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Age-Class Interactions in Atlantic Salmon and Brown Trout

Effects on Habitat use and Performance

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Konkurrens mellan åldersklasser i lax- och öringpopulationer:
inverkan på beteende, habitatutnyttjande och tillväxt

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To Anna

Age-Class Interactions in Atlantic Salmon and Brown Trout: Effects on Habitat use and Performance

Rasmus Kaspersson, 2010

ABSTRACT

This thesis investigates the underlying mechanisms and the density-regulatory effects of age-class interactions, using juvenile Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) as study species. Field experiments were performed in streams along the western coast of Sweden, in which densities of older age-classes were reduced and the response on young-of-the-year habitat use and performance (growth, movement and survival) was observed (Papers **I** and **II**). Observational data from 159 trout populations was extracted from the Swedish Electro-fishing Register to test the generality of age-class competition (Paper **III**) and observations in controlled artificial stream environments were used to establish the underlying mechanisms with regard to habitat use and behavioural interactions (Papers **IV** and **V**).

The combined findings of these studies show that age-classes of stream-living salmonids compete for limited resources in the stream habitat. This competition favours old individuals, although the behavioural observations of Paper **V** suggest that their competitive benefit may decrease at increasing densities of young-of-the-year fish.

Density-reductions of older cohorts in field increased the growth of young-of-the-year trout, an effect that was observed at the later part of the growth season (Papers **I** and **II**). The observational data-set (Paper **III**), provided further evidence of the prevalence of inter-cohort competition, reflected as a negative association between density of older cohorts and young-of-the-year body-size, in the same magnitude as on an intra-cohort level. In accordance with previous studies, juvenile salmon and trout were segregated in the stream habitat, with young-of-the-year individuals using shallow, low-velocity, habitats close to the spawning area while older cohorts were positioned in deep, high-velocity, areas (Papers **II** and **IV**). However, when experimentally reducing the density of older cohorts in field and lab (Papers **II** and **IV**), this spatial pattern was shown to be an effect of habitat exclusion rather than size-dependent habitat preference, as suggested in previous studies, with subsequent negative effects on young-of-the-year foraging activity (Paper **IV**). Thus, this finding provides a potential underlying mechanism to the negative effect on young-of-the-year performance presented in Papers **I**, **II** and **III**.

From an applied point of view, the findings of this thesis highlight the importance of taking age-class interactions into account when investigating density-dependence and habitat use among stream-living salmonids. The findings also suggest that marginal stream habitats may be essential during the first months after emergence by acting as refuges from inter-cohort competition, thus emphasizing the importance of maintaining and restoring these habitats in the wild.

KEYWORDS: Competition, inter-cohort, density-dependence, growth, habitat, *Salmo trutta, Salmo salar*, trout, salmon

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Populärvetenskaplig Sammanfattning

Under laxens (*Salmo salar* L.) och öringens (*Salmo trutta* L.) första år i sötvatten konkurrerar de yngsta individerna (årsungarna) om gynnsamma födorevir, vilket kan leda till att många individer tvingas till platser där födotillgången är sämre och där de löper större risk att dö. Det är vanligt att även äldre individer vistas inom samma begränsade område men det är dock inte känt om dessa konkurrerar om samma resurser som årsungarna och inte heller vilka konsekvenser detta kan få för populationen som helhet.

I denna avhandling försökte jag besvara dessa frågor. Fältförsök genomfördes i delar av vattendrag, där jag antingen behöll den naturliga ålderssammansättningen av öring eller flyttade bort äldre individer. Därigenom kunde jag studera om äldre individer påverkar årsungars tillväxt, rörlighet, överlevnad och habitatutnyttjande (Paper **I** och **II**). För att undersöka effekter av konkurrens mellan åldersklasser på en större skala tog jag del av data från tidigare undersökningar av 159 öringpopulationer runt om i Sverige, som lagrats i det Svenska ElfiskeRegiStret (SERS) (Paper **III**). Jag studerade även hur åldersklasser interagerar med varandra och vilka habitat de föredrar med hjälp av strömakvarier som utformades för att efterlikna naturliga miljöer, med avseende på vattenhastighet, substrat, födotillgång och temperatur (Paper **IV** och **V**).

Mina resultat tyder på att olika åldersklasser av lax och öring konkurrerar. Denna konkurrens gynnar äldre individer även om deras konkurrensfördel minskar något när antalet årsungar ökar (Paper **V**). I de sektioner av vattendragen där äldre individer tagits bort, ökade årsungarnas tillväxthastighet, vilket kan tyda på att de fått tillgång till mer föda och upplevt mindre stress (Paper **I** och **II**). Att olika åldersklasser konkurrerar bekräftades även indirekt genom data-materialet från SERS, som visade att årsungars kroppsstorlek minskar ju fler äldre individer som finns i en population (Paper **III**). Liksom tidigare studier kunde jag visa att åldersklasser av lax och öring är uppdelade i vattendragsmiljön. Medan årsungar finns i grunda, lugnflytande, habitat utnyttjar äldre individer framförallt djupa, snabbflytande, områden (Paper **II** och **IV**). I tillägg till tidigare studier tyder dock mina resultat på att årsungar tvingas till dessa habitat när de förekommer tillsammans med äldre individer, vilket minskar deras födosök och födointag (Paper **IV**).

Min avhandling visar att konkurrens från äldre åldersklasser av lax och öring påverkar både vilken typ av miljö årsungar utnyttjar och deras tillväxt. Avhandlingen visar även att tillgången på grunda, långsamflytande, miljöer kan vara avgörande eftersom dessa fungerar som skyddande refugier från konkurrens med äldre åldersklasser. Resultaten kompletterar således den befintliga kunskapen inom området och kan därmed bidra till en bättre förvaltning av lax- och öringpopulationer samt deras habitat.

LIST OF PAPERS

This thesis is a summary of the following manuscripts and published papers, referred to in the text by their Roman numerals (**I-V**). Published papers were reprinted with the permission from Blackwell Publishing (Paper **I**) and Elsevier B.V. (Paper **V**).

Paper **I**   Kaspersson R. and Höjesjö J.[1] 2009 Density-dependent growth rate in an age-structured population: A field study on stream-dwelling brown trout *Salmo trutta*.
Journal of Fish Biology **74** (10), 2196-2215.

Paper **II**   Kaspersson R., Höjesjö J.[1] and Bohlin T.[2] Habitat exclusion and reduced growth: Effects of inter-cohort competition on young-of-the-year brown trout in field.
Manuscript.

Paper **III**   Bohlin T.[2] and Kaspersson R. Differential effects of intra- and older-cohort densities on the body-size distribution in young-of-the-year brown trout.
Manuscript.

Paper **IV**   Kaspersson R., Höjesjö J.[1] and Armstrong J. D.[3] Size-related performance in juvenile Atlantic salmon: The importance of inter-cohort competition.
Manuscript.

Paper **V**   Kaspersson R., Höjesjö J.[1] and Pedersen S.[4] 2010 Effects of density on foraging success and aggression in age-structured groups of brown trout.
Animal Behaviour **79** (3), 709-715.

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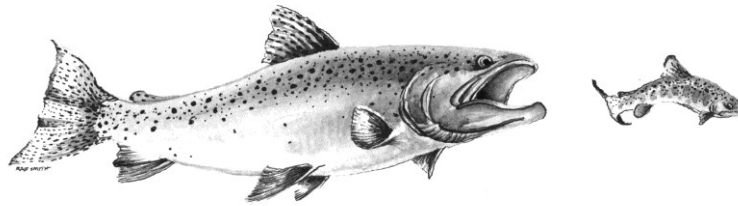
TABLE OF CONTENTS

"

I went to the woods because I wished to live deliberately, to front only the essential facts of life, and see if I could not learn what it had to teach, and not, when I came to die, discover that I had not lived

Henry David Thoreau
Life of Walden (1854)

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INTRODUCTION

Competitive interactions among conspecifics are pervasive in nature, whether occurring over habitats, food items or mating opportunities. Thus, knowledge of how, why and when competition occur is a cornerstone for understanding as well as successfully applying population ecology to the management of species and their habitats in the wild.

As a population grows, competition for limiting resources intensifies and the population experience what is often described as a negative density-dependent feedback (Hixon *et al.* 2002). Hence, the density of a given population at a given time is established in relation to the quantity of accessible resources in the surrounding environment (Begon *et al.* 1996; Murdoch 1994) by affecting either per capita input rates (density-dependent fecundity) or loss rates (density-dependent mortality and

> ”” Competition occurs when a number of animals (of the same or of different species) utilize common resources the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one or other in the process. This is the strict meaning of competition and the one which corresponds [...] to the etymology of the word, namely "together-seek." ””
>
> L. C. Birch
> The Meanings of Competition (1957)

migration) (Hixon *et al.* 2002). Simplified models often suggest that the density-dependent response is allocated equally among all individuals within a population and hence that all individuals face the same risk of having reduced fecundity and survival or increased emigration. In nature, however, populations are rarely homogenous, but rather a set of mixed phenotypes at different developmental stages, of different sizes and sexes, and presumably also with different abilities to compete for and acquire limited resources (also termed 'competitive weights' (sensu Sutherland & Parker 1992)).

In this thesis I investigate the underlying mechanisms and the population-level effects of competition in such phenotypically structured populations using two species of stream-living salmonids as study organisms: Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) (family *Salmonidae*, subfamily *Salmoninae*). In this model system, several age-classes (hereafter referred to as 'cohorts') coexist in a relatively confined habitat, suggesting potentially strong competitive interactions (hereafter referred to as 'inter-cohort competition'), an issue that, however, has received relatively limited attention in the previous literature.

The thesis is a collection of five studies (Papers **I** to **V**) that were performed between 2005 and 2009 using density-manipulations in field, controlled behavioural studies in semi-natural stream environments and observational data from previous population surveys. Before further presenting the studies performed and the obtained results, however, I will put inter-cohort competition in a somewhat wider context and consider where and why inter-cohort interactions occur in nature, how competitive success is determined and, last but not least, what effects one can expect on a population level.

Structured Populations

Size- and age-structured populations are especially apparent in organisms with flexible growth patterns, such as amphibians, fishes and certain invertebrates. Here, a later developmental stage is associated with a corresponding increase in body-size and populations may therefore contain a wide spectrum of coexisting and potentially interacting age- and size-classes (Werner & Gilliam 1984).

Since characteristics that are associated with individual performance, such as resource acquisition and predation risk, often correlate with body-size, individuals of different size- or age-classes tend to undergo what is known as ontogenetic niche-shifts; changes in resource use during the course of an individual's life-time (Werner & Gilliam 1984). The most drastic of these shifts occur in organisms with complex life-cycles (Wilbur 1980), including many aquatic invertebrates and amphibians. Larvae and adults of these animals occupy entirely different niches, with regard to diet as well as habitat, such that the stages even have been considered of different 'ecological species' (Enders 1976), hence suggesting a low risk of competitive interactions between age-groups (Smith 1990; Tschumy 1982; Werner & Gilliam 1984). While organisms that grow continuously without undergoing metamorphosis (fishes, many terrestrial insects and reptiles) also often experience ontogenetic niche-shifts, these tend to be somewhat less drastic. In fishes, ontogenetic shifts have been attributed to for example size-dependent diet preferences; where small-sized individuals are restricted from feeding upon prey of certain size, or to predation;

where juveniles use littoral habitats to avoid piscivorous predation but switch to deeper areas as they increase in size (e.g. Mittelbach 1981; Werner *et al.* 1983).

Given that size-dependent diet and habitat selection reduces the niche-overlap between cohorts, competition is often believed to occur within cohorts rather than between, also in organisms with less discrete ontogenetic shifts. However, this assumption does not hold if competition between age-classes is an underlying mechanism to the resource segregation observed in field. In that case, age-specific segregation may rather be an effect of inter-cohort competition, with potentially negative effects on performance of the age-class with the lowest competitive ability and subsequently also for density-dependence in these populations (Lomnicki 1988). However, determining whether resource use in nature is an effect of ontogenetic preferences or competitive interactions requires manipulation experiments and has therefore rarely been performed in field.

What Determines Competitive Success?

Competition in structured populations is often asymmetric, with some individuals being more capable of acquiring resources and hence facing a lower risk of being negatively affected at high densities. There are several factors that may influence competitive success, and this section aims to present the most relevant of these in the context of inter-cohort competition, categorized into internal factors (individual characteristics) and external factors (resource abundance, resource distribution in time and space as well as competitor densities).

Individual Characteristics

Body-size is an important attribute in determining the outcome of competitive interactions and especially so in organisms with indeterminate growth (Cutts *et al.* 1999; Milinski & Parker 1991; Ward *et al.* 2006; Werner & Gilliam 1984). Individuals with large body-size relative to their competitors are assumed to have increased fighting capacity and hence also higher resource holding potential (RHP) (Smith & Parker 1976) (see box 1 for further information about interference competition). A large asymmetry in body-size among contestants is also expected to settle conflicts before escalating to the point of fighting, in accordance with the size-assessment theory (Enquist & Leimar 1983).

Several studies have provided evidence of size-dependent competition success and conflict duration (reviewed in Huntingford & Turner 1987). Jenkins (1969), for example, found the largest individuals of rainbow trout (*Oncorhynchus mykiss*) and brown trout to initiate and win more than 85 % of the observed contests in a confined stream environment and similar evidence has been provided in several other fish species (Ward *et al.* 2006). Studies on fish have also shown a strong correlation between metabolic rate and competitive success, either as a consequence of higher metabolic scope (higher ability to perform energetically expensive interactions), or of higher metabolic demands (increased hunger) among large-sized individuals (reviewed in Johnsson *et al.* 2006). Thus, it has been suggested that metabolic rate may be a better predictor of competitive success when the size asymmetry among contestants is small, whereas body-size more accurately predicts the outcome of interactions as the size asymmetry grows larger (Metcalfe *et al.* 1995).

Competitive success is also associated with social and environmental perception, such as prior social experience and prior residency, characteristics that can be acquired and improved during the course of an individual's lifetime. Individuals that are prior residents in a territory are assumed to have better insight into its value, have invested more time and energy on exploring the area and are therefore expected to be more motivated in defending it against intruders (Smith & Parker 1976). In accordance, both residence duration and territory value have been shown to correlate positively with the effort spent on defence and the likelihood of winning contests against intruders (e.g. Johnsson *et al.* 2000; Johnsson & Forser 2002). The advantage of prior residency seems to decrease with an increasing body-size asymmetry between defenders and intruders (Huntingford & Turner 1987) and to be replaced by the competitive benefit of body-size if the asymmetry among contestants becomes too big (Rhodes & Quinn 1998). For example, Johnsson *et al.* (1999) found that territory-holding brown trout fry won 85 % of the contests with similar-sized individuals but lost contests when opponents had a 30 % body-size advantage. A similar effect has been found in spiders, where large individuals of the funnel web spider *Agelenopsis aperta* had an advantage in contests if the size difference between contestants was greater than 10 %, whereas prior residents won contests between similar-sized individuals (Smith & Riechert 1984). Relatively few studies have explicitly investigated the importance of prior residency among discrete cohorts (but see Anholt 1994; Eitam *et al.* 2005; Ryan & Plague 2004). Eitam *et al.* (2005) observed priority effects between cohorts of the larval fire salamander (*Salamandra salamandra inframmaiculata*), where 100 % of the youngest individuals survived in absence of older cohorts but only 13-33 % in their presence.

An individual's social experience can be improved by participating in interactions with competitors (e.g. Francis 1983; Jackson 1988), a capacity that can influence competitive success and hence also resource holding capacity to an even greater extent than prior residency (Rhodes & Quinn 1998). Jackson (1988) found individuals with a prior experience of winning conflicts to initiate more interactions than those with experience of losing in the dark-eyed junco (*Junco hyemalis oreganus*), an effect that has been detected in several other study systems (Arnott & Elwood 2009). However, an individual does not necessarily need to actively participate in contests to acquire social experience. Johnsson & Åkerman (1998) showed that juvenile rainbow trout can pre-assess a contestant's competitive ability by observing interactions (eavesdropping) thereby reducing the time to decide whether to challenge or to defeat. Intriguingly, Höjesjö *et al.* (2007a) found eavesdropping rainbow trout to assess the fighting ability of a contestant even before any interactions were initiated, possibly as a result of olfactory cues or subtle signals of social status through body or eye coloration.

In conclusion, it seems likely that old individuals of organisms with indeterminate growth may experience a competitive advantage at interference competition by having larger body-size, being socially experienced from prior interactions and by being prior residents in the shared habitat. However, while these features may favour old individuals at interference (box 1); this is not necessarily the case when competition occurs through exploitation (box 2). At exploitation competition, most individuals have access to the limited resource and favoured qualities are therefore associated with the ability to exploit the resource before neighbouring competitors, but also with the ability to withstand low resource availability (low metabolic requirements) (Persson 1985). Individuals with a large

body-size have been suggested to benefit at exploitation competition through their improved search capacity, higher foraging efficiency and wider diet range (Brooks & Dodson 1965; Werner & Hall 1988). However, evidence provided through theoretical and empirical studies suggest that some model systems, such as lentic fish populations and certain amphibians, may display the opposite pattern, with small-sized individuals having a competitive advantage through lower resource requirements and higher foraging activity (Byström & Garcia-Berthou 1999; Hamrin & Persson 1986; Persson 1985; Smith 1990; Werner 1994). Moreover, in aquatic environments where the prey is size-structured, small fish may experience a relative advantage when average prey size is grazed below what is energetically favourable for larger individuals (Post *et al.* 1999). Hence, this suggests that small individuals may have a greater effect on the growth of large individuals, such as when food supply is low, even though their overall effect on the resource supply is limited (Hamrin & Persson 1986; Persson 1985; Polis 1984; Werner 1994) (for further information about exploitation competition in age-structured populations, see pages 23, 24 and 25).

Box 1. Interference Competition

Interference competition (or contest competition) refers to a situation where individuals compete through direct behavioural interactions, from physical attacks to subtle threats (Keddy 2001). Only few superior competitors have access to the limited resource while subordinates are excluded (Milinski & Parker 1991). Thus, as opposed to exploitation competition (see box 2), the intensity of interference competition is not related to resource shortage per se but rather to the relative behaviour of neighbouring individuals (Begon *et al.* 1996; Milinski & Parker 1991). Furthermore, since few individuals always acquire sufficient amount of the resource, interference competition is assumed to stabilize population dynamics (Crawley 2007). Interference appears in several different ways: (**i**) Territoriality and habitat exclusion, where a dominant, aggressive, individual monopolizes a high-quality habitat or patch (Milinski & Parker 1991), commonly observed in fishes (e.g. Kalleberg 1958), birds (e.g. Arcese & Smith 1985; Cresswell 1997; Goss-Custard & Le V. Dit Durell 1987) and invertebrates (e.g. Crowley *et al.* 1987; Gribbin & Thompson 1990) and has been shown to be of major importance in the regulation of fitness asymmetries among coexisting individuals (Amarasekare 2002). (**ii**) Intimidation, where a subordinate individual reduces feeding activity in the presence of a superior individual, as shown in for example fishes (e.g. Griffiths & Armstrong 2002; Szabo 2002) and birds (e.g. Drummond 2006). This may also involve a shift in foraging activity to less beneficial hours to avoid competing with dominant individuals (Alanärä *et al.* 2001; Kadri *et al.* 1997). (**iii**) Mating contests, where animals compete over mates or mating opportunities (Andersson 1994). (**iv**) Filtering interference (or 'shadow competition'), where inferior individuals obtain only those food particles missed by superior individuals, as observed among invertebrates (e.g. Wilson 1974) and fishes (e.g. Elliott 2002; Nilsson *et al.* 2004); (**v**) Kleptoparasitism (or food stealing) (Elgar 1989) and (**vi**) Cannibalism, the most extreme form of interference competition (Persson *et al.* 2000; Polis & McCormick 1986). Interference competition has generally been assumed to result in a higher degree of resource monopolization as compared to exploitation competition (see box 2) (Lomnicki 1988). However, recent evidence on convict cichlids (*Archocentrus nigrofasciatus*) and goldfishes (*Carrasius auratus*) (Weir & Grant 2004), suggest that this might not be the case in all systems, thus providing an interesting future study area beyond the scope of this thesis.

Resource Characteristics and Competitor Densities

While the internal factors mentioned above are important determinants of competitive success, they are also highly context dependent, influenced by the density of resources, their predictability and distribution in time and space as well as by the number and quality of competitors in the surrounding environment (Emlen & Oring 1977; Milinski & Parker 1991).

The resource defence theory (sensu Brown 1964) (reviewed by Grant 1993) predicts that the fitness benefit of actively defending a specific resource (the 'economic defendability') should increase with its predictability in time and space. When considering resource density, however, the benefit of defence is predicted to peak at intermediate levels. More specifically, if the resource is dense, most individuals are assumed to obtain parts of the resource, independent of their competitive ability, suggesting that a territorial strategy would be a waste both of time and energy. Likewise, if the abundance of resources is very low, individuals need to use a large area in order to acquire a sufficient amount, suggesting that a territorial strategy would be too costly (Grant 1993). A similar dome-shaped pattern of defendability is predicted also when considering resource distribution, with the highest benefit of resource defence, and hence the highest frequency of aggression, at an intermediately clumped distribution in time and space (Grant 1993).

If the scenarios of resource availability described above fulfil the criteria of high economic defendability, those individuals that have superior resource holding capacities (body-size, prior residency and social experience) are predicted be most successful in acquiring the resource. If, however, the distribution or abundance of resources changes so that defence becomes increasingly costly (Nöel *et al.* 2005), territoriality may be replaced by mixed competitive strategies and eventually by pure exploitation competition (Grant 1993). Evidence for such resource-dependent shifts of competition modes has been provided from a range of species, including birds (e.g. Goldberg *et al.* 2001) and fishes (e.g. Bryant & Grant 1995; Grant *et al.* 2002; Grant & Kramer 1992; Nöel *et al.* 2005).

The same cost-benefit trade-off of interference competition is expected also when considering density of competitors. Territoriality is assumed as a costly and superfluous strategy at conditions with low population densities, since all individuals acquire a sufficient share of the limited resource without the need of direct interactions or defence. Similarly, at very high densities, the frequency of intrusions increases, suggesting that the time and energy spent on defence as well as the risk of injury makes a territorial strategy uneconomical (Grant 1993). Hence, as for resource density and distribution, the resource defence theory predicts a dome-shaped curve of aggression at increasing population densities, with the highest profitability at an intermediate population size, a pattern that has been confirmed by several empirical studies (e.g. Chapman & Kramer 1996; Jones 1983; Kim & Grant 2007). The effect of density on competition in age- and size-structured populations is, however, somewhat less well understood. In the models by Parker & Sutherland (1986) and Sutherland & Parker (1992) (the 'phenotypic scales slope' model and the 'phenotypic scales intercept' model), the relative competitive success of large and superior individuals was predicted to be constant or even to improve at increasing group sizes. However, the few studies that have tested these models empirically suggest that such response may be less common at natural conditions. For example, Tregenza *et al.* (1996) studied food intake in groups of cichlids (*Aequidens portalegrensis*) showing that although the

best competitor did better relative the rest of the group at low densities, the poorest competitors were most successful at high densities. Hence, the difference in competitive ability between dominant and subordinate individuals decreased with density, possibly due to a shift from interference at low density to exploitation at high, in correspondence with the prediction of the resource defence theory. A similar response has been detected by Humphries *et al.* (2000) and Pettersson *et al.* (1996) using cichlids (*Tilapia zillii*) and rainbow trout, respectively. Indications that the pattern of resource defence may change with body-size structure was also provided by Kim & Grant (2007), showing that the peak of aggression occurred at higher densities of different-sized convict cichlids (*Archocentrus nigrofasciatus*) than predicted from previous studies using individuals of equal size. Thus, more studies are required in order to further understand the appearance of resource defence at conditions when competitors are structured in age and size.

Box 2. Exploitation Competition

Exploitation or scramble competition refers to a situation where individuals compete for common resources in absence of direct interactions (Keddy 2001). The two terms are often used synonymously (as in this review), but according to the strict definition exploitation includes only those indirect interactions that occur without visual contact, whereas scramble refers to indirect interactions where competitors see each other and adjust their behaviour according to that of the rest of the group (Milinski & Parker 1991). The amount of resources that are distributed among individuals at exploitation competition is primarily dependent on resource availability and competitor density, while individual rank is of less importance (as opposed to interference, box 1) (Keddy 2001; Wootton 1999). Hence, since all individuals are assumed to receive parts of the limited resource, exploitation competition reduces the overall resource supply with potential large-scale effects on population dynamics (Bjornstad *et al.* 2004) and may even lead to population extinction if resources become scarce (Crawley 2007; Lomnicki 1988). Shoaling behaviour of pelagic fishes in oceans and lakes is one example of exploitation (scramble) competition (reviewed in Johnsson *et al.* 2006). The food resource of these systems, such as zooplankton, is often distributed quite evenly in space, suggesting a reduced potential for resource defence (see pages 14 and 15 for further information about resource defence). Individuals adopting a shoaling behaviour may benefit through reduced predation (risk dilution, predator confusion and early detection) and increased foraging efficiency but may also experience increased costs (reviewed in Johnsson *et al.* 2006). As argued by Begon *et al.* (1996), most study systems probably include elements of both exploitation and interference, either simultaneously or alternating in accordance to social and environmental conditions (Grant 1993).

Atlantic Salmon and Brown Trout

There are several good reasons as to why fishes in general and stream-living salmonids in particular provide ideal model organisms when investigating competition and density-dependence. (**a**) Their indeterminate growth not only generates a range of different-sized individuals, but can be used as an indicator of individual performance and occurrence of negative density-dependence; (**b**) Their high fecundity results in strong density-dependence during the first year, involving effects on growth, mortality and survival. (**c**) Competition for favourable feeding territories and shelters is intense, with body-size, prior residency and prior social experience as important correlates of dominance and resource holding capacity.

Figure 1. The life-cycle of anadromous Atlantic salmon. Illustration by Robin Ade, reprinted with kind permission from the Atlantic Salmon Trust.

Status and Distribution

The native distribution of brown trout is restricted to Europe but has since the first introduction to eastern Russia 1852 increased to include at least 24 countries world-wide (Elliott 1994; Klemetsen *et al.* 2003). The brown trout is well-known for its wide range of life-history strategies; from spending the entire life-span in the freshwater environments of lakes, rivers and streams (resident and lake-migratory populations) to performing long-distance migrations between freshwater and marine habitats (sea-migratory or anadromous populations) and this flexibility is probably a contributing explanation to its successful colonization into new areas. Although not considered a threatened species, some brown trout populations do experience declining numbers as a consequence of environmental degradation in the freshwater habitat and barriers restricting their migratory routes. Along the coastline of Sweden, populations of sea-migrating brown trout vary in their status; from being vulnerable in the Gulf of Bothnia and the Baltic Sea, to being relatively stable along the western coast (Kattegat and Skagerrak) (Fiskeriverket 2009).

The historical distribution of Atlantic salmon includes the North Atlantic Ocean and rivers along the adjacent coasts of North America and Europe. In North America, the species occurred from Hudson River (northern limit), along the coast of Quebec and Gulf of St. Lawrence to Nova Scotia and southernmost to the Connecticut River on the north-eastern coast of the Unites States. In Europe, the native distribution includes Iceland

(northern limit), Barents Sea (north-eastern limit), Baltic Sea (eastern limit) and the European coastline to Portugal (southern limit) (Klemetsen *et al.* 2003; Webb *et al.* 2007). Today, however, the distribution of Atlantic salmon has decreased substantially, and the species is now extinct from many river systems in Europe and North America (Webb *et al.* 2007) (see box 3).

Compared to brown trout, the Atlantic salmon is somewhat less flexible in its life-history, with most populations being sea-migratory. There are, however, some land-locked (resident) populations, that remain in rivers and lakes throughout their entire life-cycle. Such populations are found in for example Lake Vänern (Sweden), River Namsen (Norway), Lake Ladoga (Russia) and Lake Ontario (Canada) (Klemetsen *et al.* 2003).

The Life-Cycle
The following section provides a brief overview of the intriguing life-cycle of trout and salmon, with focus on anadromous populations. The timing of life-history events (such as spawning, emergence and smoltification) is highly variable between and within regions (Elliott 1994), and this information should therefore be treated accordingly.

Individuals adopting an anadromous life-history strategy migrate from juvenile habitats in streams or rivers to the ocean and returns to their natal freshwater habitat as sexually mature adults (Klemetsen *et al.* 2003; Milner *et al.* 2003) (figure 1). Atlantic salmon and brown trout in the Northern Hemisphere usually spawn in November and December, in gravel nests (redds) excavated by the female prior mating (Elliott 1994). These are commonly placed in riffle areas at the tails of pools (Armstrong *et al.* 2003; Armstrong & Nislow 2006) where the substrate is coarse, thus allowing the oxygenated water to reach the eggs in the gravel bed (Webb *et al.* 2007). Male hierarchies are established in cases with limited number of females, where the largest and most dominant males defend females and nesting sites with the highest quality (Klemetsen *et al.* 2003). Subordinate males may adopt an alternative sexual strategy ('sneaky-mating'), by which they attempt to fertilize some of the eggs prior to the dominant male (Webb *et al.* 2007). The eggs (*c.* 5-7 mm in diameter) (Webb *et al.* 2007) are generally distributed in two or three nests (Elliott 1994) and their numbers ranges from 100 for a small resident trout female (Elliott 1994) to several thousand for a large salmon (Webb *et al.* 2007).

The eggs hatch in the subsequent spring (February or early March) (Elliott 1994) but the juveniles remain feeding endogenously on their internal energy store (the yolk-sac) in the sheltered gravel nest for approximately five to eight weeks (these juveniles are commonly referred to as 'alevins', *c.* 15-25 mm long) (Webb *et al.* 2007) (figure 1). As the yolk-sac supply diminishes, the juveniles (now referred to as 'fry') emerges to the gravel surface (Elliott 1994) with subsequent exposure to abiotic and biotic elements in the open stream channel (Armstrong *et al.* 2003; Klemetsen *et al.* 2003; Milner *et al.* 2003) (figure 1). Emergence occurs mainly at night and is often synchronized among several hundred fry, most likely as way to reduce predation risk (Armstrong & Nislow 2006). As the fry emerges, they start feeding exogenously on invertebrate prey (Skoglund & Barlaup 2006) (sometimes referred to as the post-emergent fry stage (Einum *et al.* 2006)). During this critical period (see also page 22), the fry compete intensively for feeding territories near the spawning area and a large proportion will drift downstream where they experience increased mortality rates through starvation and predation (Elliott 1989). The limited

Box 3. Status of the Atlantic Salmon

During the last century, the Atlantic salmon in Europe and North America has experienced a gradual decline, with many populations being severely threatened or even extinct (Parrish *et al.* 1998; Webb *et al.* 2007). Populations in the southern range of the distribution seem to face a more rapid decline and several river systems in these areas have lost their entire stock of wild salmon (Parrish *et al.* 1998), such as the Elbe and the Rhine (Webb *et al.* 2007). However, also more northern populations experience declines. In the Baltic Sea, for example, salmon spawned in 80-120 rivers at the beginning of the 20th century, with an estimated production of 8 to 10 million smolts per year. Today, however, the distribution has decreased to include merely 38 rivers and a production of less than 2 million smolts per year (Eriksson & Eriksson 1993; Webb *et al.* 2007). The M74 reproduction syndrome is suggested as a major reason for this decline in the Baltic Sea, in combination with more widespread factors, such as fishing pressure, environmental degradation and migration barriers in the freshwater habitat (Webb *et al.* 2007). Moreover, recent surveys in salmon rivers along the coasts of the North Atlantic Ocean report a decrease in both number and body-size of returning adults, suggesting that also the marine phase may involve processes that are important to the decline, possibly linked to changes in the ocean climate and pH (ICES 2009a; 2009b). Today, the Atlantic salmon is listed in annexes II and V of the European Union's Habitat Directive as a species of European importance. The land-locked salmon population in Lake Vänern (spawns in the River Gullspång) is listed as endangered in the Swedish red list.

supply of feeding territories at emergence (Nislow *et al.* 1998) imposes a strong selective pressure on early emergence (prior residency) (Harwood *et al.* 2003) and body-size at emergence (Good *et al.* 2001), features that to a large extent are maternally determined (Einum & Fleming 2000). Indeed, several studies have shown a benefit of body-size and timing of emergence, where early-emerging, large-sized, fry remain closer to the spawning area (Bujold *et al.* 2004). While some dispersal occurs during the weeks after emergence, a majority of the emerging fry tend to stay within a few hundred metres from the spawning area (Armstrong & Nislow 2006).

The post-emergent fry stage is followed by the parr phase; commonly defined as the period after the yolk-sac has been fully absorbed but before smoltification (Elliott 1994). During this period, the juveniles generally develop characteristic red spots and vertical stripes on the sides of the body (Webb *et al.* 2007) (figure 1; box 4). As individuals grow or if the densities are high during the first year, territoriality may become replaced by a more flexible behaviour where the parr use home ranges and form dominance hierarchies (Keeley 2000). Although debated (Gowan *et al.* 1994; Rodriguez 2002), stream-living salmonids seems to be relatively sedentary in the freshwater habitat also after emergence, with movement distances rarely exceeding 200 metres (e.g. Bohlin *et al.* 2002; Heggenes 1988a; Okland *et al.* 2004; Steingrimsson & Grant 2003). Peak growth period generally occurs in spring and early summer at optimum temperatures of 13-18 °C (Elliott 1994).

In spring (April-May), after one to four years in the freshwater habitat, anadromous trout and salmon undergo a physiological adaptation to marine conditions, termed smoltification (figure 1). While temperature and photoperiod are assumed as important cues for initiating the smoltification process, the actual time spent in freshwater is

dependent on other factors, such as latitude and individual growth rate (Klemetsen *et al.* 2003). As smolts, the behaviour shifts from territoriality to shoaling and the body coloration turns silvery (Webb *et al.* 2007) (figure 1).

While at sea, trout are assumed to perform shorter migration routes than salmon, although knowledge about the sea-water phase is limited for both species (Milner *et al.* 2003). Mature individuals generally return to their natal stream after one to four years at sea (Elliott 1994), commonly in the late summer (August-September) but the exact timing is population-specific and also dependent on environmental variables, such as water-flow and distance to spawning grounds (Webb *et al.* 2007). Among anadromous trout populations, some individuals, mainly males, may remain stream-resident throughout their entire lives (Dellefors & Faremo 1988). As for subordinate males (see above), resident males often adopt an alternative sexual strategy including early sexual maturation and sneaky-mating (Gross 1996; Milner *et al.* 2003).

As a consequence of the life-history strategies of Atlantic salmon and brown trout, the youngest individuals will coexist with at least one older cohort within the stream habitat (box 4). Although this suggests a scope for potentially intense competition between cohorts, few previous studies have thus far investigated the prevalence of such interactions.

Habitat use in Streams and Rivers
Suitable stream habitats are often of limited supply for stream-living salmonids (Chapman 1966), and may therefore provide an important factor in determining competition intensity and hence also upper limits of population growth. Habitat profitability is mainly determined by depth, velocity, substrate composition, in-stream structure and bank-side cover, and since these are highly interrelated in a natural stream environment (Heggenes *et al.* 1999), an individual fish is likely to respond to a combination of variables rather than to just one (Armstrong *et al.* 2003).

At emergence, salmon and trout fry establish small territories (Grant *et al.* 1998), in shallow (< 10 cm) habitats close to the stream-bank where the water velocity is low (Heggenes *et al.* 1999; Nislow *et al.* 1999). There seems to be a general preference for coarse gravel (Heggenes 1988b), probably as it provides micro-habitats (interstitial spaces) with low water velocity, but also protection against predators and reduced frequency of interactions (visual isolation) between con- and inter-specifics (Bardonnet & Heland 1994; Imre *et al.* 2002). The availability of these marginal, low-velocity, habitat is often limited at emergence, especially where the natural stream channel has been homogenized through anthropogenic activities (Nislow *et al.* 1999), such as attempts to improve timber driving, and may therefore provide a plausible mechanism for the intense density-dependence observed at the point of emergence (Einum *et al.* 2008).

While young-of-the-year salmon and trout tend to remain in these marginal nursery habitats during the entire first summer, these are actively avoided by older age-classes (Armstrong *et al.* 2003; Heggenes & Borgstrom 1991). In contrast to trout, juveniles of Atlantic salmon have enlarged pectoral fins that enable them to hold position in high-flow habitats at relatively low energetic costs (Arnold *et al.* 1991). Hence, salmon yearlings and over-yearlings tend to have their main occupancy in high-velocity habitats (20-60 cm s^{-1}), whereas the distribution of older trout seems mainly directed towards deep but slow-

flowing habitats (pools) (< 20 cm s^{-1}) (Armstrong *et al.* 2003; Heggenes 1988a; Heggenes *et al.* 1999; Näslund *et al.* 1998).

As temperatures drop below 8-10°C during late fall and winter, the size-dependent segregation in habitat use may become less evident since all size-classes have been shown to move to deeper, slower-flowing (< 10 cm s^{-1}) habitats (Cunjak *et al.* 1998; Huusko *et al.* 2007; Mäki-Petäys *et al.* 1997). This habitat shift is probably associated with reduced swimming capacity at low temperatures and hence also reduced ability to avoid terrestrial and avian predators (Valdimarsson & Metcalfe 1998). In accordance, there is also a corresponding shift in the diurnal rhythm, where juvenile salmonids become increasingly nocturnal, while hiding in shelters, such as substrate interstices, during day-time (Greenberg *et al.* 1996; Heggenes *et al.* 1993; Metcalfe *et al.* 1999). Although several studies have shown decreased aggression during winter (e.g. Heggenes *et al.* 1993), recent laboratory experiments have observed competitive interactions at dawn as juveniles seek daytime shelters (Armstrong & Griffiths 2001; Gregory & Griffith 1996; Orpwood *et al.* 2003; Orpwood *et al.* 2004), suggesting that shelter availability during winter can affect the carrying capacity of natural populations.

Ontogenetic Habitat Shifts: Preference or Exclusion?

The ontogenetic shifts in habitat use or the 'bigger-fish-deeper-habitat relationship' presented above, seems to hold for many species of stream-living fishes (e.g. Davey *et al.* 2005; Mullen & Burton 1995) and is an especially common pattern in the distribution of salmonids in nature (e.g. Bohlin 1977; Bremset & Berg 1999; Greenberg *et al.* 1996; Mäki-Petäys *et al.* 2004).

Deep habitats of streams and rivers are often assumed as being more profitable than shallow, marginal, areas. For example, deep areas may provide a better environment to find and forage on drifting food items through their larger area (Hughes & Dill 1990) and lower risk of predation from bank-side avian and mammalian predators, such as heron (*Ardea cinerea*) and mink (*Mustela vison*) (Heggenes & Borgstrom 1988; Lonzarich & Quinn 1995). Deep habitats, in the centre of the stream-channel, may also have higher water velocity relative to marginal areas, resulting in a greater availability of invertebrate drift (Hill & Grossman 1993), an important food source of juvenile salmonids (Keeley & Grant 1995; 1997).

Hence, on the basis of these circumstances, the question arises as to why juvenile salmonids use shallow, and presumably also less beneficial habitats, during their first year? There seems to be at least three plausible explanations for this pattern: (**a**) **Size-dependent habitat availability**; the ability to swim and capture drifting food items is related to body-size (Nislow *et al.* 1999) and young-of-the-year trout and salmon may therefore be constrained to marginal low-velocity habitats that will maximize food intake rate at the lowest energy cost (Fausch 1983). Evidence for this has been provided from foraging-based models applied to laboratory and field settings (Nislow *et al.* 1999), where Atlantic salmon fry was shown to consistently choose low-velocity habitats (< 0.08 cm s^{-1}) despite their limited supply at emergence. (**b**) **Vulnerability to predation**; movement to deeper habitats may be restricted in streams containing piscivores, such as northern pike (*Esox lucius*) or bullhead (*Cottus gobio*), through increased risk of predation (Bardonnet & Heland 1994; Greenberg *et al.* 1997; Roussel & Bardonnet 1999). (**c**) In addition to size-dependent

swimming capacity and predation risk, habitat shifts during ontogeny may also result from **competitive exclusion** (sensu Hardin 1960). According to this scenario, young-of-the-year salmon and trout prefer deep, high-velocity, habitats but are excluded to shallow, marginal habitats, through intra-specific competition from older, more dominant, individuals. Although inter-cohort competitive exclusion has been a suggested underlying mechanism of young-of-the-year habitat use in several previous studies (e.g. Bohlin 1977; Bremset & Berg 1999), few have tested its importance in an experimental set-up (but see Bohlin 1977; Vehanen *et al.* 1999). Moreover, most observations of ontogenetic habitat utilisation in field are based on correlations between abundance or distribution and local habitat variables (see Armstrong *et al.* 2003 for a review). While these studies provide valuable information on general patterns, they do not reveal the underlying mechanisms (Nislow *et al.* 1998), which is necessary in order to separate habitat preference from exclusion (Rosenfeld 2003).

A Question of Terminology

Habitat utilisation, selection and preference are three commonly used (and misused) terms when attempting to describe the distribution of salmonids in streams and rivers. Hence, this section aims to provide a brief overview of their meanings, based on the thorough review by Rosenfeld (2003).

Habitat utilisation is an individual's use of a habitat at a given site and at a given time and is consequently an illustration of the realized niche (sensu Hutchinson 1957), that is, habitat use in presence of biotic factors such as predation and competition (Rosenfeld 2003). Habitat utilisation can never deviate from the total habitat availability (Heggenes 1988a) and will therefore differ largely within and between streams and seasons.

The relation between habitat utilisation and habitat availability is termed habitat selection and can either involve avoidance of a specific habitat, or attraction, when a habitat is used to a greater extent than the average availability (Rosenfeld 2003). Hence, investigating habitat selection requires not only knowledge of the micro-habitat at the position of each individual but also a general mapping of the overall habitat that is available to the individual.

Habitat preference illustrates an individual's fundamental niche (sensu Hutchinson 1957) and is subsequently defined as use and selection of habitats in absence of biotic factors, such as competitors or predators (Rosenfeld 2003). As opposed to habitat utilisation and selection, habitat preference is assumed to be independent of habitat availability and instead determined by for example individual behaviour or physiological constraints (Rosenfeld 2003). Hence, in order to investigate the true habitat preference of stream-living salmonids, factors that may confound the utilisation and selection must be isolated, either by experimental manipulations in field or by using controlled artificial stream environments.

Density-Dependent Processes in Salmonid Populations

In contrast to mammals and birds that invest energy in few offspring with high quality, most fishes produce a large number of eggs at each reproductive effort, greatly exceeding the carrying capacity of the local habitat (Sinclair 1989). In consequence, density-dependent mortality can be substantial during the juvenile phase, and among stream-living salmonids this is especially apparent as the fry switches from maternal provisioning to external

feeding, also known as the Early Critical Period (ECP) (Armstrong & Nislow 2006) or the Critical Period Concept (CPC) (Nislow *et al.* 2004). Mortality rates of 65 % during the first two weeks after emergence and 84 % during the first months were reported by Einum & Fleming (2000), and an even higher loss (90 %), during first 65 days after emergence, was observed by Elliott (1994) in Black Brow's Beck (The Lake District, UK).

The level of mortality at the ECP seems mainly dependent on the recruit (egg) density and competition for limited feeding territories, with fry not capable of attaining territories being displaced and experiencing increased mortality rates through starvation or predation (Elliott 1994). However, the density-dependent population loss at the ECP can also be amplified by processes that act independently of the recruit density, such as low temperatures and high discharge (e.g. Lobon-Cervia 2004). Hence, it is generally assumed that the ECP can be of major importance, not only establishing the strength of newly emerged cohorts (Lobon-Cervia 2005; Nislow *et al.* 2004) but also determining the intensity of future density regulation (Einum *et al.* 2006).

The high but transient mortality rate that characterizes the ECP has been attributed to size-dependent habitat availability (see also page 20) (reviewed by Armstrong & Nislow 2006) where newly emerged fry are restricted to marginal habitats with low food availability and high predation risk through their reduced swimming capacity (Nislow *et al.* 1998), thus leading to high mortality rates. As the fry grow, however, the availability of favourable habitats is assumed to increase and subsequently also lessen the constraints on population growth (Armstrong & Nislow 2006). Another, less investigated, mechanism underlying the ECP is inter-cohort habitat exclusion (see also page 21) whereby presence of older cohorts excludes newly emerged fry to less favourable, marginal, habitats, in the same way as size-dependent swimming capacity. Hence, although these theories provide different underlying mechanisms, both highlight the importance of marginal fry habitat in determining the intensity of density-dependence at the ECP (Einum *et al.* 2008; Nislow *et al.* 2004).

Although the high mortality rates at the ECP has been suggested to reduce population densities to an extent that further regulation is density-independent (Elliott 1994), more recent studies suggest that also later stages and other density-dependent processes may be of importance. For example, several studies have provided evidence of a second density-dependent bottleneck during the first winter (see review by Huusko *et al.* 2007). The high mortality rate at this period is probably influenced by both small body-size and low energy stores at the onset of winter, but also by density-dependent shelter availability and increased predation by mammalian and avian predators on individuals using less profitable habitats (Huusko *et al.* 2007). Moreover, evidence of density-dependent individual growth rate, provided from observational studies (e.g. Crisp 1993; Grant & Kramer 1990; Imre *et al.* 2005; Jenkins *et al.* 1999; Lobon-Cervia 2005; Lobon-Cervia 2007) and field experiments (Bohlin *et al.* 2002; Einum *et al.* 2006; Nordwall *et al.* 2001) also contrasts the view of the ECP as the only phase of density-dependence among stream-living salmonids.

However, whereas density-dependent mortality and emigration seems most prevalent at high densities in association with the ECP, evidence for density-dependent growth has been provided primarily from low-density populations after the ECP (Grant & Imre 2005; Imre *et al.* 2005; Jenkins *et al.* 1999), suggesting an ontogenetic dimension as to how density-dependent processes operate (Einum *et al.* 2006). The underlying mechanism to the somewhat unexpected occurrence of density-dependent growth at low population densities

has been investigated in several recent papers (e.g. Grant & Imre 2005; Imre *et al.* 2005; Imre *et al.* 2010; Ward *et al.* 2007). Imre *et al.* (2005) suggested that salmonid populations may be regulated via two mechanisms; exploitation competition for drifting food items at low densities, reducing the individual growth rate, and interference for limiting territories at high densities, reducing the survival rate. Hence, this would explain the lack of response on growth in Elliott's high-density population (Elliott 1994) and support for this theory has been provided in several recent papers (Grant & Imre 2005; Imre *et al.* 2010; Jenkins *et al.* 1999). For example, Grant & Imre (2005) analysed data from 19 populations of six stream-living salmonid species, with 15 showing patterns of negative density-dependent growth and 11 populations demonstrating the most rapid decline at low densities (< 1 fish m^{-2}).

In a recent study by Steingrimsson & Grant (2008), young-of-the-year Atlantic salmon were observed to use large multi-central territories within the stream habitat, rather than one single foraging station. This interesting finding suggests that stream habitats may be limiting even at relatively low densities, thus providing an additional explanation for the occurrence of density-dependence at lower densities than expected, and hence possibly also for the intricate association between density and growth rate (Steingrimsson & Grant 2008). Indeed, Ward *et al.* (2007) and Lobon-Cervia (2007), suggested that density-dependent growth can be an outcome of interference competition and territoriality if less competitive individuals are excluded to habitats with lower growth potential. Furthermore, and as suggested by Lobon-Cervia (2007) it is likely that interference and exploitation operates simultaneously in complex natural stream habitats, but that the detection of growth may be obscured in high-density populations by the severe effects on mortality. Hence, further studies are required to fully comprehend the occurrence of density-dependent growth and mortality, and their underlying mechanisms with regards to interference and exploitation competition, in populations of stream-living salmonids.

Inter-Cohort Competition: What we know so far

The close association between body-size and performance in organisms with flexible growth patterns suggests that age- and size-asymmetries can have large effect on competition intensity as well as density-dependence (Persson 1985; Smith 1990; Woodward *et al.* 2005). Indeed, inter-cohort interactions have received increasing interest during the last decades, and this section aims to provide a brief overview of some influential theoretical and empirical studies within this field.

Gribbin & Thompson (1990) found evidence of inter-cohort interference competition for favourable feeding sites among larvae of the damselfly *Ischnura elegans*, resulting in delayed moulting and decreased size-at-moult of early instars, whereas older individuals were unaffected. Reduced survival rates of young larvae in sympatry with older cohorts was observed in the dragonfly *Tetragoneuria cynosura* (Crowley *et al.* 1987) and in the lepidopteran *Plodia interpunctella* (Cameron *et al.* 2007), as an outcome of interference competition, including cannibalism. Similar evidence has been provided from amphibians, where late-emerging (young) larvae of the fire salamander (see page 12) experienced survival rates of merely 13 to 33 % in presence of early-emerging (old) larvae, while the 100 % survived in their absence (Eitam *et al.* 2005).

Box 4. Salmonid Age-classes

During the first year after emergence, juvenile salmonids are often referred to as Young-Of-the-Year (YOY), 0+ or age 0 individuals. Juveniles that have spent one year in the stream are called yearlings, 1+ or age 1 individuals, whereas older cohorts are referred to as over-yearlings, 2+, 3+ ... or age > 1 individuals. As shown by the pictures of juvenile salmon (upper photo) and trout (lower photo), these cohorts can differ considerably in body-size as a consequence of their indeterminate growth pattern (Photo: Rasmus Kaspersson).

Considering intercohort competition in fish, two major lines of research can be distinguished; either on demographically open populations of coral-reef species with interference competition as the prevalent competition mode or on demographically closed populations of northern European lentic fishes, experiencing inter-cohort exploitation competition. In the former category, Webster (2004) found young-of-the-year survival to be inversely related to adult density in populations of fairy basslets (*Gramma loreto*), while no such effect was detected on growth rate. Similar evidence was provided by Schmitt and Holbrook (1999a; 1999b) investigating settlement rates of juvenile damselfish (*Daschyllus* spp.) on coral-reef micro-habitats, and more recently by Samhouri *et al.* (2009) showing reduced survival and growth rates of juvenile goldspot gobies (*Gnatholepis thompsoni*) in presence of adult conspecifics.

In the second line of research, Hamrin & Persson (1986) presented empirical evidence that the 2-3 yr population cycles previously described in the planktivorous vendace (*Coregonus albula*) (reviewed in Persson *et al.* 1998) is an outcome of inter-cohort exploitation competition, favouring younger cohorts. More specifically, years with a strong recruiting cohort depressed the zooplankton food resource to the extent that older cohorts experienced reduced growth rates and eventually also reduced fecundity (see also page 13). More recent studies in the same ecosystem have confirmed this result (Claessen *et al.* 2000; de Roos & Persson 2003; Persson *et al.* 2000) and evidence has also been provided through theoretical models, predicting destabilized population dynamics as exploitation competition from younger cohorts reduces adult fecundity, but a stabilization as competition acts on juvenile survival (Ebenman 1987; Loreau & Ebenhoh 1994; Persson *et al.* 1998; Tschumy 1982). Empirical evidence seem to suggests, however, that reduced juvenile survival may give rise to similar year-to-year population fluctuations, through either competition or cannibalism, as shown in age-structured population of cicadas (reviewed in Persson *et al.* 1998) and cod (Bjornstad *et al.* 2004). Recent models and empirical tests in lentic fish populations have also shown how a simultaneous presence of

both inter-cohort exploitation competition and cannibalism can result in complex dynamics and even population collapses (Claessen *et al.* 2000; de Roos & Persson 2002).

Few studies have previously investigated the underlying mechanisms of inter-cohort competition, such as resource use and behavioural interactions, but there are some noteworthy exceptions (also among organisms with determinate growth). For example, in age-structured groups of doves (*Columba livia*) and willow tits (*Parus major*), removal experiments revealed inter-cohort competition as the underlying mechanism to habitat use, where young birds were excluded to less protected habitats in sympatry with older cohorts (Koivula *et al.* 1993; Sol *et al.* 2000; Sol *et al.* 1998), possibly related to asymmetries in social experience and prior residency between individuals of different age (Koivula *et al.* 1993). Similar evidence has been provided from coral-reef fishes, where young-of-the-year damselfish used feeding sites with lower food availability and increased risk of predation, in sympatry with older cohorts (Webster 2004). Indeed, exclusion to habitats with lower profitability may have a great influence on individual performance. Small-sized individuals of the fairy basslet, a coral-reef fish, experienced 60 % lower feeding rates in presence of larger, more dominant, conspecifics (Webster & Hixon 2000) and inter-cohort exclusion from predator-safe areas was shown as the main explanation for reduced survival among young-of-the-year damselfish (Holbrook & Schmitt 2002). In accordance, Szabo (2002) found young-of-the-year individuals of the marine tidepool sculpin (*Oligocottus maculosus*) to not only reduce their use of predator-safe shelters but also to lower their foraging activity and experience decreased foraging success, in sympatry with older cohorts.

Evidence from Stream-Living Salmonids
In populations of stream-living salmonids, several cohorts often coexist within a relatively confined area (Elliott 1994). This suggests potentially intense inter-cohort interactions, especially when also considering the hierarchical and territorial behaviour of juvenile salmonids and the large difference in body-size between cohorts (see box 4). Nevertheless, relatively few studies have thus far explicitly investigated inter-cohort competition in salmonid populations, providing a somewhat equivocal understanding of its importance, generality and underlying mechanisms (see table 1). In the influential studies by Elliott, based on observational time-series data on brown trout in the Black Brow's Beck (reviewed in Elliott 1994), no evidence of inter-cohort competition was provided, with the subsequent conclusion that sympatric cohorts of salmonids experience low niche-overlap. This result contrasted the findings of some previous studies (see table 1); for example, Bohlin (1977) investigated habitat use in a simple artificial pool-riffle environment, where young-of-the-year brown trout used riffles to a greater extent in sympatry with two yearlings. A similar finding was provided more recently by Vehanen *et al.* (1999) in an indoor stream environment, where older cohorts excluded young-of-the-year trout from preferred velocity shelters. Hence, more studies are required to test importance of inter-cohort habitat exclusion at more natural settings as well as at the specific periods of the first year when habitats are assumed to be most limiting to population growth.

However, the stream habitat represents merely one dimension of an individual's niche, suggesting that also food preference and temporal activity patterns may influence the intensity of inter-cohort competition (Bremset & Berg 1999; Bremset & Heggenes 2001). Stream-living salmonids are visual predators that mainly feed upon drifting invertebrates

(Kalleberg 1958; Keeley & Grant 1995), although some benthic foraging does occur to a lesser extent (Elliott 1967). Several studies investigating diet composition of stream-living salmonids provide evidence of a positive correlation between prey size and salmonid body-size, but also of an opportunistic feeding pattern, where most invertebrate taxa available in the stream environment at a given time are included in the salmonid diet (e.g. Amundsen *et al.* 2001; Bozek *et al.* 1994; Bridcut & Giller 1995; Fahy 1980; Hunt & Jones 1972; Keeley & Grant 1997; Steingrimsson & Gislason 2002). As shown by Keeley & Grant (1997), the greatest diet selectivity seems to occur among the newly emerged stages, when juvenile Atlantic salmon consistently select smaller-sized prey and taxa than the average availability, and among older parr, showing a similar strong diet selectivity but in the opposite direction. Fochetti *et al.* (2008) found different cohorts of older trout parr (age 2 and older) to forage upon significantly different invertebrate taxa and in a study by Stradmeyer & Thorpe (1987), large salmon parr (12-15 cm) used surface feeding to a greater extent than smaller individuals (10 cm). Hence, this provides additional support for diet selectivity and suggests that older cohorts may be differentiated also in foraging behaviour. However, there are also results indicating a potentially large overlap in diet among size-classes and cohorts (e.g. Amundsen *et al.* 2001; Bozek *et al.* 1994; Elliott 1967; Keeley & Grant 1997). For example, in the study by Keeley & Grant (1997), the size-range of prey in stomachs of juvenile Atlantic salmon increased continuously with body-size following emergence and young-of-the-year individuals were found to prey upon almost all size-classes of drifting invertebrates (except for the largest and smallest 5 %). In agreement, Amundsen *et al.* (2001) and Bozek *et al.* (1994), showed an extensive overlap between cohorts of juvenile Atlantic salmon (age 1-3) and cutthroat trout (*Oncorhynchus clarkii*) (age 0-2) respectively. Hence, further studies are required to fully understand the extent of diet overlap among cohorts during ontogeny as well as its influence on inter-cohort competition intensity and segregation in the habitat dimension.

Evidence of temporal segregation has been provided from groups of similar-aged brown trout held at laboratory conditions, where large-sized, dominant, individuals foraged during the beneficial hours at dusk and night while subordinate fish were active at dawn and day, when the risk of predation is higher (Alanärä *et al.* 2001). A similar pattern has been recently observed also in groups of Arctic charr (*Salvelinus alpinus*) (Brännäs 2008). These findings suggests that subordinate individuals may gain access to a food resource, and maintain positive growth rate, by foraging at times when dominants are less active, thereby reducing the risk of being involved in aggressive interactions (Alanärä *et al.* 2001). Hence, this provides a potentially important process also at inter-cohort competition, and investigating how temporal activity patterns influences habitat use and foraging activity in age-structured groups at more natural settings is therefore a field for interesting future research.

Assuming that cohorts of salmonids overlap in the preference for habitats, food items and temporal activity, and that older cohorts have prior access to the most profitable resources through their higher dominance rank, one would indeed expect a negative effect of older cohorts on young-of-the-year performance. Some evidence for this has been provided in terms of observational data (see table 1), but few previous experimental studies have to our knowledge explicitly investigated this issue in field (but see Nordwall *et al.* 2001) and especially not during the important bottlenecks of the first year.

Reference	Species	Origin (age)	Type	Experimental design	Response
Bohlin (1977)*	*Salmo trutta*	Wild, A (0-1)	L	Pool-riffle aquarium; $<1^{yr}$	Habitat exclusion
Buck & Hay (1984)	*Salmo salar*	Wild, A (0-3)	O	1 stream; 10^{yrs}	Survival
Burnet (1959)	*S. trutta*	Wild, R (0-5)	O	2 streams; 2 sections; 5^{yrs}	Density fluctuations
Côté & Pomerleau (1985)	*S. salar*	H-r, A (0-1)	E	1 stream; 6^{yrs}	No response
Egglishaw & Schackley (1982)	*S. salar* (and *S. trutta*)	Wild, A (0-2)	O	1 stream; 12 sections; 2^{yrs}	Survival
Elliott (1985)	*S. trutta*	Wild, A (0-3)	O	1 stream; 17^{yrs}	No response
Harvey & Nakamoto (1997)	*Oncorhynchus mykiss*	Wild, A (0-1)	E	1 stream, 18 enclosures; $<1^{yr}$	Growth
Imre *et al.* (2005)	*S. salar*	Wild, A (0-1)	O	1 stream; 10^{yrs}	Weak effect on growth
Gibson & Dickson (1984)	*S. salar*	H-r, A (0-1)	E	2 streams; 3 sites	No response
Kennedy & Strange (1980)*	*S. salar* (and *S. trutta*)	H-r (0-1)	E	2 streams, 8 sections; 3^{yrs}	Survival
Kennedy & Strange (1986)	*S. salar* (and *S. trutta*)	H-r (0-1)	E	1 stream, 2 sections; 3^{yrs}	Survival and growth
Lobón-Cerviá (2005)	*S. trutta*	Wild, R (0-5)	O	1 stream, 4 sites; 15^{yrs}	Growth
Nordwall *et al.* (2001)*	*S. trutta*	Wild, R (0-2)	E ^{δ}	5 streams; 5 sections; 3^{yrs}	Survival and growth
			O ^{δ}	3 streams; $\geq5^{yrs}$	Survival and growth
Paul *et al.* (2000)*	*Salvelinus confluentus*	Wild, R (1-4)	O, T	1 stream, 1 section; 15^{yrs}	Population cycles
Rosenfeld & Boss (2001)*	*O. clarki*	Wild, A (0-2)	E	1 stream, 15 enclosures; 1^{yr}	Habitat excl. / Growth
Vehanen *et al.* (1999)*	*S. trutta*	H-r (0-1)	L	Stream-aquarium; $<1^{yr}$	Habitat exclusion

Table 1. Studies investigating mechanisms and effects of inter-cohort competition in stream-living salmonids. The column 'Origin (age)' refers to the type of populations used; collected in nature (Wild), hatchery-reared (H-r), anadromous (A) or stream resident (R), and provides details concerning the age of the tested individuals (0 refers to young-of-the-year fish while 1, 2 or 3 refers to older cohorts). The column 'Type' presents the type of study performed; studies based on observational data (correlations) (O); experimental studies (density-manipulations) (E), laboratory-based studies (stream-aquarium) (L) or theoretical studies (modelling) (T). The column 'Experimental design' presents characteristics of the experiment, such as number of streams, sites and experiment duration while 'Response' presents the main findings. * indicates studies with the explicit aim of investigating inter-cohort competition. ^{δ} The study by Nordwall *et al.* (2001) includes experimental as well as observational data.

AIM OF THESIS

The overall aim of this thesis was to investigate the effects of inter-cohort competition on density-regulatory processes in populations of juvenile Atlantic salmon and brown trout as well as to explore its underlying mechanisms.

More specifically, I aimed to:

a) Establish the influence of inter-cohort competition on young-of-the-year performance (survival, growth and migration) during the critical density-dependent bottlenecks (emergence and winter) and the main growth period of the first year, by performing density-manipulations in field (Papers **I** and **II**).

b) Investigate whether the use of marginal habitats by newly emerged fry is an effect of competitive exclusion or preference, by performing density-manipulations in field and behavioural studies in artificial stream environments (Papers **II** and **IV**).

c) Explore the generality of density-dependent inter-cohort competition using associations of density and body-size distribution from several populations (Paper **III**).

d) Investigate the value of being old when competing with young individuals (Paper **V**). More specifically, we aimed to determine to what extent old (and supposedly also more dominant) trout are able to defend a food resource as the density of younger individuals increase.

METHODS

The studies within this thesis are based on field experiments, observational data from previous population surveys and behavioural studies in controlled semi-natural environments. The following section provides a brief overview of the study-systems and the specific methods used.

Field Studies (Papers **I** and **II**)

In collaboration with my co-authors, I evaluated the effect of inter-cohort competition on young-of-the-year performance (Papers **I** and **II**) and habitat use (Paper **II**) in streams along the western coast of Sweden. In Paper **I**, one stream was used (River Norumsån, figures 2 and 3), while Paper **II** was performed in seven streams (figure 3). The streams are relatively small (the approximate wetted width range from 2 to 5 m) and demonstrate a typical pattern of alternating pool-riffle habitats (figure 2). Nutrient concentrations, conductivity and pH of the streams are all within the normal range of the area (data provided by the Swedish County Administrative Board, Västra Götaland). The streams show considerable fluctuations in flow regime throughout the year (peak flow during spring and minimum flow during summer), since water bodies with the capacity to buffer such fluctuations (lakes and wetlands) are lacking from most of the catchment areas. The experimental sites of all streams were shaded by dense riparian forests, mainly consisting of alder (*Alnus* spp.) and birch (*Betula* spp.) but occasionally also spruce (*Picea* spp.), while the more distant surroundings were dominated by pasture and arable lands.

The streams have stable populations of native brown trout, which also is the dominating fish species. However, Atlantic salmon, European minnow (*Phoxinus phoxinus*), stickleback (*Gasteosterus aculeatus*), pike and eel (*Anguilla anguilla*) are present at lower densities in some of the streams. Potential terrestrial and avian predators present in the adjacent area of the streams include mink and grey heron. Most of the trout are anadromous, migrating to sea after two years in the stream, although a smaller proportion of the population (mainly males) may remain within the stream throughout their entire lives (Dellefors & Faremo 1988).

A blocked design was used in Papers **I** and **II**, where each block (replicate) consisted of two treatment sections, control and manipulated. In control sections, the natural cohort structure was maintained whereas cohorts older than young-of-the-year were removed from manipulated treatment sections and released approximately 1 km downstream the experimental sites. Each treatment section was surrounded by a buffer zone with the same treatment as the adjacent section, as a way of maintaining the treatment effect, and sections were randomly assigned to an upstream or downstream position within each block prior to the start of the experiments. Sampling of fish was performed by means of electro-fishing using a bank-side generator (straight DC, 200-400 V, LUGAB, Sweden). In all cases of measurement or tagging, fish were anesthetized using 2-phenoxyethanol (0.5 ml L^{-1}).

In Paper **I**, five blocks (10 treatment sections) were distributed within one stream (figure 3). The experiment was initiated between 21 September and 12 October 2005, when the current trout population was removed from manipulated sections and *c.* 40 young-of-the-year trout from each control and manipulated section were equipped with Passive

Integrated Transponders for individual recognition (PIT-tags; ID100, Trovan Ltd., US). This enabled us to estimate specific growth rate as well as recapture rate (survival) and individual movement patterns. The experiment proceeded during winter and recapture was performed between 16 and 31 May 2006.

In Paper **II** we used 17 blocks (34 treatment sections) distributed among seven streams (figure 3). The experiment was initiated between 26 April and 8 May 2006 (Sampling I), before young-of-the-year emergence from the gravel bed, when the current trout population was removed from each of the manipulated sections. A second field effort was performed between 12 and 21 June 2006 (Sampling II), approximately one month after emergence of young-of-the-year trout. At this sampling occasion, we used a modified electro-fishing technique (point-abundance sampling) (Copp & Penáz 1988) to collect representative data on young-of-the-year habitat use and abundance. This method has been frequently used on juvenile fishes, partly as a way to avoid displacement of fish ('fright bias') (Heggenes 1988a) and partly since quantitative electro-fishing is difficult to perform on newly emerged fry. Hence, instead of electro-fishing an entire stream section we sampled sub-sites, distributed with a metre distance, in an upstream direction. Each site was electro-fished for approximately three seconds and immobilized fish were collected with a hand net. In addition to counting and measuring the fry inhabiting each site, we also characterized the micro-habitat according to depth, distance to nearest riffle (spawning area) and distance to nearest shore. By doing this we could determine the effect of inter-cohort competition on the young-of-the-year habitat use, habitat selection and habitat preference (see page 21 for definitions). Habitat selection was calculated as the difference between available and used habitat, with a negative value representing selection of habitats that are deeper, positioned at longer distance from riffles and shores than the average available depth, distance to nearest riffle or shore within the stream section. The third and final field effort (Sampling III) was performed between 4 and 13 October 2006, when all individuals within the experimental sites were captured and measured.

Observational data (Paper **III**)

In Paper **III**, we investigated the association between intra- and older-cohort density and young-of-the-year body-size distribution (mean and standard deviation) in populations of brown trout, using data extracted from the Swedish Electro-fishing RegiSter (SERS). The database is hosted by the Swedish Board of Fisheries and contains data of most electro-fishing surveys performed in Sweden since it was launched in 1989 (today more than 35 700 surveys at 13 000 stream sites). We used data on stream-resident ($n = 51$), anadromous ($n = 81$) and lake-migratory trout populations ($n = 27$) sampled nine years or more from the whole of Sweden (in total 1973 samples). Population density estimates followed the recommendations of Bohlin *et al.* (1989) and were in most cases based on three removals. The sites were usually 50 m long with an area depending on stream width. Population samples were included in the analysis only if (**a**) sampling was conducted in August or later, (**b**) body-length was measured on at least 10 young-of-the-year individuals, (**c**) the whole width of the stream section was sampled (not only along banks, which is common in larger/deeper streams), (**d**) brown trout density was $\geq 90 \%$ of the estimated total fish density, and (**e**) each site was represented by at least nine annual observations.

Figure 2. The streams used in the field experiments were small and shaded by dense riparian forests (upper photo: River Norumsån, SW Sweden, the experimental stream used in Paper **I**. See also figure 3). Behavioural and habitat selection studies were performed in artificial indoor streams where food availability and habitat variables, such as water velocity, could be controlled (lower photo: one of 16 test arenas at the Marine Scotland field station in Almondbank, Scotland, used in Paper **IV**) (Photo: Rasmus Kaspersson).

Laboratory Studies (Papers **IV** and **V**)

In Papers **IV** and **V**, we investigated the mechanisms of inter-cohort competition using controlled, semi-natural, stream environments. The following section provides an overview of the general experimental procedures of these, separately for each paper.

*Almondbank (Paper **IV**)*

In order to investigate the habitat use and behaviour of newly emerged Atlantic salmon fry in presence and absence of older cohorts, we used an indoor semi-natural stream at the Marine Scotland field station in Almondbank, Perthshire, UK. The experiment was repeated over two periods: 20 April to 5 May 2009 (Period 1) and 17 June to 11 July 2008 (Period 2). The facility consists of a hatchery and an 80-m indoor flow-through stream-aquarium, equipped with a glass-sided outer wall to enable behavioural observations and supplied with natural stream water from the adjacent River Almond. In this experiment, we used a sub-section of the stream-aquarium, divided into 16 test arenas with stainless steel mesh screens (figure 2).

Each test arena was landscaped as two markedly different habitats; the outer half constituted a deep (23.9 ± 0.1 cm) high-velocity (42.2 ± 0.004 cm s^{-1}; range: 23 - 62 cm s^{-1}) habitat while the inner half constituted a shallow (12.2 ± 0.2 cm) low-velocity (3.3 ± 0.003 cm s^{-1}; range: 0 - 14 cm s^{-1}) habitat (mean $\pm$ SE). A shelter (sheet of opaque PVC), was positioned in the middle of each habitat (figure 2). Water temperature corresponded to that in the nearby river and natural photoperiod was simulated using an electronic timer. Thawed chironomids were delivered to each of the two habitats through an under-gravel feeding tube emerging in the upper part of the test arenas. Food items were provided in an approximate proportion to the water velocity, through a computerized fish feeder (ASU 2000) (MacLean *et al.* 2003), with the high-velocity habitat having 10 times greater food availability.

Hatchery-reared salmon fry were used at Period 1, whereas wild young-of-the-year (Period 2) and yearling salmon (Period 1 and 2) were collected from River Almond using electro-fishing. Five density treatments were used: (**a**) young-of-the-year salmon absent, one age-1 salmon; (**b**) young-of-the-year salmon absent, two yearling salmon; (**c**) eight young-of-the-year salmon, yearling salmon absent; (**d**) eight young-of-the-year salmon, one yearling salmon; (**e**) eight young-of-the-year salmon, two yearling salmon. Each group of fish were observed for five days (2 × 10 minutes each day) after which used fish were removed from the test arenas and new were introduced. During each observation, we noted number of individuals in the high-velocity (deep) habitat and in the low-velocity (shallow) habitat, aggressive interactions within and between cohorts as well as movement patterns, food availability, foraging activity and efficiency.

*Silkeborg (Paper **V**)*

In Paper **V** we investigated the resource holding capacity of yearling trout at an increasing density of young-of-the-year conspecifics. The experiment was performed between 12 August and 9 September 2007 in an indoor semi-natural recirculation stream at the facilities of DTU-Aqua, National Institute of Aquatic Resources, Silkeborg, Denmark. The indoor stream was constructed as an oval loop, consisting of two parallel straight tanks. The outer

of the two tanks was divided into six test arenas using stainless steel mesh screens and a glass-sided outer wall enabled behavioural observations from a darkened hide.

The average water depth and velocity measured 17.3 ± 0.3 cm and 12.9 ± 0.3 cm s^{-1} respectively and the latter was regulated with a paddle wheel in the back tank. The stream bed substratum of each test arena consisted of relatively fine gravel and one large stone was placed in the upper third of the test arenas to provide a profitable holding position. Natural photoperiod was simulated using an electronic timer and water temperature was set to approximately 15°C. Thawed chironomids were manually inserted into an under-gravel feeding tube that emerged in the upper part of the test arenas.

Wild trout were used in the experiment, collected from Bjergskov Bæk (a tributary to River Gudenå, central Denmark) from a mixed population of resident and lake-migratory fish. The focal individual was one yearling, held in the following four treatment groups: (**a**) no young-of-the-year trout; (**b**) two young-of-the-year trout; (**c**) six young-of-the-year trout or (**d**) 12 young-of-the-year trout. Each test arena was observed for one day (6 × 8 minutes) after which used fish were removed from the test arenas and new were introduced. During each observation, we noted yearling foraging activity, aggression, body colouration, position as well as swimming activity.

Figure 3. The streams used in the field experiments were located on the western coast of Sweden, approximately 20 to 80 km north of Göteborg. In Paper **I**, we used one stream, River Norumsån (number 4 on the map), in which five experimental blocks (replicates) were distributed. In Paper **II**, seven streams were used: Henån (1); Varekilsån (2); Stenungeån (3); Lerån (5); Vallby å (6); Kollerödsbäcken (7) and Grannebyån (8), in which 17 experimental blocks were distributed.

MAIN FINDINGS AND DISCUSSION

This section provides an overview of the main findings and a short summary of the discussion of each paper (**I** to **V**) included in the thesis.

Young-of-the-year Performance During Winter (Paper **I**)

In Paper **I**, we investigated the effect of inter-cohort competition on young-of-the-year survival, growth and movement in a long-term field experiment; from autumn, during winter to spring. The study was performed in one stream (River Norumsån; see figures 2 and 3) and the experimental site was sub-divided into sections where older cohorts were either maintained (control) ($n = 5$) or removed (manipulated) ($n = 5$), through electro-fishing.

33 % ($n = 133$) of the individually (PIT) tagged young-of-the-year trout were recaptured in spring, with no effect of presence or absence of older cohorts on the recapture rate. The first winter after emergence has been suggested as a potentially important bottleneck for juvenile salmonids, partly through increased habitat overlap among cohorts (Mäki-Petäys *et al.* 2004) which may limit the shelter availability (Armstrong & Griffiths 2001) and partly through insufficient energy stores at the onset of winter (e.g. Finstad *et al.* 2010; Finstad *et al.* 2004; Huusko *et al.* 2007). Hence, the lack of treatment response on recapture rate suggests that the presence of older cohorts did not influence overwintering survival of young-of-the-year trout in this experimental site, possibly through unlimited shelter availability.

Despite the duration of the experiment and relatively harsh winter conditions, movement distance of the PIT-tagged young-of-the-year trout was remarkably restricted, with 83 % being recaptured within 50 m from the release points and only 8 % dispersing more than 200 m, in agreement with previous studies on movement in stream-living salmonids (e.g. Bohlin *et al.* 2002). While movement was independent of older cohorts, there were significantly more immigrants (untagged individuals) in manipulated sections at recapture, suggesting that older cohorts may restrict the number of favorable habitats for younger individuals, possibly as a result of prior residency in the stream habitat.

In addition, Paper **I** provided evidence of negative density-dependent growth rate (in agreement with Papers **II** and **III**), with young-of-the-year trout growing significantly slower in sympatry with older cohorts than in sections where the density of older trout was experimentally reduced (see Nordwall 1999 for a similar result on older cohorts). Moreover, growth rate was also negatively correlated with initial density and biomass of older cohorts in control sections, while no such response was observed in manipulated sections, thus providing further evidence of a negative density-dependent response through inter-cohort competition. Given the fact that densities were approximately balanced between sections at the time of recapture, the treatment effect on growth rate was most likely established during the pre-winter period, just after the start of the experiment, rather than a 'catch-up effect' during early spring (Berg & Bremset 1998). Furthermore, young-of-the-year trout from treatments with reduced inter-cohort competition are also likely to have had higher capacity to maintain pre-winter biomass through either higher food intake rate during winter or lower stress levels (Edeline *et al.* 2010).

Habitat use and Performance at Emergence (Paper II)

In Paper **II**, we investigated the effects of inter-cohort competition at the critical phase of emergence (Sampling II; performed in June) and at the peak growth period (Sampling III; performed in October) of the first year. The study was performed in seven streams (see figure 3) and the experimental site of each stream was sub-divided into sections where older cohorts were either maintained (control) ($n = 17$) or removed (manipulated) ($n = 17$) through electro-fishing (Sampling I). Effects on young-of-the-year performance were observed at Sampling II and III, while habitat use, selection and preference were investigated at Sampling II only (see pages 21 and 30 for further details concerning these variables).

The results of Paper **II** showed that habitat utilisation was associated with body-size, with large individuals holding position at deeper habitats, further away from riffles, thus corroborating evidence provided by previous studies (e.g. Bohlin 1977; Bremset & Berg 1999; Girard *et al.* 2004; Greenberg *et al.* 1996; Heggenes 1988a). Similarly, when comparing habitat selection indices between cohorts (available-used habitat) (see pages 21 and 30), we found older trout to actively select habitats that were deeper and located further from riffle areas in comparison with younger cohorts, thus providing additional evidence for the 'bigger-fish-deeper-habitat relationship'.

While several studies have observed size- and age-dependent habitat segregation among stream-living salmonids in field, few have explicitly tested its underlying mechanisms (but see Bohlin 1977; Vehanen *et al.* 1999) and especially not in the field. By experimentally removing older cohorts from specific stream sections, thus relaxing the intensity of inter-cohort competition, we were able to show that newly emerged trout selected habitats that were deeper than in sections with a natural cohort structure. Hence, and in agreement with the findings of Paper **IV**, these results suggest that the observed habitat segregation among cohorts of stream-living salmonids in the wild cannot be explained by size-dependent preference only, but that habitat exclusion through inter-cohort competition must be considered as an additional underlying mechanism.

The results of Paper **II** also provide evidence for a negative effect of inter-cohort competition on the performance of young-of-the-year individuals, thereby confirming the results of Papers **I** and **III**, and the relatively few studies investigating inter-cohort effects on salmonid growth in the field (e.g. Nordwall *et al.* 2001). More specifically, in experimental sections with relaxed inter-cohort competition, young-of-the-year trout had significantly larger body-size at the final sampling occasion (Sampling III), while the response was less apparent at the second sampling in June (Sampling II). Although this delayed response on growth may suggest limited treatment duration, the lack of effect on growth at the Early Critical Period (ECP), is not entirely unexpected and may instead suggest that the scope for storing energy (and attaining positive growth) during the ECP is outweighed by higher energy demands to survive (Schultz & Conover 1997). Evidence supporting this theory has been provided by Einum *et al.* (2006) observing partitioning of intra-cohort density-dependent processes (growth, mortality and migration) during ontogeny in young-of-the-year Atlantic salmon. In their study, density-dependent mortality was accompanied by density-independent growth at the fry stage (immediately after onset of exogenous feeding), while negative density-dependent growth and density-independent survival was observed among juveniles later in the growth season.

In addition to an inter-cohort effect on young-of-the-year body-size, we also detected evidence of intra-cohort density-dependence, in correspondence with Paper **III** and with several recent studies (e.g. Bohlin *et al.* 2002; Einum *et al.* 2006; Grant & Imre 2005; Imre *et al.* 2005; Imre *et al.* 2010; Jenkins *et al.* 1999). More specifically, the average young-of-the-year body-size was negatively associated with intra-cohort density (Sampling III), while the body-size variation (CV) increased with density (Sampling II and III).

We found no effects on young-of-the-year density in presence or absence of older cohorts. However, since this experiment was designed to use natural trout densities, the response may have been confounded by the large variation in initial density (*i.e.* egg numbers) between treatment sections. In addition, the large number of sites investigated disabled us from individually tagging young-of-the-year trout, providing an additional explanation to the obtained result. Hence, further studies are required to investigate the effects of older cohorts on young-of-the-year survival at the time of emergence.

Effects on Body-size Distribution (Paper **III**)

Using a data-set of 159 brown trout populations from the whole of Sweden, Paper **III** investigated the generality of inter-cohort competition and, more specifically, to what extent the body-size distribution (mean and standard deviation) of young-of-the-year trout is associated with densities on an intra-cohort level as well as with densities of older cohorts. The data-set was provided by the Swedish Electro-fishing RegiSter (SERS) (hosted by the Swedish Board of Fisheries) and was selected to contain anadromous, lake-migratory and stream-resident populations, surveyed nine years or more (in total 1973 samples).

The result of Paper **III** showed that the average young-of-the-year body-size was negatively associated with both its own density and with that of older cohorts, and to a similar magnitude. When splitting this effect between population types, we found that the effect of older cohorts on young-of-the-year body-size was strongest in populations of stream-resident trout (even stronger than the intra-cohort effect), possibly explained by the lower young-of-the-year density and higher proportion of older cohorts in these populations (Bohlin *et al.* 2001). Hence, this finding is in agreement with those of Papers **I** and **II** as well as with previous field studies investigating this issue (e.g. Nordwall *et al.* 2001), but also adds to the current knowledge by suggesting that inter-cohort interactions may be a more widespread phenomenon in populations of stream-living salmonids than previously believed.

The findings of Paper **III** also showed that the association between standard deviation of young-of-the-year body-size and density is cohort dependent. While the standard deviation tended to get wider with increasing young-of-the-year density, it became narrower with increasing density of older cohorts. A wider variation of performance-related traits is to expect if competition is intense and resources are unequally distributed among competitors (Uchmanski 1985). This is in agreement with the finding of Paper **II** and with the relatively few previous studies that have investigated this issue within cohorts of stream-living salmonids (e.g. Einum *et al.* 2006; Elliott 1994; Jenkins *et al.* 1999; Keeley 2001). The negative association between standard deviation and density of older cohorts was, however, somewhat more unexpected. We suggest that a possible explanation for this response is related to the size-dependent habitat exclusion described in Papers **II** and **IV**.

At high density of older cohorts we would expect fewer young-of-the-year individuals, especially among those that belong to the 'upper tail' (dominant) group, to have access to high-growth habitats. As these dominant young-of-the-year individuals are forced to less favourable habitats, the 'lower tail' (subordinate) group would experience a similar shift to even less profitable habitats where they may experience increased risk of predation from avian and mammalian stream-bank predators (Heggenes & Borgstrom 1988; Lonzarich & Quinn 1995). Hence, this would result in a narrowed size-range of young-of-the-year individuals at high densities of older cohorts, while an opposite pattern would appear at high intra-cohort densities as more individuals have access to profitable areas of the stream.

In addition, the data-set of Paper **III** was also able to provide a more detailed insight into the relation between young-of-the-year body-size and population density, by showing that the size-density association was more negative at high young-of-the-year densities than at low, while the opposite pattern was observed when considering standard deviation. This result contrasts several recent studies showing strongest effect on body-size at low young-of-the-year densities while being less evident as densities increase (e.g. Grant & Imre 2005; Imre *et al.* 2005; Imre *et al.* 2010; Jenkins *et al.* 1999). Hence, we suggest that further studies are required to investigate the underlying explanation of this diverging response and the intriguing association between inter-cohort densities and young-of-the-year body-size variation presented in this study.

Habitat Preference and Behavioural Interactions (Paper **IV**)

The aim of Paper **IV** was to investigate the mechanisms of habitat use in young-of-the-year Atlantic salmon and, more specifically, to determine whether the use of marginal, less profitable, habitats among newly emerged fry is an effect of inter-cohort competition or size-dependent swimming capacity.

I used a controlled semi-natural stream environment with continuous supply of natural stream water and controlled food availability. Each test arena ($n = 16$) was landscaped into two habitat types; a deep, high-velocity, area and a shallow, low-velocity, area, with food provided in an approximate proportion to the water velocity. The following five density treatments were used: (**a**) young-of-the-year salmon absent, one age-1 salmon; (**b**) young-of-the-year salmon absent, two yearling salmon; (**c**) eight young-of-the-year salmon, yearling salmon absent; (**d**) eight young-of-the-year salmon, one yearling salmon; (**e**) eight young-of-the-year salmon, two yearling salmon. The experiment was repeated over two periods: 20 April to 5 May 2009 (Period 1) and 17 June to 11 July 2008 (Period 2).

The findings of Paper **IV** showed that young-of-the-year Atlantic salmon preferred the deep, high-velocity, habitat at both observation periods (Period 1 and 2). Individuals using this habitat had a similar foraging efficiency as those using the shallow, low-flow, areas but a markedly higher foraging activity (food intake and attempts), suggesting that the additional food availability outweighed the potential costs of foraging at these conditions. Hence, these findings seem to contrast previous evidence suggesting size-dependent constraints to habitat use among newly emerged salmon (e.g. Nislow *et al.* 1999).

In sympatry with yearlings, however, young-of-the-year salmon were excluded to the low-velocity habitat, thus experiencing a subsequent decrease in foraging activity. This pattern was observed despite the fact that yearlings showed indiscriminate habitat

preference at Period 1, suggesting that the mere presence of an older individual may induce avoidance behaviour among younger ones. In addition, the frequency of aggressive interactions between cohorts was low, thus providing further support for intimidation as the underlying mechanism to the observed response (see Griffiths & Armstrong 2002).

The exclusion of young-of-the-year salmon from profitable, high-flow, areas correspond with the findings of Paper **II**, where young-of-the-year trout used shallower habitats in presence of older cohorts. Hence, these findings provides a plausible underlying mechanism to the negative effects of inter-cohort competition on young-of-the-year growth and final body-size detected in field (Papers **I** and **II**) as well as to the negative size-density associations revealed by the observational data-set (Paper **III**).

In agreement with Nislow *et al.* (1999) and Einum *et al.* (2008), the result of Paper **IV** (and Paper **II**) suggest that marginal habitats may be essential for the recruitment of salmonids at the point of emergence, however, not necessarily by being preferred by the newly emerged fry but by acting as refuges from competition with older cohorts.

The Costs of Defence (Paper **V**)

The aim of Paper **V** was to explore the benefit of being old at increasing young-of-the-year densities. Density of competitors is assumed as a key factor in determining the capacity to defend limited resources, such as mating opportunities, shelters or feeding territories (Grant 1993). Few studies have, however, investigated the effect of density on resource defence in groups with large asymmetries in competitive ability, as a consequence of for example age or body-size.

In Paper **V**, I used a semi-natural stream environment with fixed food availability and controlled environmental variables (temperature, water-velocity, light-regime and substrate). The focal individual was one yearling, held at the following four density treatments: (**a**) no young-of-the-year trout; (**b**) two young-of-the-year trout; (**c**) six young-of-the-year trout or (**d**) 12 young-of-the-year trout.

The result of Paper **V** showed a progressive increase in yearling aggression, as the young-of-the-year density increased. This finding disagrees with the resource defence theory (Brown 1964) and is subsequently also inconsistent with several previous studies that provides evidence of a dome-shaped pattern of aggression with increasing competitor densities (e.g. Chapman & Kramer 1996; Fenderson & Carpenter 1971; Jones 1987; Keenleyside & Yamamoto 1962; Kim & Grant 2007; Syarifuddin & Kramer 1996). A possible explanation for this unexpected response is the body-size structure (Kim & Grant 2007). More specifically, a large difference in body-size between defenders (in this study exemplified by yearling trout; 99.1 ± 0.91 mm long) and intruders (young-of-the-year trout; 66.5 ± 0.75 mm long, mean ± SE) may involve a lower cost of aggression than what would be expected if the competitors were of equal size and may therefore have enabled yearlings in our study to defend the food resource also at high densities of intruders. Hence, this would shift the peak of aggression (*i.e.* the economic defendability) to higher densities than expected if the group were composed of equally sized individuals.

However, the findings of Paper **V** also showed that yearling trout made significantly more unsuccessful foraging attempts and adopted a darker body colouration at high young-of-the-year densities. Dark body colouration is commonly observed among subordinate

salmonids signalling social submission (Keenleyside & Yamamoto 1962; O'Connor *et al.* 1999), but has rarely been linked with changes in density, and especially not among more dominant individuals. Hence, the reduced foraging efficiency and the darkened body colouration suggest that older individuals experienced higher stress levels at increasing young-of-the-year densities. This finding is in agreement with previous studies suggesting increased costs of aggression as competitor densities increase, through for example social stress (Praw & Grant 1999) and lost time foraging (Krause & Ruxton 2002), processes that may translate into reduced individual performance (Nöel *et al.* 2005). In accordance, these high-cost conditions are assumed to turn interference competition into exploitative interactions, as predicted by the resource defence theory, and may therefore also benefit individuals lacking features that are associated with successful resource defence, such as large body-size (Tregenza *et al.* 1996).

Aggression is generally assumed to increase the ability to defend a limited resource (e.g. Adams *et al.* 1998; Bryant & Grant 1995; Harwood *et al.* 2002) and the increasing number of unsuccessful foraging attempts at high aggression detected in our study was therefore somewhat unexpected. A possible explanation for this response is that although the yearling trout experienced increased costs of less successful foraging, this did not outweigh the benefit of using aggression at the body-size structure and density conditions used in this study.

This is one of few previous studies showing that young-of-the-year salmonids can impose a competitive pressure on older cohorts, suggesting that further experiments are required in order to fully understand the underlying behavioural interactions of inter-cohort competition at increasing competitor densities.

GENERAL DISCUSSION AND CONCLUSIONS

This thesis investigates the effects and the underlying mechanisms of inter-cohort competition in juvenile Atlantic salmon and brown trout using experiments in field, controlled behavioural studies and observational data. These issues have attracted relatively limited attention in the previous literature (table 1). Moreover, there is a general shortage of experimental studies on salmonids in field and especially few studies have been performed at natural densities, which may limit the ability to establish the effects and mechanisms of competition, niche segregation as well as of density-dependent regulation (see Fausch 1998 and references therein). The studies presented here were designed with these circumstances in mind, and may in that way add to the current knowledge in the field of salmonid ecology.

In conclusion, the result of my studies suggests that cohorts of stream-living salmonids compete for limited resources in the stream habitat. This will be in favour of old individuals, although the result also suggests that their competitive benefit may decrease at increasing densities of young-of-the-year fish (Paper **V**). I support this conclusion on the following three main findings:

(**a**) Density-reductions of older cohorts in field increased the growth and the final body-size of young-of-the-year trout, an effect that appeared some months after emergence and the early critical period (Papers **I** and **II**). In order to test the generality of these findings,

we used observational data from previous trout population surveys. The results of this study provided evidence of a negative association between density of older cohorts and young-of-the-year body-size, in the same magnitude as the negative size-density association within the young-of-the-year cohort (Paper **III**). Hence, the inter-cohort effect on young-of-the-year body-size corresponds with the few previous studies investigating this issue in field (e.g. Nordwall *et al.* 2001) and adds to previous knowledge by showing that inter-cohort competition may be more prevalent among stream-living salmonids than previously believed.

The negative response on young-of-the-year growth and final body-size in sympatry with older cohorts may be explained by several processes, some of which are already mentioned. For example, older cohorts may exclude young-of-the-year individuals to areas with low food availability (as shown in Papers **II** and **IV**), presence of older individuals may reduce young-of-the-year foraging activity through intimidation (e.g. Greenberg *et al.* 1997; Griffiths & Armstrong 2002; Szabo 2002), increase young-of-the-year stress levels and thereby reduce growth rate indirectly (e.g. Edeline *et al.* 2010), in combination with more general density-dependent effects, such as reduced overall food availability, decreased territory size and increased costs of defence (Grant 1993; Klemetsen *et al.* 2003; Krause & Ruxton 2002).

From a more general perspective, the negative density-dependent effects on growth and final body-size detected in this thesis (Papers **I**, **II** and **III**) is in accordance with previous evidence provided by a number of observational as well as experimental studies on stream-living salmonids (e.g. Bohlin *et al.* 2002; Crisp 1993; Einum *et al.* 2006; Grant & Imre 2005; Grant & Kramer 1990; Imre *et al.* 2005; Lobon-Cervia 2005; Lobon-Cervia 2007). However, in contrast to several recent studies (e.g. Grant & Imre 2005; Imre *et al.* 2005; Imre *et al.* 2010), we found the most negative size-density associations to occur at high, rather than low, population densities (Paper **III**), hence providing an interesting opportunity for further investigations. An area for future research is also to elucidate the mechanisms underlying the unexpected and novel finding of cohort-dependent effects on body-size variation, as presented in Paper **III**.

(**b**) As in several previous field studies (e.g. Bohlin 1977; Bremset & Berg 1999), we found evidence of an ontogenetic segregation in habitat use in field (Paper **II**), where young individuals used marginal habitats close to the spawning area while old individuals were positioned in deeper habitats. Size-dependent swimming capacity has been suggested as a possible underlying mechanism to this pattern, where young fish are constrained to a small fraction of the stream where the water velocity is low (Armstrong 1997; Armstrong & Nislow 2006; Elliott 1989). Empirical evidence in support of this theory has been provided through field and laboratory tests of foraging-based models, suggesting that young-of-the-year salmonids use the shallow habitat to maximize the pay-off of swimming-costs and food intake rate (Nislow *et al.* 1998; 1999; 2000), even though these habitats may be limited at the time of emergence (Nislow *et al.* 1999). However, the result provided here (Papers **II** and **IV**) suggests that the underlying mechanism of young-of-the-year habitat use may be more complex than just size-dependent swimming capacity. First, we are able to show that even relatively newly emerged salmon fry not only have the capacity to hold position and forage at high velocities, but also prefer these habitats over those with lower water velocity (Paper **IV**). Second, density-reductions of older cohorts in field and behavioural

observations in an artificial stream environment (Papers **II** and **IV**) provide evidence of overlapping habitat preferences between cohorts, where young-of-the-year trout and salmon used less profitable habitats in sympatry with older cohorts. Hence, this suggests that presence of older cohorts in the shared stream habitat influences the ontogenetic size segregation observed in field. Inter-cohort competitive exclusion of young-of-the-year salmon to less profitable low-velocity habitats was also shown to reduce the foraging activity (Paper **IV**). Hence, this response may therefore provide an insight into the possible linkage between exclusion to habitats with low food availability (Papers **II** and **IV**) and the reduced growth in sympatry with older cohorts (Papers **I**, **II** and **III**).

(**c**) Testing the resource holding capacity of yearling trout at increasing densities of young-of-the-year competitors showed that older cohorts were less successful in foraging and adopted darker body coloration, suggesting that they faced increased stress levels at high under-yearling densities. Despite this, the level of aggression increased, hence indicating that the body-size difference between the intruders (young-of-the-year trout) and the defender (yearling trout) enabled yearlings to use a territorial strategy at higher densities than expected if all competitors were of equal size (Paper **V**).

Methodological Considerations

The methods used in this thesis have all been tested and evaluated in previously published papers. There are, however, some methodological details that may benefit from additional explanation and justification.

In Papers **I** and **II**, we investigated the existence of inter-cohort competition by reducing the density of older cohorts in a priori selected stream sections while the young-of-the-year cohort was maintained at natural levels (also known as a 'minimal additive design') (Fausch 1998). Although this experimental set-up has the weakness of not providing insights into the relative importance of intra- and inter-cohort competition, it enabled us to investigate the presence or absence of inter-cohort competitive interactions without any further manipulations of the natural density conditions. Several previous field studies have studied competition and density-dependence in populations of stream-living salmonids populations by experimentally increasing population densities, in some cases above the carrying capacity of the local habitat. Although providing valuable information, these conditions do not necessarily reflect those occurring at natural densities (Brännäs *et al.* 2004).

As a result of large water-flow fluctuations in the experimental streams (see page 29) of Papers **I** and **II**, we were unable to screen the treatment sections with nets. Instead, we used buffer zones to isolate density-manipulations and to avoid fish from moving between sections, a technique that has been applied in previous field experiments (e.g. Bohlin *et al.* 2002; Nordwall *et al.* 2001). In a Scottish stream, Armstrong *et al.* (1994) studied redistribution of juvenile salmonids after experimentally depleting three sites (60, 20 and 20 m in length) surrounded by control areas with natural densities (120, 20 and 20 m), thus using a similar approach as in Papers **I** and **II**. They found no re-colonization of fish from buffer zones, or from areas outside, to the depleted 60 m site when re-sampling the area 14, 28 and 69 days after depletion. In the smaller areas, some re-colonization occurred, but only 30-44 % of the pre-removal densities were reached at the final sampling 35 days after

depletion. Hence, these findings of limited re-colonization rates to depleted areas correspond with that of Paper **II**, where the density-reductions of older cohorts were maintained between sampling occasions (1 and 3 months respectively). In Paper **I**, however, the reduction was compensated for at recapture, probably as a consequence of relatively harsh winter-conditions but also of the much longer duration between density reduction and re-sampling (7 months) (see pages 29 and 30), hence suggesting that the method of buffer zones to isolate treatment sections may be more efficient on a shorter time-scale. What may appear as a contrasting finding to the re-colonization of sections with reduced density in Paper **I**, movement of target fish was remarkably restricted, with 80 % of the fish being recaptured within 50 m from the point of release and only a few migrating longer distances than 200 m, despite the fact that some displacement of fish can occur during electro-fishing (Nordwall 1999). This restricted movement is in accordance with previous studies in the same river (e.g. Bohlin *et al.* 2002; Höjesjö *et al.* 2007b) as well as in other systems (e.g. Heggenes 1988a; Steingrimsson & Grant 2003; Sundström *et al.* 2004) and may therefore provide further support for the ability to perform experimental density-manipulations in an open stream-system, provided that buffer zones cover the short-scale movement pattern. In Papers **I** and **II**, we released older trout that were captured in manipulated treatment sections approximately 1 km downstream from the experimental area. A similar design was used by Heggenes (1988a), who displaced 130 resident brown trout (captured 1100 m or 3300 m from the release site) and found only two individuals returning to their natal stream area, after one and four months respectively, despite higher densities at the release sites. Several, more recent, studies have, however, shown that stream-living salmonids have the capacity to migrate back to their natal site after experimental displacement (e.g. Armstrong & Herbert 1997; but see Belanger & Rodriguez 2001). However, such homing seems most evident when fish are displaced shorter distances and among older life-stages in association with spawning activity, suggesting that these findings may not represent the study-system used here. While our studies provide little insight into the movement pattern of displaced fish, this provides an interesting opportunity for further investigation.

In Paper **II** we collected data on total habitat availability as well as on young-of-the-year habitat use in each of the experimental sections. As argued by Heggenes *et al.* (1991), the observation method for investigating habitat use in field should be selected with the aim of minimizing disturbance (which may influence habitat use prior data collection), and being equally efficient in all available stream habitats, for all available size-classes of fish. Commonly used methods for actively observing habitat use of salmonids include underwater observations by snorkelling (e.g. Nakano *et al.* 1999) and river bank observations (e.g. Heggenes *et al.* 1991). However, the restricted width and depth of the streams used in Paper **II** (see page 29) and the often highly turbid water suggest that these methods would result in both disturbance of fish and biased habitat data. Hence, as an alternative to these methods, we used a modified electro-fishing technique (point-abundance sampling) that has been frequently used to investigate habitat use of stream-living fishes (e.g. Copp & Penáz 1988; Davey *et al.* 2005; Heggenes 1988a; Mäki-Petäys *et al.* 1997) and is suggested to have low effects on the displacement of fish from their original habitat (Heggenes 1988a; Mäki-Petäys *et al.* 1997).

In order to control food availability, competitor density, habitat availability and to enable behavioural observations, we used artificial stream environments when investigating the underlying mechanisms of inter-cohort competition (Papers **IV** and **V**). Such laboratory-based systems have an important function in improving our knowledge of salmonid behaviour. In order for the obtained results to correctly reflect a natural situation, however, it is essential to strive for a correspondence with the natural stream environment. With this in mind, we used test arenas landscaped with gravel and equipped with holding stones or shelters, food items were provided as to resemble the availability of drifting invertebrates and temperature and light conditions were set in the same range as those in nature at the time of the experiment. Moreover, in Paper **IV**, we used a flow-through semi-natural laboratory facility with natural stream water from an adjacent river (River Almond) that further increased the resemblance with natural conditions, by providing olfactory cues and natural temperature fluctuations.

Concluding Remarks

In line with the findings of this thesis, the question arises as to if, and how, the effect of inter-cohort competition on young-of-the-year growth (Papers **I**, **II** and **III**) and habitat use (Papers **II** and **IV**) may translate also into population-level effects.

Several studies have provided evidence of how a reduction in growth rate can result in both direct and indirect negative effects on fitness, by for example reducing fecundity (Hutchings 1993), delaying or cancelling smoltification (e.g. Bohlin *et al.* 1993; Bohlin *et al.* 1996; Hutchings 1993; Hutchings & Jones 1998; Metcalfe 1998), reducing the competitive ability (Ward *et al.* 2006) and delaying the timing of ontogenetic shifts, which may further enhance the density-dependent response (e.g. Rincon & Lobon-Cervia 1999). Several studies have also shown a direct association between body-size and survival rate (Lorenzen 1996; Wootton 1999), where small individuals generally experience higher mortality rates, by being more susceptible to starvation (e.g. Schultz & Conover 1997; Schultz *et al.* 1998), predation (e.g. Hyvärinen & Vehanen 2004) and environmental factors, such as water flow (Good *et al.* 2001) (but see Carlson *et al.* 2008). However, the extent to which a reduced body-size translates into negative population growth is also dependent on the capacity of individuals to compensate for an impaired growth at a later stage (compensatory growth) (e.g. Johnsson & Bohlin 2005; Metcalfe & Thorpe 1992), which in turn is likely to be influenced by overall population density, food abundance as well as availability of profitable habitats (Ali *et al.* 2003).

The findings of this thesis suggest that inter-cohort competition can restrict newly emerged fry to less profitable stream habitats. Since limited availability of fry territories is assumed as a key factor for establishing cohort strength of stream-living salmonids (Armstrong & Nislow 2006), it seems likely that inter-cohort competition may affect also the intensity of the Early Critical Period. While the results obtained here provide no direct evidence of reduced fry survival at presence of older cohorts, this may be a consequence of uncontrolled initial variation in egg density, which is likely to obscure such effects (Paper **II**). In addition to being excluded to less profitable habitats, it is also likely that newly emerged salmonid fry may experience increased mortality through cannibalism from older cohorts. However, while cannibalism has been frequently observed among lentic fish

populations (including salmonids) (e.g. Amundsen 1994; Amundsen *et al.* 1995; Labee-Lund *et al.* 1992), little is known of its prevalence among stream-living salmonids (but see Elliott 1967; Vik *et al.* 2001). Hence, the effect of older cohorts on the behaviour and performance of fry at emergence provides an intriguing and important area in need of further investigation.

From an applied point of view, the findings of this thesis highlight the importance of taking inter-cohort interactions into account in order to understand the true habitat preference of stream-living salmonids, and hence to successfully manage and restore their habitats in the wild. In agreement with Nislow *et al.* (1999; 2000; 2004) and Einum *et al.* (2008), we suggest that maintaining or recreating marginal habitats may be an important way of increasing the survival of newly emerged salmonid fry, by acting as refuges from inter-cohort competition.

"

Rivers and the inhabitants of the watery elements are made for wise men to contemplate and for fools to pass by without consideration

Izaak Walton
The Complete Angler (1653)

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