Life history types and strategies

Case studies on brown trout (*Salmo trutta*) and alewives (*Alosa pseudoharengus*), involving physiological differences and interspecific interactions.

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Preface

This dissertation has been submitted to the National Institute of Aquatic Resources at The Technical University of Denmark (DTU Aqua) in partial fulfilment for the degree of Doctor of Philosophy (Ph. D.)

The pages printed in this thesis are based on the results from labours that were carried out from primo 2009 to ultimo 2011 at Lake Hald (Denmark) and from a stay at the "Post Lab" (Yale University, New Haven, Connecticut).

Contents

Acknowledgements

Objectives

This dissertation relates to life history strategies of brown trout (*Salmo trutta*) and alewives (*Alosa pseudoharengus*). The first part focuses on the brown trout population in Lake Hald, Jutland, Denmark. The second part relates to the effect of life history differences of alewives in lakes in Connecticut, North America.

Part one aimed at revealing the mechanistic basis of life history strategies of trout (MS I). Limited knowledge exists on the underlying factors leading to potamodromous *vs* anadromous life history strategies in brown trout. The objective of this part of the study was to obtain more knowledge on the differences between migratory strategies. In Lake Hald, brown trout exhibits three distinct life history strategies and is therefore a very suitable study system addressing this topic. Specifically, life history strategies of brown trout were identified and retrospectively correlated to physiological indicators. This investigation was tied up on a telemetry approach, using passive integrated transponders (PIT), where PIT data loggers monitored the movements of juvenile trout between the tributaries, the lake and the lake outlet, respectively.

The brown trout population in Lake Hald has declined in recent years. This has coincided with a rapid increase in numbers of nesting cormorants (*Phalacrocorax carbo sinensis*) in an adjacent breeding colony. Generally, the knowledge of the quantitative effect of avian predation on salmonid populations in European freshwater systems is limited. Thus, avian predation on a lake resident brown trout population was studied (MS III). PIT telemetry was used to identify the habitat where predation occurred and thereby exploring if avian predation pressure is equal between life history strategies.

PIT telemetry was a central tool in this study. Therefore potential adverse effects of PIT tagging were evaluated in a field study based of numerous recaptures of pit tagged brown trout (MS IV).

The objective of the second part of this thesis was to relate the life history differences in alewives to the ontogeny of co-occurring largemouth bass (*Micropterus salmoides*). Alewives can have different life history strategies, being either anadromous or landlocked, and therefore affect zooplankton communities in different ways. Largemouth bass depend on zooplankton availability during the juvenile stages and it was expected that different alewife life histories will have different influence on the ontogeny of largemouth bass (MSII).

In the introduction the main findings of my study are presented and set in to context of other studies. In addition to the main findings from the 4 manuscripts listed below, I also include some results that so far have not been included as manuscripts. These will be referred to as *unpublished results*.

MS I   Boel, M., Aarestrup, K., Baktoft, H., Larsen, T., H. Madsen, Malte, Skov, C., S.S., Svendsen, J.C. and Koed, A. The physiological basis of partial migration in the brown trout (*Salmo trutta*) (manuscript)

MS II   Boel, M., Brodersen, J, Koed, A and Post, D.M. Life history differences in alewives (*Alosa pseudoharengus*) alter the ontogenetic trajectory of juvenile largemouth (*Micropterus salmoides*) (manuscript)

MS III   Boel, M. & Koed, A. Habitat specific avian predation on brown trout (*Salmo trutta*) (manuscript)

MS IV   Boel, M., Aarestrup, K., Koed, A., Baktoft, H. and Skov, C.. Field based evaluation of the effect of 23 mm passive integrated transponder (PIT) tags on the length-mass relationship in wild juvenile brown trout (*Salmo trutta*) (submitted manuscript: *Fisheries Management and Ecology*)

Introduction

Behavioural biology, also known as ethology, generally involves placing animal behaviours into various contexts that will provide explanations to animals expressing certain behavioural characteristics. To answer this biologists have applied laboratory and field approaches that extend over many biological disciplines. These sometimes overlap and stretches from the more uncompromising and functional disciplines, such as neurobiology and physiology, to the more observational end, such as sociobiology. Though very different, these approaches are used to answer questions about the relevance of different phenotypes in matters of survival, evolution and interactions (Griffiths et al. 2008). Tinbergen (1963) states four major questions in biology. First, regarding proximate causation of behaviours; identifying external and internal factors that encourage a behavioural phenotype. Second, regarding the function of behaviours; in what ways behaviours increase survival and fitness. Third, regarding evolution; using comparative approaches to identify selection on behavioural types. Fourth, ontogeny of behaviours; how do the behaviours develop /change through life stages and what causes these changes. Simply observing behaviours often raises more questions than it provides answers and it is of imperative importance to combine behaviour with other approaches to generate a more complete understanding of behaviours; for example using telemetry in combination with physiology or functional genomics, may help to provide the mechanistic understanding of what motivates different behaviour types (Cooke et al. 2008).

1 Study organisms

1.1 Brown trout

Brown trout (*Salmo trutta*) is native to Europe and the natural range stretches to the western parts of Asia and northern parts of Africa. Brown trout is a very plastic species, displaying a variety of life history strategies, which makes them very adaptable to alternative environments. This adaptability

in combination with human introductions of brown trout around the world, can explain why brown trout currently is a worldwide species thriving in many different environments outside its natural range (MACCrimmon & Marshall 1968; MACCrimmon et al. 1970; Klemetsen et al. 2003).

The salmonid family displays a variety of life history strategies that involves differences in breeding and migration patterns. Especially in brown trout populations multiple life history strategies are common and often one or more strategies coexist within the same population. Strategies range from residents that reside in their native stream (resident fluvial); potamodromous migrants that reside in downstream river parts (fluvial-adfluvial) or lakes (lacustrine-adfluvial); or anadromous migrants that migrate to saltwater environments of fjords or the sea (Eliott 1994; Klemetsen et al. 2003). Spawning takes place in winter, where females dig their nests in the coarse gravel of streams or rivers. The females lay their eggs in the nests while one or more males fertilize the eggs. Subsequently the nest is covered with gravel by the female. After the eggs hatch in the spring, the migratory part of the population spend 2-6 years in the natal stream before migrating to the sea, time increasing with higher latitudes (Jonsson & Labeelund 1993). Migrants eventually return to spawn in the gravel of their native river or stream, closing the migration cycle. The migration period outside the native river/stream habitat can vary from 6 months to one or several years (Eliott 1994; Klemetsen et al. 2003). Anadromous trout undergo the parr-smolt transformation (smoltification), which is related to preparatory changes for living in a saline environment. It involves an active up regulation of the hypo-osmoregulatory ability (McCormick & Saunders 1987; Hoar 1988) correlating with increases in gill Na/K ATPase activity (McCormick et al. 1995; Nielsen et al. 2003; Nielsen et al. 2004). Those that resides in the natal streams do not show this up regulation and hence gill Na/K ATPase activity can be used as a proxy for future migration propensity (Nielsen et al. 2004). However, it cannot be used to distinguish between coexisting

potamodromous and anadromous brown trout as smoltification appear to be characteristic to both (MS I;(Pirhonen & Forsman 1998).

Brown trout populations often segregate into that individuals that become stream residents, while other individuals migrate to rivers (Cucherousset et al. 2005), lakes (Jonsson 1985; Forseth et al. 1999; Olsson & Greenberg 2004) or the sea (Jonsson 1985; Cucherousset et al. 2005). The mechanistic explanations for residency and migratory behaviour have received more and more attention in recent years. However, the explanation of multiple migratory forms (i.e. potamodromous and anadromous) have so far received very little attention. The brown trout population of Lake Hald, which was investigated in this study, is located in the centre of Denmark (Figure 1). The lake houses brown trout with resident, potamodromous and anadromous life history strategies and poses an excellent model system to answer questions about differences life history traits. However, the population has been landlocked for centuries, due to a migration barrier downstream of the lake. The design of this barrier allows for the smolts to leave the lake and migrate towards the sea, but prevents adult sea trout from returning. Despite of this, to this day an annual smolt run persist through the lake outlet. In this study the resident, potamodromous and anadromous life history strategies of brown trout were compared on physiological indicators for nutritional status, stress, tissue damage and smoltification (MS I). The trout population of Lake Hald has been declining since the settling of a cormorant colony on the lake shore and hence an evaluation of avian predation pressure on trout in the tributaries and the lake was done (MSIII). This thesis focus is on the juvenile life stage where the life history strategy is expressed by migratory differences, i.e. juveniles migrate as smolts and become potamodromous or anadromous or become residents in the natal stream.
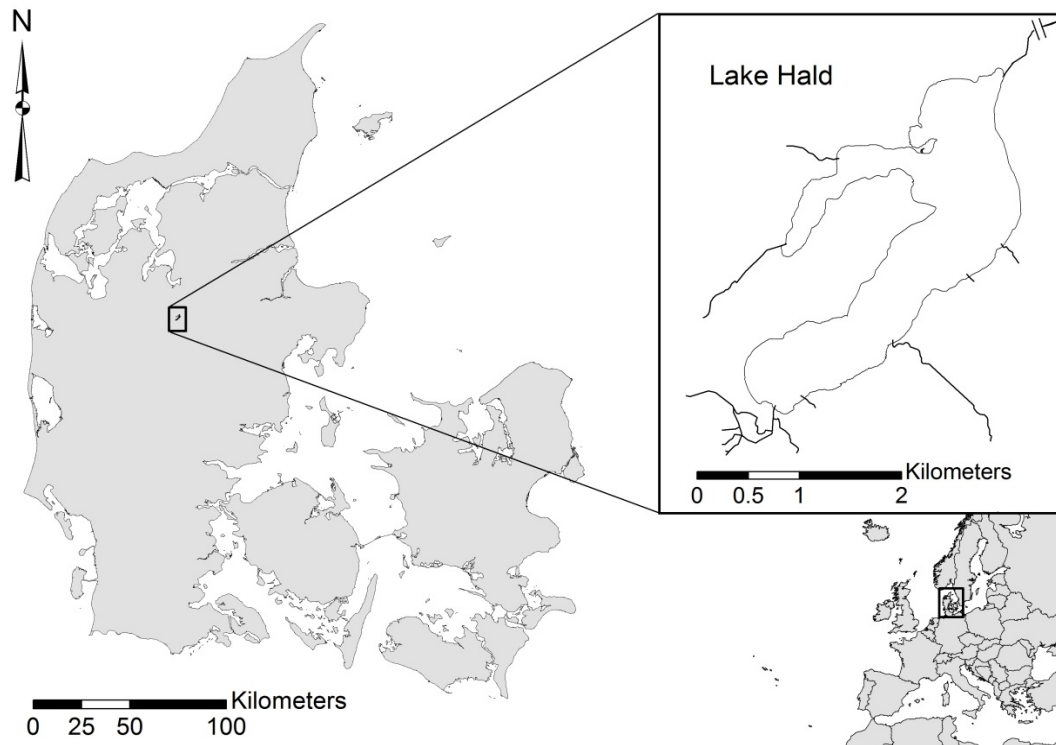
Figure 1: Location of Lake Hald in the central part of the Jutland peninsular of Denmark, Europe.

1.2 Alewives and Largemouth bass

Alewives (*Alosa pseudoharengus*) are generally an anadromous species which is native to the Atlantic coastal habitats of North America, ranging from South Carolina (Neves & Pardue 1983) to Canada (Cocker et al. 2001). If migration is hindered by natural or anthropogenic causes, or if stocked in isolated lakes, they are able to complete their lifecycle in lakes, thriving as landlocked populations. Since this life history is not voluntary, the alewife life histories are here referred to as life history types and not strategies. In Connecticut, where part of this study took place, multiple landlocked populations have independently evolved on several occasions; some 5000 years ago and others coincident with colonial dam building 300-500 years ago (Palkovacs & Post 2008). The locations of the lakes used in this study (MS II) are presented in figure 2, including lakes with landlocked alewives, anadromous alewives and with no alewives.
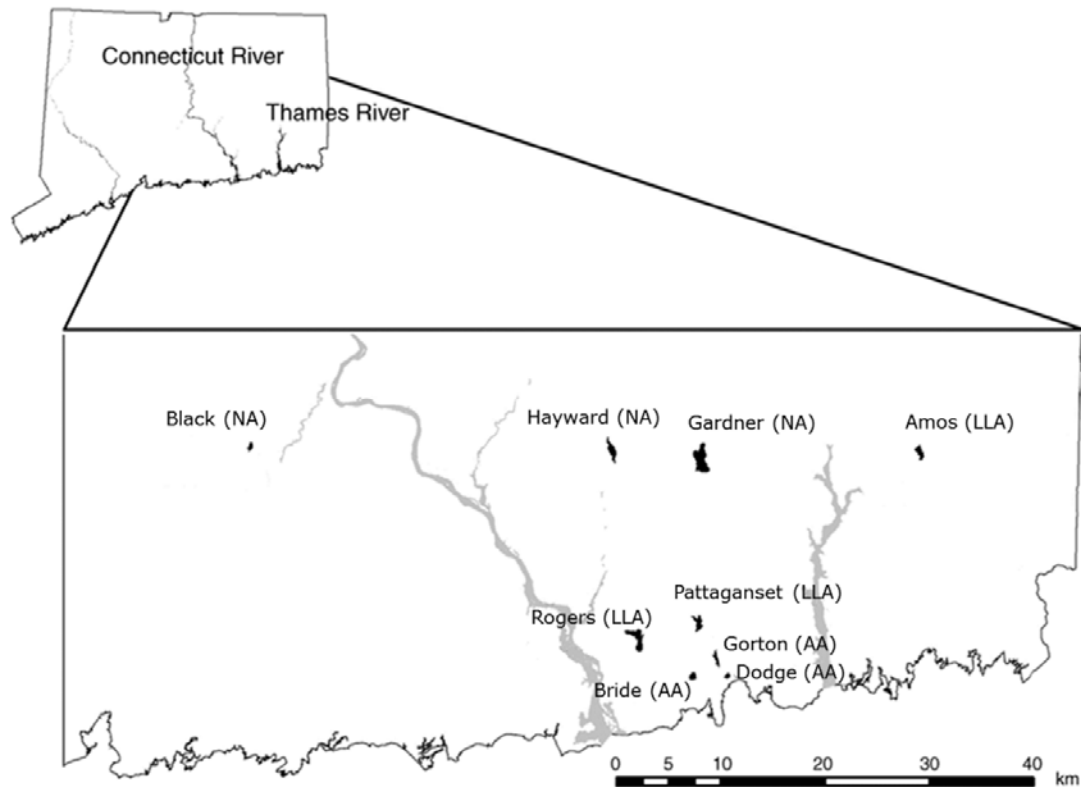
Figure 2: Location of study lakes in Connecticut, USA. Lakes are labelled according to whether alewives (*Alosa pseudoharengus)* were present and according to their life history type; no-alewives *NA*, landlocked *LLA* and anadromous *AA* (figure modified from Post *et al.* 2008).

Adult anadromous alewives migrate from the ocean through connecting rivers to lakes and ponds in late March until July, where spawning occurs from April till July. Immediately after spawning they return to the ocean (Loesch & Lund 1977). In the Connecticut area, the returning adult spawners range from 3 to 8 years in age (Loesch & Lund 1977). Like salmonids can detect their natal stream, returning adult alewives are capable of distinguishing water from their natal pond from that of nearby ponds and return to their natal waters to spawn (Thunberg 1971). In northern parts, Nova Scotia and New York around 60% are returning spawners (Joseph & Davis 1965). Juveniles generally emigrate from lakes to the sea between June and November as young-of-the-year (Kissil 1974). Landlocked alewives perform similar spawning cycle, but for obvious reasons they remain in the lake they were spawned. The seasonal presence of anadromous and year round presence of landlocked alewives results in profoundly different structuring effects on

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zooplankton communities, where zooplankton sizes and abundances are reduce when alewives are present (Post et al. 2008) (*see section 4.1*). These differences in structuring effects has prompted morphological changes in the landlocked alewives, making them more adapted to feeding on small bodied zooplankton that are predominant in these lakes, compared to anadromous alewives which have remained adapted to feeding on large bodied zooplankton; an eco-evolutionary feedback where the alewife influence on their food source induces changes in the feeding morphology of the alewives themselves (Palkovacs & Post 2008).

Largemouth bass (*Micropterus salmoides*) are top predators as adults, but in their first year juveniles go through ontogenetic diet shifts from feeding on zooplankton to macro invertebrates and ending up feeding on fish (Ludsin & DeVries 1997; Post 2003). Reaching piscivory increases growth and decreases mortality (Buijse & Houthuijzen 1992; Olson 1996). The final shift to piscivory depends on an interaction of resource availability and growth in the preceding stages (Persson & Greenberg 1990; Wu & Culver 1992; Bystrom et al. 1998; Hoxmeier et al. 2004) and thus the specific structuring effect on zooplankton according to alewife life history type may have consequences for coexisting largemouth bass. The effects of alewife life history type on planktivore competition are covered in later sections (*see 4.1, 4.2 and MS II*).

2 Salmonid life history strategies

2.1 Migration

The migration pattern of a given individual reflects its life history strategy. Hence, migration is a central theme when exploring the mechanistic basis of life history strategies in brown trout. Migration involves coordinated movement of several individuals from one habitat to another, with a fundamental expectation of return to a previous occupied habitat. It is often defined according to Northcote (1978) who referred to migration as "the movement of a substantial number of individuals occurring with regular periodicity between two or more separate habitats". Migratory

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behaviours are in many cases an adaptation for avoiding resource depletion and utilize seasonal peaks in resources elsewhere and it can be observed over a wide range in the animal kingdom, e.g. birds, mammals, insects, and fish (Alerstam et al. 2003). Fish migrations between freshwater and saltwater are termed *diadromy*. This includes *anadromy* and *catadromy*. Anadromous fish perform majority of feeding, growth and maturation in saltwater and reproduction in freshwater, while the opposite is true for catadromous fish (Mcdowall 1997). Anadromous fish species are predominant where the sea is more productive than freshwater habitats, whereas catadromous species are often found where freshwater productivity is higher than the sea (tropical regions) (Gross et al. 1988). Though associated with higher risks, migrations are presumed to provide better feeding and growth opportunities that ultimately optimize the overall lifetime fitness (Gross 1987; Gross et al. 1988; Jonsson & Jonsson 1993). In salmonids, there is often a prevalence of females in migration and males in residence, which probably relates to female fitness having a higher dependence on body size than male fitness (Jonsson & Jonsson 1993). Anadromous salmonids generally attain larger body sizes and greater average egg production, compared to those residing in freshwater (Hutchings & Morris 1985). This is also the case for resident alewives. Landlocked alewives in lakes, but also river dwelling alewives, have relatively smaller adult sizes (Walton 1983) and show reduced female fecundity compared with their anadromous counterparts (Scott & Crossman 1973).

In many species only a part of the population migrates while another part reside. This is generally referred to as "partial migration" and is often influenced by e.g. resource seasonality and competition, predation, migrations costs and physical barriers (Alerstam et al. 2003). In salmonids, both genetic and environmental factors are suggested to be involved in the decision-making of partial migration (Jonsson & Jonsson 1993). Despite that no or little genetic differences are found between concurrent residents and migrants strategies (Hindar et al. 1991; Petersson et al. 2001), recent approaches have shown that life history strategies can be related to differences at the

expression level of genes (Giger et al. 2006), which suggests that life history strategies are characterized by differences in the regulation of physiological processes that relates to the expression of these genes (*see 2.3*).

In juvenile Atlantic salmon (*Salmo salar*) the decision whether to migrate in spring is made already at the end of the preceding summer, where the past and current growth trajectories are probably assessed. If growth performance surpass a decision threshold in autumn, migration is initiated in the following spring (Metcalfe 1998). Individuals that reach this threshold are characterised by obtaining high position in the social hierarchy and having high growth rates, while lower order and slow growing individuals are more likely to postpone migration at least one more year (Metcalfe et al. 1990; Thorpe et al. 1992). Being dominant and having high metabolic rate may give a growth advantage over the summer that enables them to surpass the decision threshold and migrate in the next spring (Metcalfe 1998). Through the subsequent winter fast growing individuals maintain growth by allocating resources towards protein anabolism, while simultaneously reducing protein catabolism, and not towards lipid storage as in slow growers (Morgan et al. 2000; Morgan et al. 2002).

2.2 Proximate migration causes

2.2.1 The physiological basis of migration in salmonids

While optimization of fitness is the underlying reason (ultimate cause) for performing niche shifts (e.g. migrations), these may be initiated by internal and external incentives (proximate causes) (Forseth et al. 1999; Bauer et al. 2011).

High metabolism appears to have a pivotal role in the migratory decision as it favours fast growth (Forseth et al. 1994) and high feeding rates (Martin-Smith et al. 2004), which are characteristic to migratory salmonids. Compared with residents, higher consumption rates and faster growth is characteristic to potamodromous (Forseth et al. 1999; Cucherousset et al. 2005) as well as

anadromous migrants (Morinville & Rasmussen 2003; Cucherousset et al. 2005). However, relative to consumption, migrants have lower growth efficiencies, underlining that they have higher metabolic demands (Forseth et al. 1999; Morinville & Rasmussen 2003). Individuals with high metabolism and fast growth are only at an advantage when food is abundant as low food availabilities will limit these individuals sooner than those with low metabolism, making migrants more prone to starvation than residents (Jonsson & Jonsson 1993; Økland et al. 1993; Forseth et al. 1999). Several studies have shown that fish that are unable to meet their resource needs in their given surroundings will become more inclined to migrate as they become unable to allocate sufficient amounts of resources towards growth (Nordeng 1983; Forseth et al. 1999; Morinville & Rasmussen 2003; Olsson et al. 2006). Moreover, low food availability especially reduces body condition in migrants (males and females) and residents (Wysujack et al. 2009), which may give further explanation to the prevalence of females among migrants as they will feel the restraints from unfavourable conditions sooner than males.

2.2.2 The continuum of migratory strategies

Generally, the physiological characteristics of potamodromous and anadromous trout appear to be similar. Both have faster growth and higher metabolic demands relative to residents and later migrating individuals (Forseth et al. 1999; Olsson & Greenberg 2004; Cucherousset et al. 2005). Further, these two migratory strategies have similar regulation of genes related with de novo lipid synthesis and lipid metabolism (Giger et al. 2008). In MS I, we compared resident, potamodromous and anadromous brown trout on variables indicative of nutritional status, stress, tissue damage and smoltification. Compared to resident trout, both potamodromous and anadromous had lower nutritional status and were equally smoltified. Thus potamodromous and anadromous trout appeared to be physiologically very similar and might suggest that they face the same constraints in nursery areas relating to metabolism and resource availability mentioned above,

relative to residents. Then, what makes anadromous individuals migrate further than the potamodromous? Coucherouset (2005) suggested that brown trout migration will continue until finding a habitat that provides sufficient resources to maintain a sufficient growth rate relative given their intrinsic metabolic rate. Our results from MS I showed that potamodromous trout were more lipid depleted than anadromous trout, suggesting that the energy reserves available for the individual could play a role in the continuation of migration and hence whether to become potamodromous or anadromous. This supports indications from earlier studies on cyprinid (Brodersen et al. 2008) and coregonid fishes (Poulsen et al. 2010), where migration and dispersal propensity were positively correlated to energy reserves and feeding status. It further supports that migratory propensity decrease with migration cost (Bohlin et al. 2001; Jonsson & Jonsson 2006) and distance (Kristoffersen et al. 1994). Here energy reserves may be a decisive factor. We suggest in MS I that depleted energy reserves may incline a migrating fish to terminate migration to commence feeding at an earlier point than a fish with larger energy reserves.

2.2.3 Environmental cues

In salmonids, the initiation and timing of the smolt migration and the related physiological changes is under the influence of environmental cues. The smolt migration in spring is synchronized by the increasing photoperiod (Hoar 1988). The physiological changes related to smoltification are initiated by increasing photoperiod while temperature is involved in the rate of development (McCormick et al. 2002) and is advanced by longer photoperiods (Johnsen et al. 2000; McCormick et al. 2002) and higher temperatures (Sykes & Shrimpton 2010). The initiation and cessation of the actual smolt migration have been shown to occur earlier at faster temperature increases, but rather than a specific temperature threshold , the initiation and cessation of migration appears to be controlled by a certain number of degree-days, the experienced cumulative temperature over time (Zydlewski et al. 2005; Sykes et al. 2009; Sykes & Shrimpton 2010). Besides temperature and

photoperiod, smolt migrations are also known to be initiated by increases in water flow, often in combination with temperature increases (Bohlin et al. 1993; Hvidsten et al. 1995; Hembre et al. 2001). Flow has no effect on the rate of physiological changes related to smoltification and will not have any influence in the absence of a temperature increase (Sykes & Shrimpton 2010). Others have found that flow was non important in migration initiation, but that it played an important role in controlling the duration of the migration period (Sykes & Shrimpton 2010), possibly even serving as a termination cue (Sykes et al. 2009). Furthermore, migration initiation may also be influenced by changes in moon phase (Hvidsten et al. 1995).

2.2.4 Temperature dependence of migrations from Lake Hald

The winter temperature regimes of the three years of investigation were quite different. The between year variation in the pattern of brown trout movements from the tributaries to the Lake Hald and from the lake to the lake outlet (Figure 3) indicate that temperature to a wide extent controls the timing of migration (*Boel unpublished results*). The initiation of the main smolt emigration from the tributaries in springs from was increasingly delayed from 2008 to 2010, which can be linked to differences in winter temperatures. For the area of Lake Hald, the Danish national weather institute (DMI) describes the winter of 2007/2008 as "warmer than normal with considerable precipitation" and with an average air temperature of 4.3°C through January and February 2008; the winter of 2008/2009 was "slightly warmer than normal with low precipitation" and with an average air temperature of 0.7°C for January and February 2009; and the winter of 2009/2010 was "extremely cold with low precipitation" and with an average air temperature of minus 3.2°C in January and February (source: DMI). Unfortunately, we do not have a complete series of water temperature for the winter of 2007/2008, but the differences in air temperatures from January and February 2009 and 2010 was evident in the water temperatures of the tributaries. The

average water temperature in the tributaries January and February 2009 and 2010 were 5.5 °C and 4.4 °C respectively.
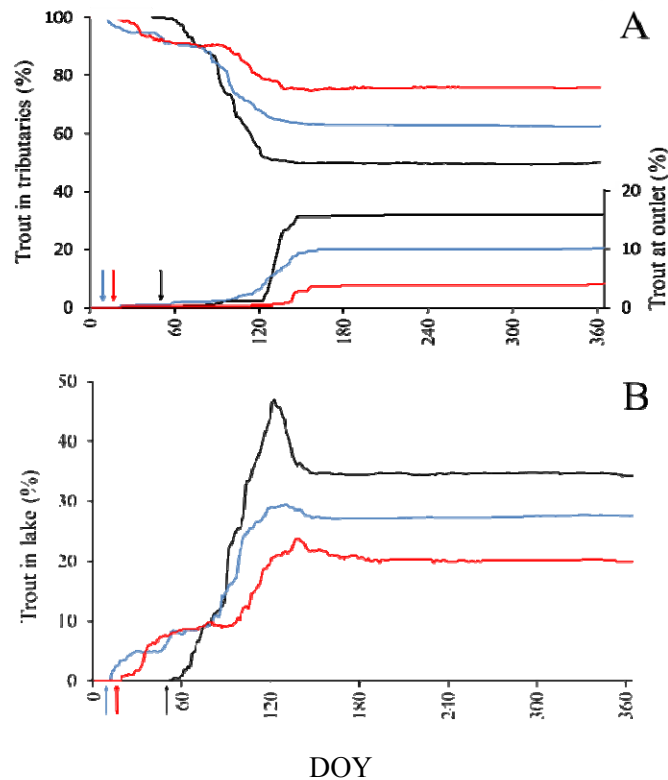
Figure 3: Movement of trout are illustrated as percentage of the number tagged for tagging events in the winters of 2007/2008 (black line), 2008/2009 (blue line) and 2009/2010 (red line). Time is presented as day-of-year and runs from tagging and appoximately one year forward. *A* the percentage of trout that were present in the tributaries (primary vertical axis) and percentages that passed the lake outlet (secondary vertical axis). *B* the sum of the movements in and out of Lake Hald are presented as the percentage of tagged trout retgistered to be in the lake at a given time. Arrows indicate respective tagging events according to colour.

In the spring migrations of 2009 and 2010 we found indications that support that migrations are governed by the experienced cumulative temperature over time (Zydlewski et al. 2005; Sykes et al. 2009; Sykes & Shrimpton 2010). Presented as a function of day-of-the-year, the onset of the main smolt migration period from the tributaries to the lake in 2010 was temporally delayed relative to 2009 (Figure 4A). This delay was further evident by distributions of the days-of-the-year that

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migrations occurred, which was significantly different between 2009 and 2010 (Kolmogorov–

Smirnov test, $p<0.001$). When displaying the migration as a function of cumulative degree-days, the

curves for the two years aligned (Figure 4B). Furthermore, the distributions of degree-days on

which migrations occurred were not found significantly different between 2009 and 2010

(Kolmogorov–Smirnov test, $p<0.14$), indicating that migration occur over the same range of degree-

days.
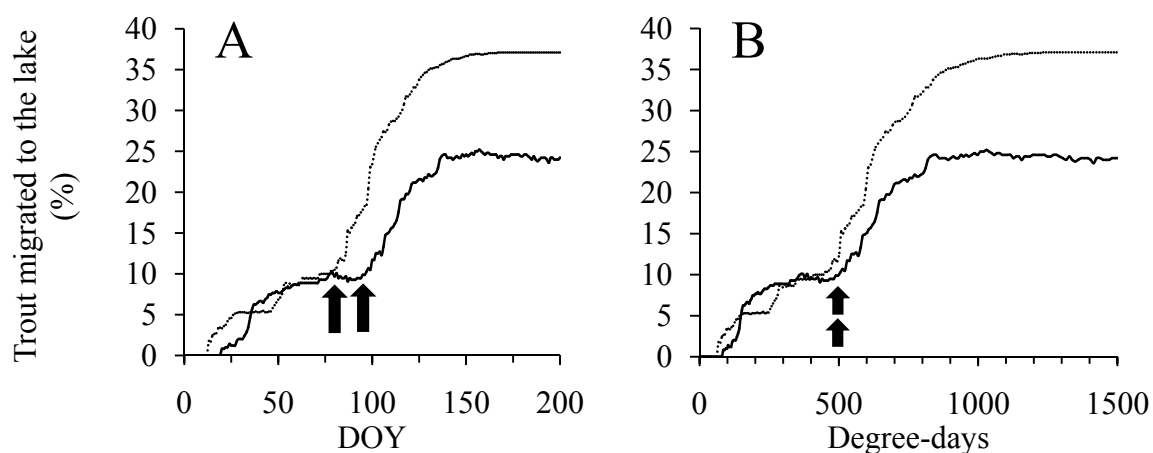
Figure 4: Temperature effect on migration patterns. Percentage of trout in year 2009 (solid line) and 2010 (dotted line) that were present in Lake Hald presented by day-of-year *A* and cumulative degree-days since January 1st *B*. Arrows indicate the initiation of the main smolt-migration period.

2.3 The molecular basis of life history strategies

Another way to explore life strategies relates to genetic methodologies. Gene

expression studies have recently revealed candidate genes for resident and migratory life history

strategies; some of these genes can be related to the regulation of physiological processes (Amstutz

et al. 2006; Giger et al. 2008). Transaldolase 1 and Endozopine are expressed at lower levels in

potamodromous and anadromous compared to resident individuals (Amstutz et al. 2006; Giger et al.

2006; Giger et al. 2008). The expression of Transaldolase 1 is temporally correlated with

smoltification and reductions of body condition and may be associated with depletion of lipid stores

and reduction of *de novo* lipid synthesis (Amstutz et al. 2006). Endozopine may likewise have a role

in *de novo* lipid synthesis (Giger et al. 2008) and lipid metabolism (Yang et al. 2001). Thus these

genes poses a potential link between the lipid depletion and changes in lipid metabolism (Sheridan

et al. 1983; Sheridan et al. 1985; Sheridan 1989) and the low energy allocation towards lipid storage

that is characteristic to the migratory strategy in salmonids (Morgan et al. 2000; Morgan et al.

2002). Additionally, the expression of HSP HSC70-1 is greater in potamodromous and anadromous

individuals, relative to residents (Giger et al. 2008), which is insensitive to heat and colds shock, but

sensitive to Cadmium stress in carp (*Cyprinus carpio*) (Ali et al. 2003). The function of this in life

history is yet to be determined, but it could be related to intensified stress responsiveness (Barton

2002) and higher basal level cortisol during smoltification (Carey & McCormick 1998). Compared

to resident and potamodromous, the expression of nucleophosmin is lower in anadromous trout

populations (Giger et al. 2008). Nucleophosmin is involved in multiple cellular processes, but the

functions relating to anadromy are so far unknown (Giger et al. 2008). In summary, the above

mentioned studies provides evidence, at the gene expression level, that resident, potamodromous

and anadromous life history strategies can be linked to differences in physiological processes. Some

of these involve lipid metabolism and synthesis, as well as stress. Thus the plasma indicators for

nutritional, lipid and stress which were used in MS I should have great potential for distinguishing

life history strategies.

It is noteworthy that the population of Lake Hald was included in the study made by

Giger et al. (2008). However, they ignored the presence of an anadromous life history strategy and

migrants were counted only as potamodromous trout. For the Lake Hald population,

Nucleophosmin, the candidate gene differentiating between freshwater and saltwater strategies, was

expressed at a level that was in the middle between what was found for saltwater and freshwater in

other populations in that study. This might indicate that this group was in fact a mix of potamodromous and anadromous trout. Though the PIT tag approach used in MS I does not provide a perfect separation of life history strategies, due to possible mortalities of anadromous individuals before reaching the outlet of the lake. However, a clearer separation of strategies might have been possible for Giger et al. (2008) if they had separated potamodromous from anadromous.

3 Life history strategies and related mortality

3.1 Predation risk in relation to life history strategies

Considerable losses to fish populations can be caused by predation from piscivorous fish in lakes (He & Kitchell 1990; Findlay et al. 2000), mammals (Heggenes & Borgstrom 1988; Aarestrup et al. 2005) and birds (Rudstam et al. 2004; Coleman 2009; Dorr et al. 2010). In lakes, cormorant species are especially efficient and have more than other predators been linked to declines in fish populations and fisheries in lakes (Klein 2000; Rudstam et al. 2004; Klein 2005; Fielder 2008; Coleman 2009; Dorr et al. 2010; Fielder 2010). In this study, cormorants are suspected to be the cause of the decline in the landlocked brown trout population of Lake Hald (MSIII). Multiple evaluations of cormorant predation have been carried out that provide qualitative data. However, there is a general lack of data on the quantitative effect on fish populations (Jepsen et al. 2010). Traditionally the impact of piscivorous birds has been evaluated by diet contents (Draulans 1988), but in more recent years models incorporating data on stable isotopes, bioenergetics or consumption have been utilized (Gremillet et al. 2003; Rudstam et al. 2004; Dorr et al. 2010; Maranto et al. 2010; Jones et al. 2010). Methods involving tag recovery (or tag detection) in nesting colonies may provide better quantitative estimates. Tag recovery estimates has so far been based on PIT tags (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Ryan et al. 2008), coded wire tags (Jepsen et al. 2010), carlin tags (Feltham & MacLean 1996) and radio tags (Dieperink et al. 2001; Koed et al. 2002; Dieperink et al. 2002; Koed et al. 2006). These methods rely on the transportation of tags

to the bird colonies and resting areas, but since not all tags can be expected to end up in these areas they only provide minimum predation estimates (Ryan et al. 2003; Ryan et al. 2008; Jepsen et al. 2010). In MS III, we used information from PIT tag registrations to assign individual trout to life history strategies, i.e. fish that were last registered in the lake were potamodromous whereas fish in the tributaries were residents. This information was combined with the accumulation of PIT tags in the colonies of cormorants and herons (*Ardea cinerea*), which were regularly examined using a pole-mounted PIT detector. This provided us with minimum predation estimates for resident and potamodromous trout over the three year study period. In the potamodromous group, the average minimum predation from herons and cormorants were respectively 16.2 % and 21.0 %. This was in contrast to the minimum predation on resident trout in the tributaries, which was significantly lower, respectively 7.8 % and 2.3 % for the herons and cormorants (MS III). Hence, our data suggests that avian predation risk may differ between groups of fish with different life history strategies. In MS III we did not consider the predation on anadromous trout. The spatial distribution of anadromous trout made it difficult to make comparisons with resident and potamodromous trout, as anadromous trout could move outside the foraging range of the cormorants and herons at Lake Hald. Additional to avian predators in Lake Hald, also piscivorous fish may contribute to trout losses ((He & Kitchell 1990; Findlay et al. 2000) and tagged trout were occasionally reported in the stomachs of large pike (*Esox lucius*) and lake trout (MS III). Also in the tributaries there appeared to be other predators present. This was illustrated by very low recapture rates of tagged fish one year after tagging (1.3 - 5.7 %). This was far below the recapture rates that could have been expected if avian predation was the sole cause of mortality. Comparably, annual survival in tributaries has been found much higher, e.g. approximately 13% for 1+ trout (Egglishaw & Shackley 1977) and for stocked salmon 15-33% for age 1+ and 30% for age 2+ (Letcher et al. 2002). Therefore we may either be underestimating predation from cormorant and heron in the

tributaries or other predators may be present. Otter (*Lutra lutra*) and invasive mink (*Mustella vison*) are present in the area and could explain some of the losses. In rivers and streams, a monthly predation of 34% on brown trout has been attributed to otters (Aarestrup et al. 2005) and as high as 87% for mink (Heggenes & Borgstrom 1988).

The results presented from MS III indicate that the trout populations in Lake Hald need management attention. Traces of a genetic bottleneck have previously been seen in the Lake Hald trout population, originating from small populations size caused by unfavourable conditions in the lake and tributaries in the 1989's (Jensen et al. 2005). Currently the spawning activity of the brown trout in Lake Hald is at the same low level as when the bottleneck occurred (see MS III). The trout population is yet again in danger of losing genetic variability and with that the adaptability to cope with changing conditions (Hansen et al. 2000). We therefore suggest that management solutions should be implemented in both lake and tributaries to minimize the losses to predation. Managing the colony size of avian predators or reducing foraging by harassment has previously been proven very effective (Coleman 2009; Dorr et al. 2010; Fielder 2010). Additionally, intensifying the eradication of invasive mink might prove effective in the tributaries.

3.2 Detrimental effects of migration barriers on potamodromous and anadromous fish

There are many examples showing that migration barriers cause severe losses to the potamodromous and anadromous part of salmonid populations. Weirs, dams and hydropower installations obstruct migration and have led to severe reductions in number of smolts entering the sea (Rasmussen & Geertz-Hansen 2001). This is a bidirectional problem, where both the emigration of smolts and kelts as well as the return of the adults are affected (Calles & Greenberg 2009). Migration barriers can be impossible to pass for spawners and even when bypass solutions are installed and fish are able to locate it, many will refrain from using it (Thorstad et al. 2003; Aarestrup et al. 2003). Consequently, they will not reach their intended spawning habitat. For the

downstream migration of smolts, delays at barriers may cause de-smoltification while still in freshwater. Thus, they may become resident or arrive to the sea having lost their hypo-osmoregulatory ability (McCormick et al. 1998; Shrimpton et al. 2000; Aarestrup & Koed 2003). Another problem with barriers relates to injuries from the actual passage of the migration barriers. Passing through the turbulent environments of spillways, which is a common feature at barriers, makes smolt more vulnerable to predation (Neitzel et al. 2004) and further may result in physical injuries from hitting hard stationary structures (Aarestrup & Koed 2003; Miracle et al. 2009). Hasler et al. (2009) introduced a toolbox for evaluating negative physical effects of passing hydro power plants, which included the use of plasma aspartate aminotransferase (AST), a relatively simple indicator of tissue damage. AST levels was used in the current study in MS I where it showed no differences in the comparison of groups with different life history strategies. These groups were all captured and sampled in the tributary and none of them had passed any barriers. Comparing these with trout that had been captured after having passed the spillway drop-off at the dam at the lake outlet (c. 1.3 meter drop), indicated that the spillway passage was associated with physical injuries. Smolt captured downstream the dam had significantly higher AST levels and hence indicating tissue damage (Figure 5) (*Boel unpublished results*).
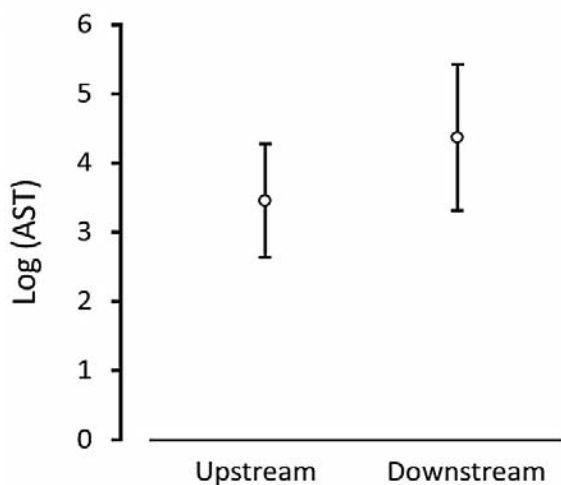
Figure 5: AST enzyme activity in migrating brown trout captured in fyke traps upstream and downstream of a millpond with approximate 1.5 meter spillway drop. Log-transformed AST activity is presented as means of log transformed data with standard deviations. AST levels of trout captured at the downstream site had significantly higher than those at the upstream site (ANOVA: ($F_{(1,89)}$= 25.391, p< 0.00001).

This indicates that the anadromous trout that migrate through the lake and pass the spill drop pay an additional price in terms of tissue damage compared to fish selecting the potamodromous life strategy.

While the large dams and hydropower plants often receives the major of focus regarding fish passage issues, small dams are very numerous and may have negative effects (Aarestrup & Koed 2003; Sheer & Steel 2006). A guestimate suggests more than several thousand dams in Denmark (Aarestrup et al. 2006). Many of these potentially harbour the risk of inflicting injuries and mortalities. The unpublished results on tissue damage presented here emphasize the need for management solutions facilitating safe downstream passages, even at relatively small weirs and dams to reduce mortality and injuries of migratory fish.

4 Life history types in alewives and interspecific interactions

The occurrence of certain species, keystone species, can have great influence on community structure and ecosystem functions (Brooks & Dodson 1965; Carpenter et al. 1987; Jones et al. 1994; Power et al. 1996; Naiman et al. 2002; Whitham et al. 2006). Variations in life history of such species can be expected to have different ecosystem effects. However, only few studies have so far addressed the ecological consequences of intraspecific phenotypic variation (Treseder & Vitousek 2001; Proffitt et al. 2005; Wimp et al. 2005; Post et al. 2008). Specialist planktivorous fish are well known to indirectly influence on coexisting species through their structuring effect on their zooplankton prey (Neill 1975; DeVries & Stein 1992; Olson et al. 1995; Post et al. 2008). Recent examples on alewives have shown that life history types, landlocked and anadromous, have different structuring effects on the zooplankton community (Post et al. 2008; Walsh & Post 2011). These differences mediated by alewives life history type may extend to influence other species that rely on zooplankton.

4.1 Effects of Alewife life history on zooplankton availability

Alewives are dominant planktivores and a key stone species in many lakes of New England and can

structure the communities of lower trophic levels (Brooks & Dodson 1965). The biomass and size

composition of zooplankton is affected not only by the presence of alewives, but also according to

which alewife life history type that is present in a given lake (Figure 6 & 7) (Post et al. 2008).

Figures 6: Mean length (±SE) of *a* cladocerans and *b* copepods in landlocked, anadromous, and no-alewife lakes in spring and summer. Different uppercase letters indicate significant differences ($P \leq 0.05$) among lake types in spring or summer. Significant differences in cladoceran and copepod length between spring and summer were found only in anadromous alewife lakes. Asterisks indicate that the comparison between the two values had a *P* value of 0.0503 (*Figure 3 from Post et al. 2008*).
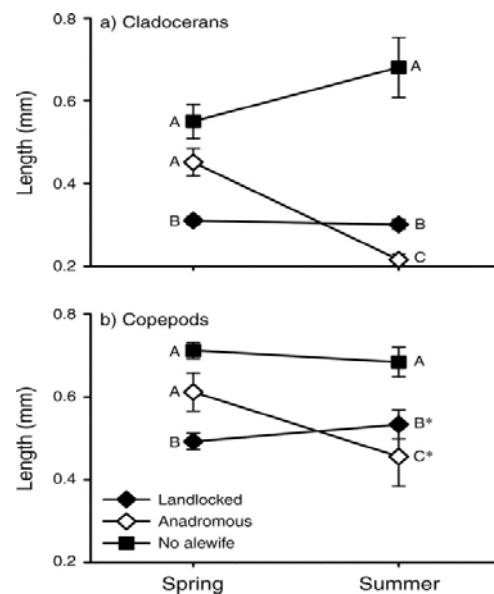
Lakes with no alewives, *NA,* have large-bodied zooplankton year-round; lakes with landlocked

alewife, *LLA,* have small-bodied zooplankton year-round; and lakes with anadromous alewife, *AA,*

have zooplankton communities that cycles between large-bodied zooplankton in the winter and

spring and small-bodied zooplankton in the summer months (Post et al. 2008). Furthermore,

differences in feeding morphology between alewife life forms, causes zooplankton biomass to be

lower and body sizes to be smaller in AA lakes than in LLA lakes when reaching the summer

months (Post et al. 2008). These differences in the influence on zooplankton size and availability

are likely to exert different competition effects on other fish species which depend on zooplankton

as prey.
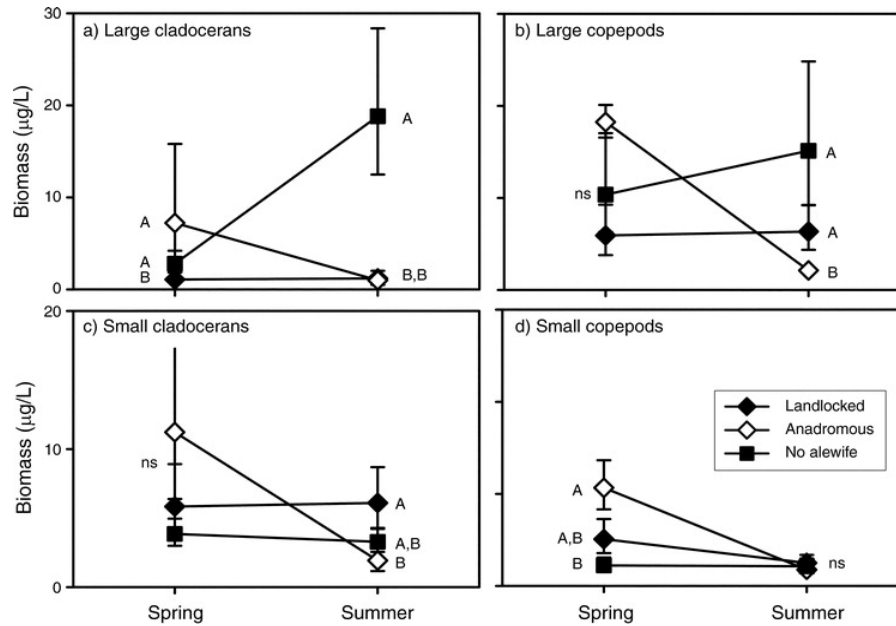
Figure 7*:* Mean biomass (±SE) of *a* large cladocerans, *b* large copepods, *c* small cladocerans, and (Dahlgren & Eggleston 2000) small copepods in landlocked, anadromous, and no-alewife lakes during spring (March and April) and summer (July–September). Note the difference in scale between large, *a* & *b,* and small, *c* & *d*, zooplankton. Different uppercase letters indicate significant differences ($P \leq 0.05$) among lake types in spring or summer. Significant differences in biomass between spring and summer were found for anadromous alewife lakes in all cases, and for large cladocerans *a* in no-alewife lakes. All other comparisons between seasons within lake types were not significant (ns) (*Fig. 5 from Post et al. 2008).*

4.2 Piscivore-planktivore competition

Since most fish has a juvenile stage where they depend on zooplankton, the predation pressure on zooplankton from alewives can potentially impact the early ontogeny of coexisting fish species. Reductions in zooplankton availability cause reductions in juvenile fish growth (Persson et al. 2000; Hoxmeier et al. 2004; Milstein et al. 2006) and depending on the alewife life history type that is present, growth may be differently affected. One species where early growth may be affected is largemouth bass, which often inhabit the same lakes as alewives. Largemouth bass generally make the transition to piscivory in their first or second year, but prior to this they go through a stage feeding on zooplankton and macro invertebrates (Ludsin & DeVries 1997; Post 2003). It is

important for young largemouth bass to make the transition to piscivory as early as possible, preferably within the first year, as it increases growth and reduces size related mortality (Buijse & Houthuijzen 1992; Olson 1996). The shifts preceding piscivory depend on an interaction of resource availability and fish size (Persson & Greenberg 1990; Wu & Culver 1992; Bystrom et al. 1998; Hoxmeier et al. 2004), which makes rapid growth, and hence zooplankton availability, a key component for young largemouth bass to gain a size advantage over prey species and finally reaching piscivory (Olson 1996). In MS II, we found that the presences of alewives slowdown the rate of growth; delay the transition to feeding at higher trophic position; and delay the transition to piscivory of largemouth bass, relative to lakes without alewives. We further found that this delay in growth and trophic position was stronger in lakes with landlocked alewives relative to lakes with anadromous alewives, showing that the effect of alewife life history type on the zooplankton influences the ontogeny of concurrent largemouth bass. This potentially has different consequences for recruitment to the adult populations. The fact that largemouth bass had slower growth and delayed transition to piscivory in lakes with either type of alewife life history, can be expected to lead to higher size related predation. As growth and trophic increase were delayed the most in lakes with landlocked alewives, the size related mortality for largemouth bass might be higher in these lakes relative to lakes with anadromous alewives. The growth of adult piscivores, however, is positively correlated with the abundance of planktivorous fishes (DeVries & Stein 1992; Olson et al. 1995; Hjelm et al. 2000) and the largemouth bass that make it to adulthood may then benefit from alewives as prey. In summary, this study showed that considering life history is important when investigating ecosystem effects and interspecific interaction.

5 Methods introduction

5.1 PIT telemetry

The exploration of fish behaviours has previously relied on external markings and capture in habitats or bottleneck passageways between habitats (Lucas & Baras 2001). Telemetry is a common name for a number of tools that are effective to quantify movements and study individual behaviours. Telemetry is based on various forms of technologies that e.g. register the movements between habitats while others records data such as depth or temperature. The technological development has made possible the mass production of smaller and smaller electronic tags and hence the number of telemetric approaches has greatly increased during recent years (Cooke et al. 2008). One such development is the radio frequency identification (RFID), a wireless technology which relies on tag-readers and relatively small tags that contains a unique code. The basic concept was developed during World War II as an aid for radar operators to recognize friend from foe in incoming aeroplanes. When a aeroplane received radar signals, the broadcasting of an identifier signal was initiated (Landt 2005). Active RFID tags are powered by a battery, while passive tags are powered by rectification of a radio signal from the tag-reader. The latter are inexpensive, come in small sizes and have indefinite life span (as long as the tag remains intact). These are known as passive integrated transponders (PIT) (Landt 2005). PIT tags was used in MS I to assign individual life history strategies and in MS III to determine in which habitat individuals were predated. PIT technology has been used in multiple studies on fish migration (Zydlewski et al. 2001; Olsson & Greenberg 2004; Skov et al. 2010), where data loggers are placed at strategic bottleneck passages, i.e. the entry point of tributaries into a lake. Two swim through antennas a few meters apart and covering the entire width of a passage way, providing a sequential detection of tagged fish and thereby both direction and time of movements can be registered at the individual level.

In studies involving tagging, it is a required assumption that the organism in question is not adversely affected by tagging procedures and from carrying the tag (Cooke et al. 2008). Hence, it is important that researchers evaluate adverse effects of tagging and strive to minimize such adverse effects. In studies of natural behaviour, such effects must be evaluated in the field where the stressors may be entirely different than under laboratory conditions (Jepsen & Aarestrup 1999). For the 23mm PIT used in the current studies, relatively few have addressed the effects under natural conditions, e.g. salmonids (Zydlewski et al. 2003) and cyprinids (Skov et al. 2005). In MS IV we compared the body conditions of recaptured tagged trout with concurrently captured untagged trout of comparable sizes in a field study (MS IV). This revealed no adverse effects of tagging individuals with total lengths >120mm, tagged with 23 mm PIT tags, which indicated that tagged and untagged trout had managed equally well in the period leading up to capture/recapture.

5.2 Stable isotopes

It can be a challenging task to gain insights in to the dynamics and structure of food webs. The traditionally used direct analyses of stomach contents provide high taxonomic resolution, but only provide snapshot information that is not necessarily representative of the average consumption. Using stable isotopes on the other hand can provide temporally integrated information about complexities of food web structure and dynamics, but with no or very low taxonomic resolution. Diets and isotopes work well in combination as one can compensate for the weaknesses of the other (Post 2003; Winemiller et al. 2007; Layman & Post 2008; Post et al. 2008).

The discovery that animals have higher $^{15}N:^{14}N$ ratios ($\delta^{15}N$) than their diet (Deniro & Epstein 1981) has enabled ecologist to estimate trophic positions of animals and food chain lengths. This is a secondary effect from the protein synthesis where higher excretion of ^{14}N leaves the consumer more enriched in ^{15}N relative to the diet (Kling et al. 1992), where the mean enrichment per trophic level is 3.4 ‰ (Post 2002). Additionally, ^{13}C allows estimation of habitat specificity.

The base of ^{13}C relates to the photosynthetic carbon fixation, where the fractionation is different between benthic algae, found in the littoral zone, and phytoplankton in the pelagic (Hecky & Hesslein 1995; France 1995a; France 1995b). Furthermore, the $^{13}C:^{12}C$ ratio ($\delta^{13}C$) of secondary consumers is very similar to that of their diets (Fry & Sherr 1984; Wada et al. 1993), with a mean enrichment per trophic level of 0.4 ‰ (Post 2002). Thus, using more than one stable isotope species is advantageous, e.g. nitrogen and carbon. The nitrogen isotope is used as an indicator of trophic level whereas the carbon isotope reflect which plant group has provided the basis of what has been consumed (Peterson & Fry 1987). The application of trophic baselines, for example phytoplankton for pelagic and periphyton for the littoral food web, has allowed for estimates of trophic position and relative food web use that are comparable between separate ecosystems (Vander Zanden et al. 1997; Post 2002). Post (2002) made further developments to the use of isotopic baseline concept by using secondary consumers, which provides temporally integrated baselines. Furthermore, a two-end-member-mixing model (with pelagic and littoral baselines) was devised. Using mean enrichments per trophic level of 3.4‰ (1 SD = 1‰) for ^{15}N and 0.4‰ (1 SD = 1.3 ‰) for ^{13}C, this model can provide information on patterns both trophic position and relative food web utilization of a secondary consumer (Schreck 1982) (Schreck 1982):

$$\text{Trophic position}_{sc} = \lambda + (\delta^{15}N_{sc} - [\delta^{15}N_{base1} * \alpha + ^{15}N_{base2} * (1 - \alpha)]/\Delta_n$$

Here λ is the trophic position of the baseline organism (e.g., $\lambda = 1$ for primary producers), α is the proportion of nitrogen in the secondary consumer ultimately derived from food web one (base1) and Δn is the trophic fractionation of nitrogen. Under the assumption that movement of nitrogen and carbon is similar through the food webs, carbon isotopes can be used to estimate proportional food web use $\alpha_{sc} = (\delta^{13}C_{sc} - \delta^{13}C_{base2})/(\delta^{13}C_{base1} - \delta^{13}C_{base2})$. This approach was used in MS II, where isotope analysis was combined with diet and growth data to unravel if the incidence of alewife life history types was associated with ontogenetic differences on concurrent largemouth bass.

Biochemical profiling of blood plasma can be used to gain insights into the current physiological status of an individual. In fish, it has previously been used in a variety of approaches of individual comparisons as well as in evaluating effects of treatment and environmental differences. Wagner & Congleton (2004), using a wide array of plasma indicators in a multivariate approach, identified functional groups that were indicative for nutrition, lipid metabolism, stress, tissue damage and smoltification in migrating wild and hatchery reared Chinook salmon (_Oncorhynchus tshawytscha_). Such indicators have for example been used to compare environmental effects on physiological status of hatchery and wild snakehead (_Channa argus_) (Gul et al. 2011); effect of tagging on wild largemouth bass (Caputo et al. 2009); comparison of anaesthetics on perch (_Perca fluviatilis)_ (Velisek et al. 2009); and comparison of breeds of _Cyprinus carpio_ (Svobodova et al. 2009). In MS I we used a similar array of plasma indicators were used to discriminate life history strategies of brown trout. Measurements of gill Na, K-ATPase activity, body condition, for assessment of smoltification status, and biochemical profiles of blood plasma (sodium, potassium, chloride, total protein, glucose, AST, inorganic phosphorus, cholesterol, triacylglycerides and calcium) were used for assessment of nutritional-, stress- and tissue damage status (Wendelaar Bonga 1997; Wagner & Congleton 2004). These were combined with tracking of individual migration histories, using PIT telemetry (MS I). A retrospective assignment of life history related traits to samples was used to reveal the degree of physiological similarity between assignment groups. The relevance of stress and nutritional indicators in life history differentiation are further supported from gene expression studies (Amstutz et al. 2006; Giger et al. 2008) (_see previous section 2.3 The molecular basis of life history strategies_).

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Summary

This thesis focused on life history strategies and types in migratory freshwater fish, using brown trout and alewife as study organisms. Firstly, we investigated underlying mechanisms of resident and migratory life history strategies of salmonids, using indicators for nutritional status, stress, tissue damage and smoltification. Secondly, avian predation pressure on the groups with different life history strategies was explored in their respective habitats. Thirdly, we demonstrated that the life history type of alewives, through regulation of zooplankton availability, influence the ontogeny of concurrent largemouth bass. Finally, a field study approach was used to evaluate the effect of PIT tagging on body condition of brown trout.

Within a salmonid population several life history strategies can be found, each of which involves variations in migration and residency. Migratory life history strategies are often viewed as an adaptive behaviour to optimise the overall lifetime fitness when resources and predation risk varies between habitats. In salmonids, some individuals migrate to seawater (anadromous), others migrate to freshwater habitats such as lakes (potamodromous), while a others may stay behind in the streams and become residents. In MS I, the physiological status of potamodromous and anadromous fish was examined and it was found that these strategise were generally very similar. It was indicated that both potamodromous and anadromous fish were smoltified and in lower nutritional status relative to resident fish. Moreover, it was found that lipid reserves were lower in the potamodromous trout compared with anadromous trout. Lower lipid reserves in potamodromous trout might provide a mechanistic explanation to why this group cease migration at an earlier point compared with anadromous conspecifics.

The lakedwelling trout population in Lake Hald has undergone a rapid decline in recent years. This has coincided with the arrival of cormorants to the area. It is well known that predation may cause substantial losses in fish populations. However quntitative information on the

impact of avian predators is relative scarce. In MS III the minimum predation from cormorants and herons was estimated over a three year period on the brown trout population of of Lake Hald. The magnitude of the predation pressure from both bird species were very similar and when summed up, the avian predation accounted for an average minimum of 37.2 % of the annual brown trout mortality in the lake and 10.1 % in the tributaries. This result illustrates that avian predation in the lake can be quite substantial and potentially plays an important role in the population dynamics of brown trout. Cormorants alone were responsible 21.2% in the lake and the allrival of these birds to the area are likely to have an important role in the decline in the lake dwelling trout population in Lake Hald. Further it illustrates that individual predation risk is life history specific, i.e. potamodromous brown trout face higher risk of avian predation than resident individuals. However, the total mortality of the resident trout might be underestimated, i.e. the losses in the tributaries estimated by electrofishing surveys were substantially higher than the avian predation suggested, indicating additional predation losses from ex. mink and otter.

Alewives are specialist planktivore fish that profoundly structure the abundance and size of their zooplankton prey. This can influence the ontogenetic development of concurrent juvenile piscivorous fish, e.g. largemouth bass. The structuring effect of alewives varies according to the life history type, i.e. whether they are landlocked or anadromous. Lakes with landlocked alewife have small-bodied zooplankton year-round; lakes with anadromous alewife have zooplankton communities that cycles between large-bodied zooplankton in the winter and spring and small-bodied zooplankton in the summer months; whereas lakes with no alewives have large-bodied zooplankton year-round. In MS II, we show that this influences the ontogeny of largemouth bass. The ontogenetic development of largemouth bass was compared between lakes with landlocked, anadromous and no alewives. In lakes with alewives young-of-the-year largemouth bass had slower growth and slower transition to feeding at higher trophic position, compared with

lakes without alewives. Thus, the alewife presence delayed the transition to piscivory in largemouth bass. Moreover, we found that this slowdown of both growth and progression in trophic level was stronger in lakes with landlocked alewives relative to lakes with anadromous alewives. This shows that the life history type of alewives has significant influence the ontogeny of concurrent largemouth bass through regulation of zooplankton availability.

In MS IV the effect of surgically implanted 23 mm PIT tags on juvenile brown trout was evaluated in a field study. The effect of carrying a PIT tag under natural conditions was evaluated during four time periods ranging from 97-328 days. The length to body mass relationship was compared between tagged and concurrently captured untagged trout of comparable sizes. We found no effect of tagging on the length to body mass relationship. This suggests that tagged and untagged fish had managed equally well in the period leading up to the concurrent capture.

MS I

The physiological basis of partial migration in the brown trout (Salmon trutta)

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Key words: life history strategy, partial migration, migration, migratory continuum, decision making, smoltification, landlocked, biochemical profile, metabolism, nutritional status.

Abstract

Partial migration is common in many animals, yet there is only scant knowledge about the mechanistic basis. Among salmonids, brown trout (*Salmo trutta*) exhibit some of the most complex patterns of partial migration. The objective of this study was to identify physiological differences in sympatric resident, potamodromous and anadromous brown trout to provide a better mechanistic understanding of these three life histories. To this end, this study measured multiple elemental plasma levels, indicative of stress, tissue damage and nutritional status and indicators of smoltification status in wild brown trout prior to downstream migration. Subsequently, resident, potamodromous and anadromous brown trout were identified using passive telemetry. The results showed that Na, K-ATPase activity, condition factor, plasma cholesterol and inorganic phosphorous all differed when the resident fish were compared with potamodromous and anadromous fish. These findings indicated that both potamodromous and anadromous fish were more smoltified and energetically depleted than resident fish. Interestingly, the physiological traits of potamodromous and anadromous fish were generally similar, although triacylglycerides were lower in the potamodromous fish. Lower triacylglycerides in the potamodromous fish may provide a mechanism explaining the cessation of further seaward migration. Collectively, these findings are consistent with the hypothesis that patterns of partial migration are strongly influenced by the magnitude of energy stores in individual fish.

Introduction

Partial migration is characterized by migration of part of the population while other parts are resident. This phenomenon is commonly seen in many animal taxa and is regarded as an adaptation for avoiding resource depletion and exploit richer resources elsewhere (Alerstam et al. 2003). However, migration is energetically costly and is associated with increased mortality. The negative consequences of migration however can be balanced by better feeding and growth opportunities, which ultimately leads to equal or better lifetime fitness (Gross 1987; Gross et al. 1988).

Although the factors causing migration and residency are widely studied, the continuum of migration has received relatively little attention. Earlier studies on salmonids have compared resident to either anadromous or potamodromous strategies, but only few deal with the underlying physiology of potamodromous and anadromous life history strategies. Studies on gene expression have suggested physiological differences that are characteristic to resident, potamodromous and anadromous salmonids (Amstutz et al. 2006; Giger et al. 2008), but the exact function of these difference remains to be explained in detail.

Generally, migration in salmonids is related to growth, food availability and metabolic demands. Previous studies have shown a negative correlation between the migrant:resident ratio and food availability in juvenile salmonids (Nordeng 1983; Olsson et al. 2006; Wysujack et al. 2009). Anadromous brook trout (*Salvelinus fontinalis*) (Morinville & Rasmussen 2003) as well as potamodromous brown trout (Forseth et al. 1999) have higher consumption rates and growth, but lower growth efficiencies, compared to residents. Indirectly these suggest a general link between high metabolic rate and migration, which has recently been shown for juvenile Atlantic salmon (*Salmo salar*) (Seppanen et al. 2010). Fish with higher metabolic rates are expected to become limited at low food availabilities sooner than fish with low metabolic rates. This mechanism causes high metabolic rate fish to migrate to avoid unfavourable conditions (Jonsson & Jonsson 1993;

Økland et al. 1993). But what causes some migrants to discontinue migration when having the opportunity to go further? It has been suggested that the migratory continuum of brown trout relates to locating a habitat that provides sufficient resources to maintain a suitable growth rate according to their intrinsic standard metabolic rate (Cucherousset et al. 2005). At a broader level, migratory propensity is associated with migratory costs (Bohlin et al. 2001; Jonsson & Jonsson 2006) and migratory distance (Kristoffersen et al. 1994). Hence, migratory continuum may involve both escaping unfavourable growth conditions to find more suitable ones, but may also involve decision-making relating to the trade-off between the growth benefits and the costs of migration.

Few previous studies on the mechanistic basis of partial migration have included a continuum of migratory strategies. To address this knowledge gap, we examined the physiological basis of three different life history strategies in the brown trout. Specifically, we tested the hypothesis that wild resident, potamodromous and anadromous brown trout can be distinguished based on their pre-migratory physiology. To this end, we measured multiple elemental plasma levels, indicative of stress, tissue damage and nutritional status as well as indicators of smoltification status. Levels of stress and tissue damage and nutritional status were assessed by elemental levels of blood plasma (sodium, potassium, chloride, total protein, glucose, inorganic phosphorus, cholesterol, triacylglycerides (TAG), calcium and aspartate aminotransferase activity (AST)). Gill Na, K-ATPase activity and condition factor were used for assessment of smoltification status. Resident, potamodromous and anadromous groups of brown trout were subsequently identified using passive telemetry.

Methods

Study area and experimental setup

The study was conducted in Lake Hald and connecting tributaries, which is part of River Gudenaa in Denmark (Figure 1). The tributaries serve as spawning and nursery grounds for a landlocked population of resident and lake-dwelling (potamodromous) brown trout. Two barriers downstream
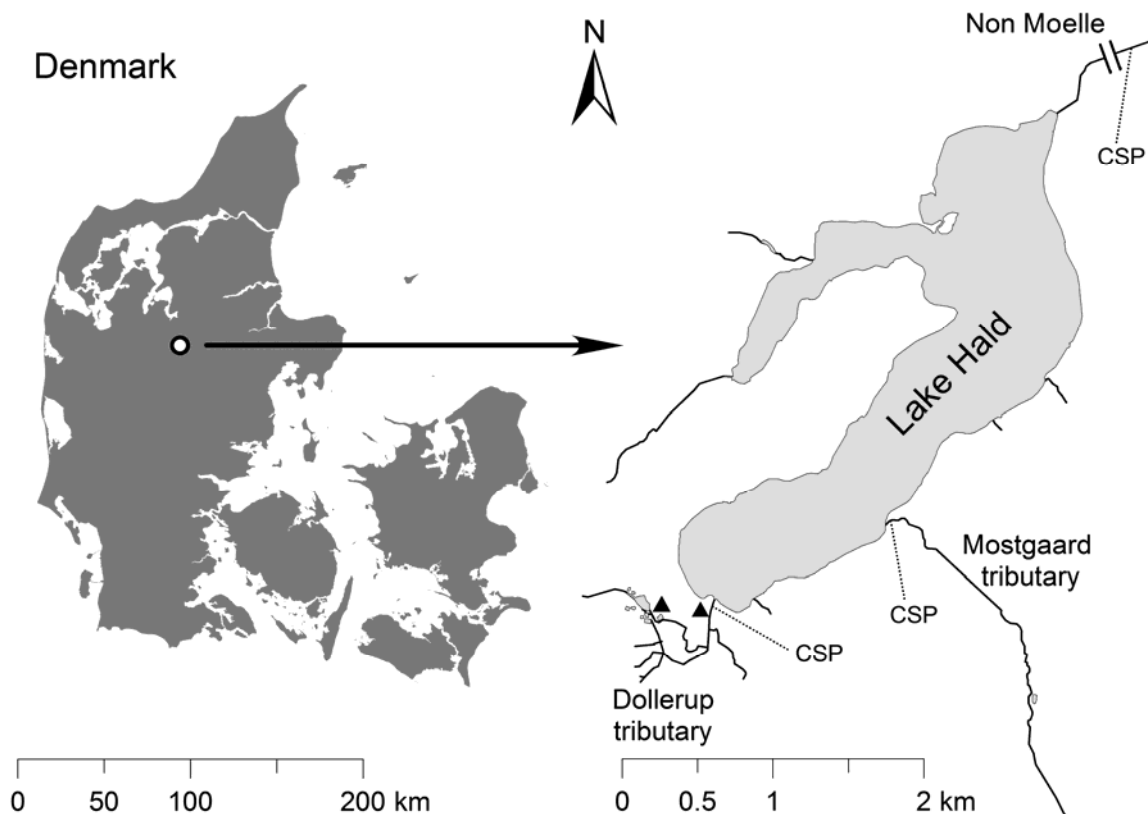
Figure 1: Map of the experimental area showing the position of Lake Hald, the tributaries and the locations of the cross-stream PIT-antennas (CSP) in the two major tributaries and the outlet. The one-way passage at the outlet, Non Moelle, is indicated by the disconnected line (⊣ ⊢). The ▲ indicates the capture/release location in the Dollerup tributary system.

of the lake allow downstream migration, but prevent the return of adult anadromous trout. The inlets from the two largest tributaries, the Dollerup and Mostgaard tributaries, as well as the lake outlet, Non Moelleaa, were equipped with cross stream antennas (CSP) that monitored the

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directional movements of fish tagged with passive integrated transponder (PIT) tags (Figure1) (Zydlewski et al. 2001).

Capture and sampling procedure

Migrating juvenile brown trout were captured from the start of April until the end of May 2009 using a fyke net trap placed in Dollerup tributary (Figure 1). Additionally, juvenile brown trout were caught in upstream stretches of the tributary by electrofishing in the same time period. After capture, trout were anaesthetized (benzocain 0.004 %). Total length (TL) and body mass (BM) were measured (to nearest 1 mm and 0.01 g, respectively). The trout were tagged and the individual tag-number was registered. Tagging was performed on trout > 120 mm using intraperitoneal insertion of a PIT tag (Texas Instruments, RI-TRP-RRHP, half duplex, 134 kHz, length 23.1 mm, diameter 3.85 mm and weight 0.6 g (air)) through a lateral-ventral incision (5 mm) approximately 10 mm posterior to the pectoral fins (Skov et al. 2005). A blood sample, (mixed arterial-venous blood), was drawn from the caudal vessel using a heparinised syringe. To ensure recovery of the fish, sampled volumes were kept below 0.1% of the fish body mass. Finally, gill biopsies were collected from the gill filaments. Shortly after recovery from the anaesthesia fish were released at the capture location. Gill biopsies were preserved in SEI buffer (pH=7.5, 150 mmol L-1 sucrose, 10 mmol L-1 EDTA, 50 mmol L-1 imidazole) following Nielsen et al. (2003). Gill samples were instantly frozen in liquid nitrogen and blood samples were immediately stored on ice and transported to the laboratory (60-180 minutes). Blood samples were centrifuged at 10.000 × g for 5 minutes and the blood plasma, the supernatant, was separated using a pipette. Samples with gill filaments and blood plasma were preserved at minus 80°C until further analysis. Finally, an additional sample of brown trout was captured the following year. Early in June 2010, at the end of the end of the migration period, trout were captured by snorkelling with a scoop net in the lake. Simultaneously, trout were caught by fyke net trapping at the lake outlet. Scale samples were taken and analysed under a

microscope to determine the growth in the immediate past. Handling and surgery were performed in accordance with guidelines from the Danish Animal Experiments Inspectorate.

Life history strategy assignment

Individual life history strategy was assigned according to capture location and individual migration history, derived from the PIT tag records. Migration data were collected until the end of July 2009 to ensure that the data collection period covered the migration period. Brown trout were assigned to one of three different strategies: 1) residents; trout that resided in the tributary; 2) potamodromous, fish that migrated to the lake, but did not leave through the lake outlet; and 3) anadromous, fish that migrated to the lake and subsequently continued migration by leaving the lake through the outlet (Figure 1). From year 2010, trout that were captured in the lake were considered as potamodromous and those captured at the lake outlet as anadromous.

Analysis of physiological samples

Na,K-ATPase activity (μmol ADP (mg protein)$^{-1}$ h^{-1}) was analysed at 27°C following the procedure of McCormick et al. (1993) using a microtitre plate reader (Spectramax, Molecular Devices, Sunnyvale, CA, USA). Protein content of gill homogenates was measured according to Lowry et al. (1951) and adjusted for 96-well plates for analysis with microtitre plate reader. Blood plasma was analysed for total protein, glucose, aspartate aminotransferase activity (AST), inorganic phosphorus, cholesterol, triacylglyceride (TAG), and calcium according to standard procedures using Siemens® Clinical Methods for ADVIA 1650. Sodium, potassium and chloride were determined by Ion Selective Electrodes (ISE) employing the same equipment. Intra- and inter assay precisions and accuracy were in all instances below 4.0 CV%.

Data analysis

Linear discriminant analysis was used to identify the linear transformations of the predictor variables, which yielded maximal separation of the three groups (resident, potamodromous and anadromous), by maximising between-group variance and minimising within-group variance, resulting in two discriminant functions. Variables used in the analysis (sodium, potassium, chloride, glucose, AST, calcium, inorganic phosphor, total protein, TAG, cholesterol, Na,K-ATPase activity and Fulton's K) are presented in (Table 1). Body condition, Fulton's K, was calculated from total length and body mass ($K = 100BM(g) * TL(cm)^{-3}$). Wilk´s statistics was used to evaluate the overall group effects in the original variables and in the discriminant scores. ANOVA was used to evaluate the group scores on the discriminant functions, separately for each discriminant function, and subsequently Tukey HSD (Honestly Significant Difference) for group comparisons. The overall significance level was set to 0.05. Assumptions of multivariate normality, homocedacity and multicollinearity were evaluated from normal QQ-plots, standardized residuals and correlation analysis, respectively. The explanatory power of predictor variables was assessed by the loading of each variable on the respective discriminant functions; loadings >[0.40] were considered substantive for interpretation purposes (Hair et al. 2010). Permutation tests were performed to validate robustness of discriminant classification procedure. Transformations by natural logarithm were applied in a few cases to improve normality or homocedacity. Extreme outliers that were outside 3 × the inter-quartile-ranges were scrutinized. Only values that could be attributed to measurement errors were removed as recommended by Cardinal & Aitken (2006).

Statistical analyses were performed in R, version 2.13.0 (R Development Core Team 2011) and using the MASS package version 7.3-14 (Venables & Ripley 2002).

Results

The detection records of individual PIT tag revealed that a part of the population in the tributaries migrated to the lake from March to May. A portion of these fish continued the migration and left the lake through the lake outlet during May. No migration was observed from June and onwards. This resulted in three groups that were regarded as residents, potamodromous and anadromous. Groups and sample results are summarized in table 1.

Variable	Residents Mean	SD	Potamodromous Mean	SD	Anadromous Mean	SD	Units
Sodium	158	6	162	8	161	7	mmol*L^{-1}
Potassium	2.7	1.0	3.0	1.6	3.1	1.4	mmol*L^{-1}
Chloride	123	4	121	5	122	4	mmol*L^{-1}
Glucose	4.30	0.72	4.80	1.53	4.88	1.46	mmol*L^{-1}
AST	41	19	33	24	34	24	IU
Calcium	2.32	0.17	2.20	0.29	2.19	0.28	mmol*L^{-1}
Inorg. Phosphor	3.33	0.32	3.06	0.43	3.10	0.54	mmol*L^{-1}
Total Protein	23.0	3.8	21.3	5.6	21.9	5.9	g*L^{-1}
TAG	1.34	0.73	0.86	0.57	1.27	0.69	mmol*L^{-1}
Cholesterol	4.18	2.19	2.27	1.86	2.90	1.93	mmol*L^{-1}
Na,K-ATPase	3.93	3.25	7.40	4.27	6.66	3.16	μmol ADP mg protein^{-1} h^{-1}
Fulton's K	0.96	0.08	0.86	0.05	0.89	0.08	g*100/cm^3
TL	139.3	2.0	142.8	1.9	137.8	1.2	mm
BM	27.8	15.1	26.3	12.2	23.7	5.8	g
N	32		29		11		N

Table 1: Summary of non-transformed variables and number of individuals assigned to the three life history strategy groups, presented as arithmetic means (Mean), standard deviation (SD).

Analysis of the physiological data indicated a significant overall group effect in the discriminant model (Wilk's; $p<0.001$). The discriminant analysis resulted in two discriminant functions, the first explaining the majority of the between-group variance and the second explaining the remaining variance (Table 2).

	Eigenvalue	Variance (%)
Function 1	6.205	77.42
Function 2	1.810	22.58

Table 2: Eigenvalues and the between-group variance explained by discriminant functions, Function 1 and Function 2.

The individual discriminant scores (Figure 2) showed significant group differences in both the first discriminant function (ANOVA: $F_{(2, 69)}=38.51$; $p< 0.001$) and the second (ANOVA: $F_{(2, 69)}=3.27$; $p< 0.05$). Subsequent multiple comparisons test (Table 3) showed that the scores of the potamodromous and anadromous groups on the first discriminant function were significantly different from the resident group. There was no significant difference between the two migratory groups. On the second discriminant function, there was a significant difference between potamodromous and anadromous trout, while residents were not found significantly different from either of the other two groups.

		Mean	SD	
	Residents	-1.178	1.136	*a*
Function 1	Potamodromous	0.964	0.852	*b*
	Anadromous	0.886	0.931	*b*
	Residents	-0.009	0.901	*c, d*
Function 2	Potamodromous	-0.251	0.951	*c*
	Anadromous	0.687	1.360	*d*

Table 3: Mean group scores (Mean) and standard deviations (SD) on the discriminant functions, Function 1 and Function 2. Group comparisons of residents, potamodromous and anadromous were performed with a Tukey HSD (significance level $p<0.05$). Different postscripts denotes significant group differences (Function 1: *a* and *b*, $p< 0.0001$ & Function 2: *c* and *d*, $p< 0.05$).
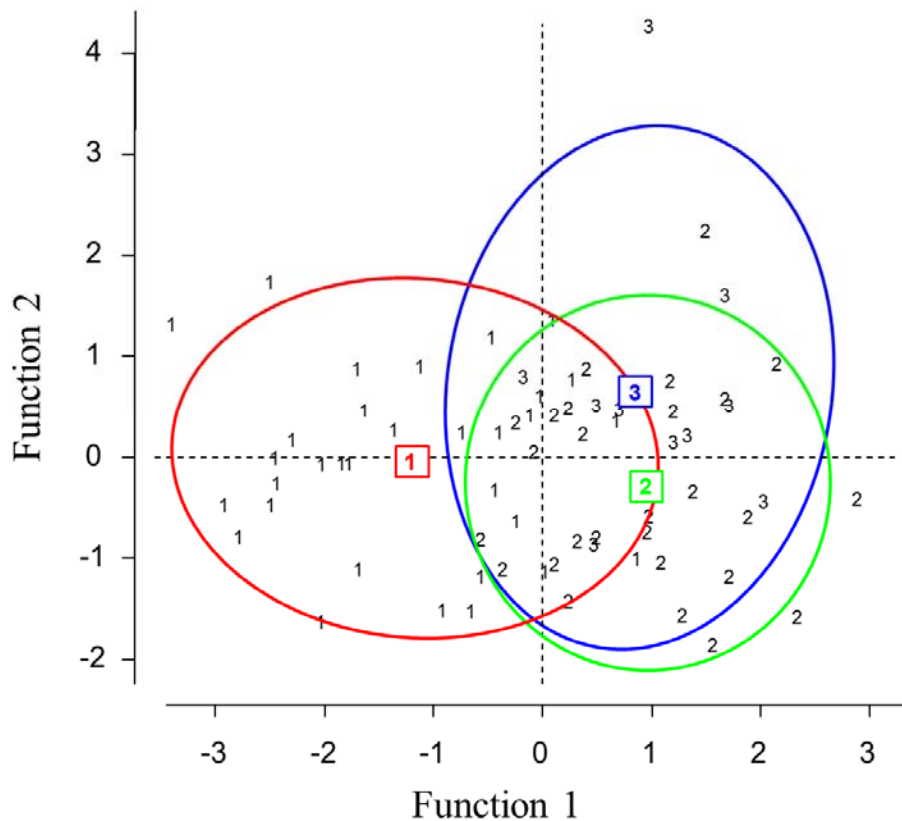
Figure 2: Bivariate plot of discriminant functions one and two from the linear discriminant analysis on groups of resident, potamodromous and anadromous trout, using variables that are indicative for nutritional status, stress, tissue damage and smoltification. The scores of individual fish from resident, potamodromous and anadromous groups are presented as 1, 2 and 3, respectively red, green and blue. The framed numbers signify the group centroids and encircled area represent the 90% tolerance regions (the region containing 90 % of the group).

Inorganic phosphorous, cholesterol, Na,K-ATPase activity and Fulton's K had directional loadings with substantial explanatory power of the group differences on first discriminant function. These showed that potamodromous and anadromous trout, relative to the residents, were characterized by low inorganic phosphorus, cholesterol and Fulton's K as well as high Na,K-ATPase activity. Calcium, total protein, TAG, sodium, chloride, potassium, glucose and AST showed no loadings with explanatory power on the first discriminant function and hence did not explain the group differences. On the second discriminant function, only the loading of TAG had substantial explanatory power on the group differences (Table 4). The direction of this loading

showed that anadromous trout had higher TAG levels than potamodromous. The loading of

Fulton's K was close to having explanatory power on the second function, which might indicate that

potamodromous trout had marginally lower condition factor relative to anadromous trout.

Category	Predictor Variable	Discriminant Loadings	
		Function 1	Function 2
Nutritional	Calcium	-0.328	-0.044
	Inorganic phosphor	**-0.425**	0.069
	Total protein	-0.214	0.122
	Cholesterol	**-0.544**	0.282
	TAG	-0.366	**0.642**
Stress	Sodium	0.328	-0.086
	Potassium	0.133	0.114
	Chloride	-0.236	0.197
	Glucose	0.292	0.084
Tissue dmg.	logAST	-0.355	0.069
Smoltification	logNa,K-ATPase	**0.589**	0.011
	Fulton's K	**-0.740**	0.379

Table 4: Discriminant loadings of the predictor variables, from blood and gill samples, which are categorized by their properties as indicators for nutritional status, stress, tissue damage and smoltification. Loadings above than [0.4] (bold) are considered to have substantive explanatory power on the respective discriminant functions.

Classification accuracy of the discriminant model, i.e. correct classifications according

to group membership, was 75 %. Validation of within-group classifications, by permutation test

(Table 5), showed that classification in the resident and potamodromous groups were significantly

different from random, with accuracies of 84 % (p< 0.05) and 86 % (p< 0.01), respectively, and

that these groups were clearly unique. Classification accuracy of the anadromous group was 18 %

and not significant from random classification (p= 0.38), but notably 64 % from this group was

significantly misclassified as potamodromous trout (p< 0.01), indicating that these two groups were

generally very similar. The remaining misclassifications were either significantly lower than random classification or contained within the random classification distribution.

	Classifications			Permuted Classifications			
					95% C.I.		p
Original	Predicted	N	%	Mean (N)	Lower	Upper	(2-tailed)
	Resident	27	84.38	22.25	18	26	**0.015**
Resident	Potamodromous	4	12.50	8.49	5	12	**0.022**
	Anadromous	1	3.13	1.26	0	3	0.615
	Resident	3	10.34	9.99	6	14	**0.002**
Potamodromous	Potamodromous	25	86.21	17.83	13	22	**0.001**
	Anadromous	1	3.45	1.18	0	3	0.603
	Resident	2	18.18	4.24	1	8	0.124
Anadromous	Potamodromous	7	63.64	3.35	1	6	**0.005**
	Anadromous	2	18.18	3.41	0	7	0.386

Table 5: Classifications from linear discriminant analysis and permutation test, presented as number of individuals (N) and as percentages (%). Distributions of permuted group classifications are presented as the mean number of individuals and with 95% confidence limits. The 2-tailed test indicate if the predicted classifications to groups were significantly different ($p < 0.05$) from the random classification distribution.

Scales of potamodromous trout that were captured in the lake indicated that they had grown rapidly in the immediate past leading up to capture. In contrast, all the scales of anadromous trout, captured at the lake outlet, showed no particular change in growth in the immediate past. The average date of capture did not differ between these two groups of fish.

Discussion

Little is known about the physiological basis of partial migration, in particular in populations of salmonids expressing a continuum of migratory strategies. The results of the present study revealed substantial physiological differences   between the resident, potamodromous and anadromous brown trout. The physiological fingerprinting is consistent with the hypothesis that the continuum of partial migration in brown trout is strongly influenced by the magnitude of energy stores in individual fish.

The variables that best explained the group differences between the resident group and the potamodromous and anadromous trout were related with nutritional status and smoltification. Potamodromous and anadromous trout were characterized by having lower plasma levels of inorganic phosphorus and cholesterol as well as lower Fulton's K, and higher Na,K-ATPase activity, relative to residents. The classification of individuals to their predefined groups showed that residents and potamodromous trout were distinctive. The significant misclassification of anadromous trout to the potamodromous group indicated that these two strategies were generally similar. Interestingly, only the levels triacylglycerides (TAG) revealed a difference between these groups.

Our results provide evidence that both potamodromous and anadromous trout were smoltified before leaving the tributary. High gill Na,K-ATPase activity and lower condition factor are widely used indicators for the anadromous life history strategy and the smoltification process (McCormick et al. 1985; Cunjak et al. 1990; McCormick & Bjornsson 1994; Reis-Henriques et al. 1996; Sigholt et al. 1998). Na,K-ATPase activity is generally lower in residents, which makes it a useful tool to estimate future propensity for anadromous migration (Nielsen et al. 2004). Relative to residents in the present study, both potamodromous and anadromous trout exhibited lower condition factor and higher Na,K-ATPase activity, indicating that both of these groups were

smoltified. Smoltification of the potamodromous trout corroborates earlier findings that up regulation of Na,K-ATPase activity (Pirhonen & Forsman 1998) and reduction of condition factor (Champigneulle et al. 1988) occur in potamodromous brown trout. Consequently, smoltification characteristics cannot be used to distinguish between coexisting potamodromous and anadromous brown trout.

We found several indications that potamodromous and anadromous trout were lipid depleted and had lower nutritional status relative to the resident. These findings may relate to a combination of relative starvation effect due to metabolic demands, differences in the energy allocation towards lipid storage and the smoltification process. In salmonids, the migratory propensity increase at low food availabilities (Nordeng 1983; Olsson et al. 2006; Wysujack et al. 2009) and is related to migrants having higher consumption needs (Forseth et al. 1999; Morinville & Rasmussen 2003). This mechanism could make them more prone to starvation and lead to lower lipid and nutritional status. In salmonids, this can become evident as low plasma levels of cholesterol, total protein and phosphorous, but sometimes also as low calcium and TAG (Congleton & Wagner 2006). However, smoltification may also result in lipid depletion, indicated by low TAG and cholesterol (Sheridan et al. 1983; Sheridan 1989) and therefore may also explain these lipid depletions. Additionally, early smolting salmon (*Salmo salar*) have lower allocation toward lipid storage, compared to late smolts (Morgan et al. 2000; Morgan et al. 2002), which may also be characteristic to migratory brown trout. We found no indications of low TAG in potamodromous and anadromous trout relative to the residents. We did find however that low plasma cholesterol indicated lipid deprivation in the potamodromous and anadromous trout, relative to the residents. This was further corroborated by the low levels of phosphorous, which is known to correlate with increased enzyme activity that is related with lipid breakdown (Wagner & Congleton 2004). The

levels of plasma calcium and total protein, likewise indicative of nutritional status in salmonids, showed no explanation of the groups in this study.

   This study showed that the potamodromous trout were relatively more lipid deprived than both resident and anadromous trout. Low TAG levels are generally associated with lipid deprivation of smolts (Sheridan et al. 1983; Sheridan 1989). However, as stated above, plasma levels of TAG did not support the lipid deprivation in the smoltified potamodromous and anadromous trout, relative to residents, as indicated by low cholesterol and low phosphorus. Instead TAG indicated that potamodromous trout were more lipid deprived than the anadromous trout. It is possible that energetic status is an important factor that influences the migratory decision-making in resident vs. migratory fish, but also in the next step potamodromous vs. anadromous fish. While migratory behaviour in salmonids is initiated to avoid energetic limitations (Nordeng 1983; Forseth et al. 1999; Olsson et al. 2006; Wysujack et al. 2009), the continuum of migratory strategies in brown trout is suggested to relate to finding a habitat that provides sufficient resources to maintain an appropriate growth rate given their inherent high standard metabolic rate (Cucherousset et al. 2005). However, at a broader level migratory propensity is also inversely correlated with migration distance (Kristoffersen et al. 1994) and the costs of migration (Bohlin et al. 2001; Jonsson & Jonsson 2006). The present findings along with earlier findings indicate an emerging pattern where lipid status might be a decisive factor influencing the migratory distance. State-dependent migratory decision making has been shown in roach (*Rutilus rutilus*), where migratory propensity was positively correlated with body condition and feeding status (Brodersen et al. 2008). Additionally, anadromous juvenile houting (*Coregonus oxyrinchus*), delay dispersal when exposed to short term food deprivation (Poulsen et al. 2010). These studies indicate that cessation or delay of the migration may be associated with energetic insufficiencies. Moreover, the scale samples from year 2010 indicated that potamodromous trout had grown rapidly in the period leading up to being

caught in the lake, whereas the anadromous trout had not grown much during the lake passage. This suggests that the potamodromous trout were more inclined to feed than anadromous trout. Based on these observations, we propose that within the migratory strategy, a fish with severely depleted energy reserves might terminate migration and commence feeding at an earlier point than a fish in a better condition, depending on the habitat conditions that are encountered. Rather than a matter of resident or migratory strategies, partial migration could be considered a migratory continuum from resident over potamodromous to anadromous.

Our results showed no indications of differences in stress or tissue damage between resident, potamodromous and anadromous brown trout. Smoltification is correlated with intensified stress responsiveness (Barton 2002) and thus, stress indicators may also provide clues to life history related strategies. However, we found no group related differences in the levels of plasma sodium, potassium, chloride and glucose that are indicative of stress (Wendelaar Bonga 1997; Wagner & Congleton 2004). Nor did we find any indications of differences in AST levels, indicative of tissue damage (Wagner & Congleton 2004).

In summary, this study revealed substantial physiological differences between resident, potamodromous and anadromous brown trout. The physiological fingerprinting is consistent with the hypothesis that the continuum of migration in brown trout is strongly influenced by the magnitude of energy stores in individual fish.

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MS II

Life history differences in alewives alter the ontogenetic trajectory
of juvenile largemouth bass

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Abstract

Phenotypic variation in important species has been shown to influence ecosystem interactions. Anadromous and landlocked alewives (*Alosa pseudoharengus*) differ in migratory behaviour and feeding traits which result in differences in the structuring effect on zooplankton communities. Consequently there are differences in zooplankton availability, which potentially influence coexisting species. Availabilities of zooplanktons are low year-round in 'landlocked' lakes; high in spring and low in summer in 'anadromous' lakes; and generally higher year-round in lakes without alewives. In this study we compared the ontogenetic trajectory of young-of-the-year largemouth bass (LMB; *Micropterus salmoides*), which depend on zooplankton in the early life stages, in three lake types: with landlocked; with anadromous; and without alewives. We found that the presence and phenotype of alewives had effects on growth, trophic position and diet of LMB. Growth and increase in trophic position of LMB were faster in lakes with anadromous alewives, relative to lakes with landlocked alewives. LMB from lakes without alewife had the fastest growth and trophic increase and diet analysis showed that LMB in this lake type were the only ones to reach consistent piscivory by the end of the summer. Diets generally shifted from pelagic towards littoral based food items and then to fish prey, but in lakes with landlocked and anadromous alewives only a short lived period of piscivory occurred. These divergences can all be related to differences in zooplankton availabilities during early ontogeny, caused by alewives, which shows that both presence and phenotypic variation of alewives has important impact on interspecific interactions.

Introduction

Only few studies have so far addressed the ecological consequences of intraspecific phenotypic variation a keystone species (Treseder & Vitousek 2001; Proffitt et al. 2005; Wimp et al. 2005; Post et al. 2008; Walsh & Post 2011). Alewives (*Alosa pseudoharengus*) are specialist zooplanktivores, and a keystone species, which can have strong impacts on the zooplankton community (Brooks & Dodson 1965; Post et al. 2008). Across the eastern North America, there are populations of alewives that differ with respect to life history, e.g. anadromous alewives, which spawn in freshwater and feed and grow in the ocean, and landlocked alewife, which spend their entire life in lakes. Post et al. (2008) showed that this intraspecific phenotypic variation drives differences in zooplankton availability and size structure. Both the presence and life history of alewives influence the zooplankton availability: lakes with no alewife (NA) large-bodied zooplankton year-round; lakes with landlocked alewife (LLA) have small-bodied zooplankton year-round; and lakes with anadromous alewife (AA) have zooplankton communities that cycles between large-bodied zooplankton in the winter and spring and small-bodied zooplankton in the summer months (Post et al. 2008). Zooplanktivorous fish species directly affect the density and size-structure of their zooplankton prey and through this they can indirectly influence the foraging behaviour, growth, and survival coexisting fish species that rely on the same resources (Neill 1975; DeVries & Stein 1992; Olson et al. 1995; Post et al. 2008). These differences in zooplankton size structure and density are likely to have different influence coexisting species.

Young-of-the-year (YOY) piscivorous fish, such as largemouth bass (LMB, *Micropterus salmoides*), undergo ontogenetic diet shifts from feeding on zooplankton, to feeding on macro invertebrates and finally to feeding on fish (Werner & Gilliam 1984; Olson 1996; Post 2003). These shifts in diets and trophic level introduce stage structure, where each stage has different community interactions (Werner & Gilliam 1984; Olson 1996). The timing of these ontogenetic

shifts largely depend on body size and therefore influences on early growth are expected to affect the timing of future ontogenetic transitions (Olson 1996; Parkos & Wahl 2010).

In the zooplanktivorous stage of juvenile fish growth rate is positively correlated with zooplankton availability (Persson et al. 2000; Hoxmeier et al. 2004; Milstein et al. 2006) and competition at this early life history stage can reduce growth and survival and subsequently the recruitment of juvenile fish into the adult population (Werner 1977; DeVries & Stein 1992; Olson et al. 1995; Bystrom et al. 1998; Hjelm et al. 2000). Additionally, low zooplankton availabilities, for example caused by competition, can promote an early shift to macro invertebrate prey (Persson 1983; Persson 1986; Persson & Greenberg 1990; Wu & Culver 1992; Bystrom et al. 1998; Hoxmeier et al. 2004). In perch (*Perca fluviatilis*), the competition induced niche shift to macro invertebrates has been shown to reduce growth and body condition (Bystrom et al. 1998), suggesting prematurely induced shifts to larger prey may be associated with greater handling costs (Werner 1977; Mittelbach 1981).

In LMB rapid growth during invertebrate feeding phase is critical to gain the predatory size advantage required to reach piscivory (Olson 1996). Generally LMB make the transition to piscivory in their first or second year (Ludsin & DeVries 1997; Post 2003) and making this transition as early as possible increases growth and survival (Buijse & Houthuijzen 1992; Olson 1996). Delays in the transition to piscivory leads to loss of growth and subsequently to increased size-related predation and winter mortality (Ludsin & DeVries 1997; Post 2003).

We hypothesise that the differences in zooplankton communities imposed by alewives (Post et al. 2008) will influence the ontogenetic trajectory of concurrent YOY LMB. The greater availability of larger zooplankton in spring in AA lakes, though decreasing toward summer, may result in higher zooplankton availability, relative to in LLA lakes. Thus we expect relatively faster

growth and ontogenetic transitions of YOY LMB in AA lakes. The greater biomass and larger sizes

of zooplankton prey in NA lakes, compared to both LLA and AA lakes, is expected allow LMB in

NA lakes to have faster growth and ontogenetic shifts. These differences may be visible in the

timing of the dietary niche shifts from zooplankton (pelagic food web) to macro invertebrates

(littoral food web) and ultimately in the timing of reaching piscivory. Here we test these predictions

using stable isotopes, measures of summer growth rates and direct diet analyses. We used stable

isotopes of nitrogen and carbon to estimate the trophic position (TP) and the proportional affiliation

from littoral and pelagic food webs (alpha) of YOY LMB, using a two-source model with littoral

and pelagic endmembers (Post 2002). Direct diet data were used to provide higher resolution

information on ontogenetic shifts. Measurements of standard length (Slagter & Sheridan 1999) over

the summer were used to infer differences in growth rates.

Materials and procedures:

Study Area and Lake Types

We collected YOY LMB from nine lakes in Connecticut. These lakes were categorized as three

types according to the presence and life history type of alewives, reflecting two levels of spatial

openness and three different food web configurations: lakes isolated from the coastal ocean with

either no alewives (NA: Black, Gardner, Hayward) or with landlocked alewives (LLA: Amos,

Pattagansett, Rogers), and lakes connected to the coastal ocean with anadromous alewives (AA:

Bride, Dodge, Gorton). A full description of the lakes and a map is available in Post et al. (2008).

There is no significant difference in fish community composition between the lake types (Howeth et

al. in review), except that non-alewife planktivorous fish are more abundant in LLA lakes, relative

to AA lakes (Palkovacs & Post 2008). Largemouth bass (*Micropterus salmoides*) and chain pickerel

(*Esox niger*) are the top predators in these systems, and bluegill (*Lepomis macrochirus*), golden

shiners (*Notemigonus crysoleucas*), pumpkinseed (*Lepomis gibbosus*) and yellow perch (*Perca flavescens*) are the most common non-alewife planktivorous fishes (Palkovacs & Post (2008); Howeth et al. in review).

Fish collection

YOY LMB was collected on multiple occasions over the period from June 4th to November 19th 2009. We collected bass using dip net (while snorkelling), scoop net (from boat), beach seine and electrofishing boat. The range of sampling period, sample sizes and size range of captured YOY LMB varied between lakes, due to variability in captures and the growth rate of bass in each lake. We sampled LLA lakes from DOY 161-299 in Amos (N=48 and length: 17.8-98.0); DOY 160-308 in Pattagansett (N=42 and length: 19.7-82.0); and DOY161-303 in Rogers (N=79 and length =17.8-60.0). We sampled AA lakes from DOY 164-300 in Bride (N=94; length: 17.4-67.0); DOY 155-323 in Dodge (N=71; length: 8.5-108.0); and DOY 155-323 in Gorton (N=56; length: 13.1-73.0). We sampled NA lakes from DOY 159-293 in Black (N=34; lenght: 15.5-107.0); DOY 159-323 (N=45; length=10.0-92.0) in Gardner; and DOY 159-308 in Hayward (N=41; length =13.3-89.0). LMB were euthanized and placed on ice for transport to the lab, where they were preserved at −20 °C until further processing. All the preserved fish (N=511) were used for growth analysis by standard length (Slagter & Sheridan 1999) measurements. Subsets from each lake on each of the sampling dates were haphazardly selected for diet (N=221) and stable isotope analysis (N=291).

Stable Isotope analysis

Following Post (2002 and 2003), we used stable isotopes of nitrogen ($\delta^{15}N$) to provide evidence for ontogenetic shifts in trophic position and carbon ($\delta^{13}C$) shifts in diet from pelagic to littoral food sources. Here we report isotope values in the standard δ notation where $\delta X \permil = [(R_{sample}/R_{standard})-$

1] 10^3; δX is either $\delta^{15}N$ or $\delta^{13}C$ and R is the ratio of $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively. Samples, the whole body minus the head and guts, were dried at 45-55°C for approximately 48 hours. The samples were subsequently ground into a fine powder either by mortar, after having been freeze dried in a vessel submerged in liquid nitrogen, or in a freezer mill. One milligram from each sample in tinfoil capsules were analysed on a Europa Geo 20/20 combustion continuous flow isotope ratio mass spectrometer. Each run included a house standard (trout muscle tissue) interspersed every 5–9 samples to correct for drift and to provide an estimate of instrumental error. $\delta^{13}C$ values were lipid-corrected following Post et al. (2007). Cayuga brown trout (*Salmo trutta*) was used as working standard, $\delta^{13}C$ = -25.1 and $\delta^{15}N$ = 17.3. Global standard for $\delta^{13}C$ was PeeDee Belemnite and atmospheric nitrogen for $\delta^{15}N$. Lipid-corrections were applied to $\delta^{13}C$ values when C:N ratios >3.3, following (Post et al. 2007). We used zooplankton for the pelagic baseline and periphyton for the littoral food webs and assumed a trophic fractionation of 3.4‰ for $\delta^{15}N$ and 0‰ for $\delta^{13}C$ following Post (2002). We estimated trophic position as TP = λ + ($\delta^{15}N_{LMB}$ - [$\delta^{15}N_{pelagic}$ ° alpha + $\delta^{15}N_{littoral}$ ° (1 - alpha)]) / 3.4], where λ is the trophic position of the organism used for $\delta^{15}N$ baseline (e.g. 1 for primary producers) and where alpha is a proportional measure of the use of benthic and pelagic food web, estimated as alpha = ($\delta^{13}C_{LMB}$ - $\delta^{13}C_{littoral}$) / ($\delta^{13}C_{pelagic}$ - $\delta^{13}C_{littoral}$) (Post 2002). Alpha was constrained between zero and one, respectively indicating a strictly benthic and a strictly pelagic food web affiliation.

Stomach contents

We analysed the stomach contents of five YOY LMB´s from each sampling date and location (when possible). Items in the stomach contents were identified to the lowest relevant taxonomic group and counted. Prey types were evaluated as: large zooplankton (*Daphnia* spp., *Epischura lacustris, Mesocyclops edax*); small zooplankton (*Bosmina* spp., *Polyphemus pediculus, Chydorus*

spp., various Copepoda, *Ceriodaphnia* ssp. and *Diaphansoma* ssp.); Littoral-benthic macro fauna (various Chironomidae pupae and larvae, various Ephmeroptera nymphs, various Odonata nymphs, various Amphipoda, various Trichoptera nymphs, various Hemiptera nymphs, various Plecoptera nymphs and Asellus sp.); and fish (possibly bluegills or yellow perch). A standard dry mass (DM) was estimated for each type of prey item: for zooplankton DM we used estimates for small or large size categories form Downing & Rigler (1984); for macro invertebrates, we converted body length or head widths to DM following (Benke et al. 1999); and for fish prey we converted length to DM using a regression created with data from juvenile bluegills (Wahl & Stein 1991; Einfalt & Wahl 1997). DM for fish prey was estimated according to the average lengths of well-preserved specimens from the respective time periods in the study. The standardized DM´s were multiplied by the number of respective food items that were counted. The DM´s of stomach contents were for each sampling day converted into proportions according to their food web affiliation (littoral or pelagic) or as fish. The temporal trends in proportional stomach contents was presented for the three lake types in the study as a weighted centred moving average, centred around three sampling days and weighted according to number of individuals for a given day.

Data treatment

The nested experimental design of lakes within lake type favours the use of mixed effects models which we performed following procedures from Zuur et al. (2009). We analysed the dependent variables of SL and TP with linear mixed effects (LME) models and alpha with generalized additive mixed model (GAMM). We were not interested in the specific lakes, but rather the effect of lake type, and therefore we used lake identity as random effect. This, furthermore, permits more general conclusions about lake type differences. To satisfy model assumptions in the analysis of growth, we used log transformation on the covariate, DOY, to obtain linearity in the increase of SL. The LME

models were fitted with restricted maximum likelihood (REML). For choosing the appropriate structure of the random effects, Akaike's information criterion (AIC) was used to evaluate the model goodness of fit in model selection. The resulting in models with random intercept for each lake provided the best fit for analysis of both TP and SL. The full model for LME models was as follows:

Dependent variable = β + Lake Type + DOY + (Lake Type : DOY) + random effect (Lake) + ε

For the modelling of SL a variance structure was fitted, which allow the variance to increase as a function of the fitted values within each lake type. The optimal fixed structure found by model reduction by backwards selection excluding terms from the fixed structure that did not explain significant variation of the response variable. Competing models in the reduction procedure were fitted by maximum likelihood (ML) and compared with a likelihood ratio test. The final models were refitted with REML. For the LME models the final models were not reduced relative to the full model.

We used a generalised additive mixed model (GAMM) to describe the change in food web affiliation over time for the three lake types, following Zuur et al. (2009). To account for repeated measurements, lake identity was included as a random effect. We tried models with one smoother for all three lake types, one smoother per lake type, but the AIC indicated that the best model had one smoother for LLA and NA and another for AA lakes, thereby modelling an interaction between lake type and DOY. The full GAMM model was given as:

alpha = β + Lake Type + s(DOY, by LLA & NA) + s(DOY, by AA) + random effect (Lake) + ε

As the dependent variable was given in proportions the model was fitted with a quasibinomial distribution (logit-link). The maximum degrees of freedom allowed to the smoothing functions, defined as number of knots (Kannan et al. 2004), was limited (k = 4) to simplify interpretation of

the results. For modelling within the data range, the intercept was set at DOY=155. Insignificant explanatory variables were removed one at a time until all remaining variables were significant (p < 0.05). Throughout the paper, we present p-values that are considered significant at the 0.05 level. Statistical analyses were performed using R version 2.13.0 (R Development Core Team 2011) using the nlme 3.1-97 (Pinheiro et al. 2010) and the mgcv 1.7-2 (Wood 2006) packages.

Results

For standard length (Slagter & Sheridan 1999) there was a significant interaction between lake type and log(day-of-year) (F=26.35, p<0.0001), showing significant differences in the increase in SL over time (growth rate) between the three lake types (Figure 1). As hypothesized, the growth rate of YOY LMB in both
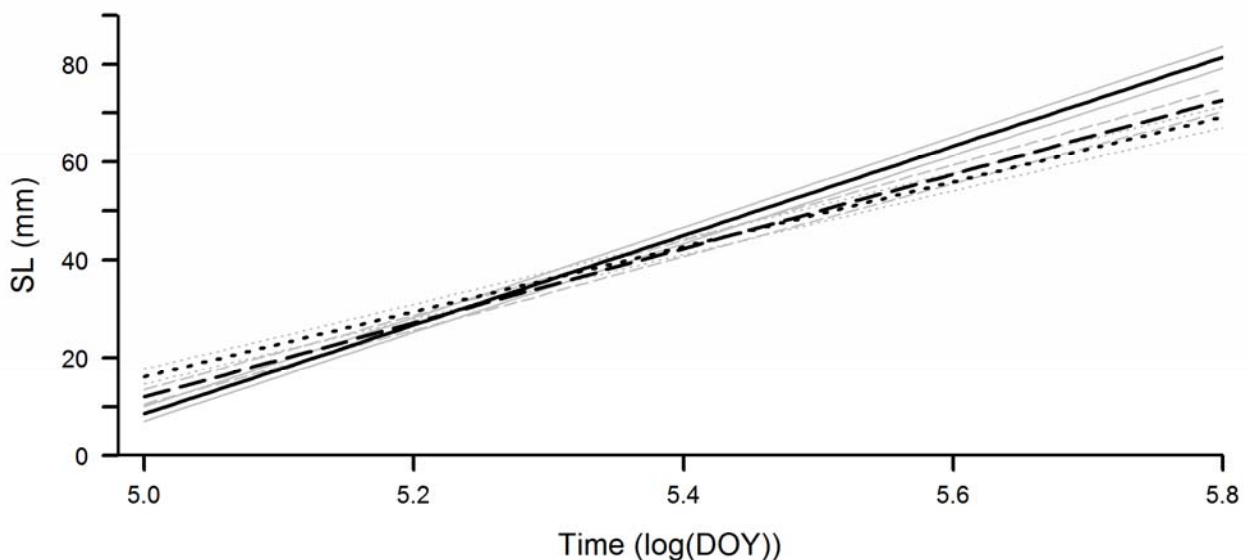
Figure 1: The change in standard length (Slagter & Sheridan 1999) over time of young-of-the-year largemouth bass in three lake types: lakes with landlocked (broken lines), with anadromous (dashed lines) and lakes without alewives (solid lines). To illustrate the modelled data the study period, from June 4th to November 19th (2009), is presented as log transformed day-of-year (log(DOY)). The lines, the fitted values (black lines) with standard errors (grey lines) obtained from a linear mixed effects model, represents the

modelled linear effect of lake type over time, where the slopes were significantly different between all three lake types.

LLA and AA lakes were suppressed, relative to NA lakes. Between lake types, the growth rate was significantly higher in the NA lakes, relative to both LLA (t =7.34, p<0.0001) and AA lakes (t=4.37, p<0.0001). Moreover we found growth was significantly higher for LMB from AA lakes compared to LLA lakes (t=2.71, p=0.0069). This indicates that the presences of alewives slow down the growth of LMB relative to those in NA lakes and, moreover, that this effect is significantly stronger in LLA relative to AA lakes.

We found significant interaction between lake type and day-of-year (F=28.87, p<0.0001), indicating differences in the rate of increase in trophic position (TP) over time of LMB in the three lake types. Similar to growth rate, the rate of increase in TP was highest in NA lakes, followed by AA and then LLA (Figure 2).

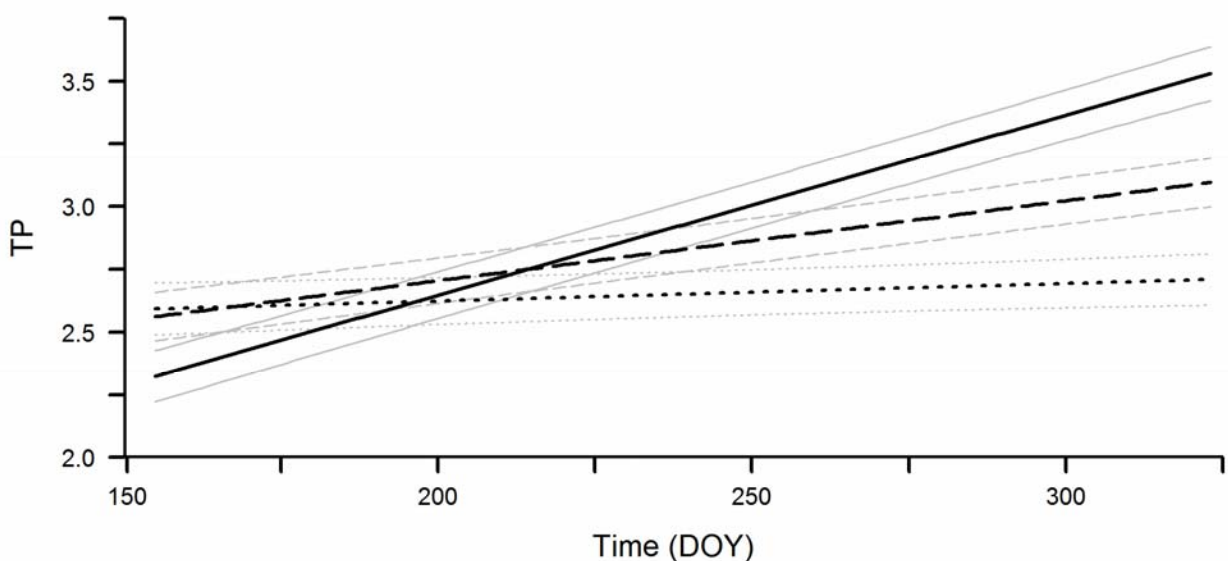**Figure 2:** The change in trophic position (TP) over time of young-of-the-year largemouth bass in three lake types: lakes with landlocked (broken lines), with anadromous (dashed lines) and lakes without alewives (solid lines). To illustrate the modelled data the study period, from June 4th to November 19th (2009), is presented as day-of-year (DOY). The lines, the fitted values (black lines) with standard errors (grey lines)

obtained from a linear mixed effects model, represents the modelled linear effect of lake type over time, where the slopes were significantly different between all three lake types.

For LMB in AA and NA lakes the increase in TP over time were significantly greater than zero (respectively: $t=6.67$, $p<0.0001$ & $t=11.63$, $p<0.0001$), but not in LLA lakes ($t=1.13$, $p=0.25$). The rate of increase in TP was significantly higher in NA than in both LAA ($t=7.53$, $p<0.0001$) and AA ($t=5.13$, $p<0.0001$). Moreover, the rate of increase in TP was significantly higher in AA relative to LLA ($t=3.25$, $p=0.0013$). This indicates that the presences of alewives slow down the transition to feeding at higher trophic position for LMB relative to those in NA lakes and, moreover, that this effect is significantly stronger in LLA relative to AA lakes.

We found that the proportional use of littoral or pelagic sources, as given by alpha, was different of LMB in the three lake types. The one smoother of the resulting model, representing LLA and NA lakes, was linear and showed no change over time (edf=1, $F=1.56$, $p=0.212$) (Figure 3). The other smoother, representing AA lakes, showed a significant nonlinear change in alpha (edf=2.44, $F=11.64$, $p< 0.00001$) (Figure 3). While for LLA and NA lakes the smoothers for alpha suggested an initial equal affiliation between the pelagic and littoral food webs, which did not change over the study period, the smoother for AA lakes showed a shift from a proportional more affiliation to the pelagic to a more affiliation to the littoral food web.

The trends in diets were relatively similar in LLA and AA lakes. Diets gradually shifted from pelagic towards littoral-benthic food sources and both with a short period of piscivory in mid-August that quickly subsided (Figure 4 A&B). However, proportional transition to littoral prey appeared more rapidly in AA relative to LLA lakes. In NA lakes the initial dominance of pelagic food items in diet transitioned towards littoral items and piscivory (Figure 4 C). Pelagic food items occurred in diets until the autumn where only fish material was found in these diets. Furthermore, the onset of piscivory in NA lakes coincided with several occurrences of empty

stomachs, whereas empty stomachs were not found in AA and LLA lakes. Due to low sampling

frequency and the
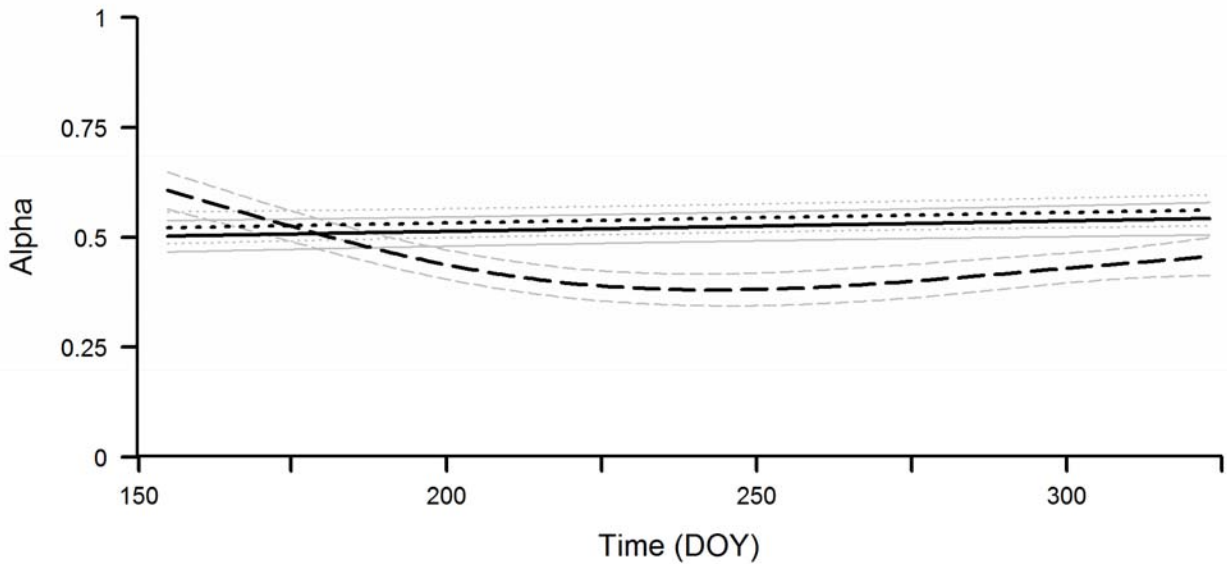
Figure 3: The trend in proportional use of pelagic food web, represented by alpha, of young-of-the-year
largemouth bass from three lake types: lakes with landlocked (broken lines), with anadromous (dashed lines)
and lakes without alewives (solid lines). To illustrate the modelled data, the study period from June 4th to
November 19th (2009) is presented as day-of-year (DOY). The effect of time (DOY) on alpha, the fitted
values (black lines) and standard errors (grey lines), were obtained by modelling with a generalised additive
mixed model (quasibinomial) and subsequent inverse logit-transformation. The best model fit was found
through a model with two smoothers, thereby modelling an interaction between lake type and DOY: a
smoother representing the linear trends of alpha in lakes with landlocked alewives and in lakes without
alewives; and a smoother representing the nonlinear trend of alpha in lakes with anadromous alewives.

presentation by weighted centred moving average, the events in diet patterns appears earlier and

stretches longer in the graph than in the actual data and hence the diet transitions should be regarded

only as trends. The prey items found in diets were often greatly dissolved and accurate species

determination was therefore rarely possible. However, skin colouration suggested that many were

juvenile bluegill.
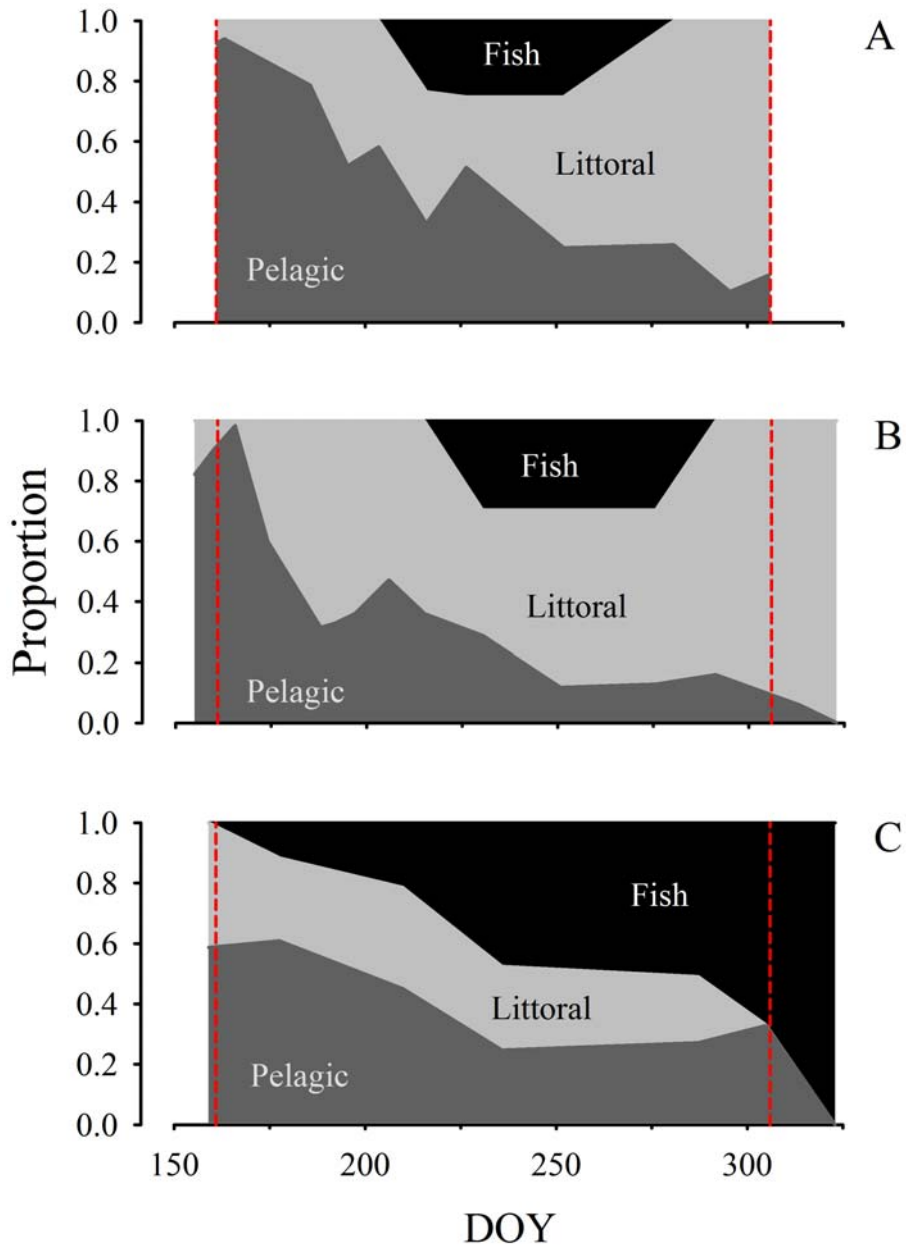
Figure 4: Illustration of the proportional trends in stomach contents for YOY LMB over the experimental period for from lakes with landlocked *A* and anadromous alewives *B* and lakes without alewives *C*. Stomach contents are illustrated as dry mass proportions of invertebrate prey, according to the food web association (pelagic and littoral), and piscivory. The trends in diet are smoothed by weighted centred moving average. The broken vertical lines represent the shared reference period.

Discussion

There is considerable variation in the availability of zooplankton for YOY LMB among our three lake types (Post et al. 2008). There are more large-bodied zooplankton in summer in NA lakes than in lakes with alewife, and more large-bodied zooplankton in the spring and early summer in AA than LLA lakes (Post et al. 2008). We found that the ontogenetic trajectories of young-of-the-year (YOY) largemouth bass (LMB) are different between lake ecosystems with the incidence of landlocked (LLA), anadromous alewife (AA) and no-alewife (NA).This was evident from differences in growth, trophic position (TP), food web use (alpha) and diet. Our results therefore suggest that intraspecific variation in alewife, a specialist planktivore, influence the zooplankton level and that this has further effects on the ontogeny of concurrent species.

Early growth is largely dependent on zooplankton availability (Persson et al. 2000; Hoxmeier et al. 2004; Milstein et al. 2006). Therefore the greater availability of zooplankton prey in spring and early summer in AA compared to LLA lakes is likely to provide a growth advantage that explains the relatively faster growth of YOY LMB in AA lakes. Furthermore, early growth differences affects the ontogenetic trajectories (Olson 1996; Parkos & Wahl 2010) and hence is potentially the causing the greater rate of increase in TP in AA lakes relative to LLA lakes. Faster initial growth of may additionally explain the more pronounced shift to littoral macro invertebrate prey, indicated in the diets and food web affiliation relative to LLA lakes, as this shift depend on gaining a size advantage over the prey (Werner 1977; Mittelbach 1981). This is further corroborated by the more rapid increase in TP in AA lakes, compared to LLA lakes, as the benthic invertebrate prey included many larger predatory species. Hence, our results show that life the history of a dominant planktivore species affects interspecific interactions and suggest that this is mediated though differences in zooplankton availability in the spring. This affects early growth of LMB and

prevents them from gaining a size advantage to make the shift to larger preys, resulting in delays in further growth and a slower increase in TP.

The abundances of large zooplankton in NA lakes are generally higher in spring and especially higher in summer, compared to lakes with LLA and AA (Post et al. 2008). This greater availability of zooplankton in the summer may provide a relative growth advantage for LMB in NA lakes. Similar to the differences between LLA and AA lakes, finding the fastest growth and most rapid increases of TP in YOY LMB from NA lakes underlines the importance of zooplankton availability for early ontogeny and, furthermore, suggests an additional importance of the high summer availability of large-bodied zooplankton. Fast growth in the early ontogenetic stages is crucial for reaching piscivory (Olson 1996; Parkos & Wahl 2010), and the faster growth and increase in TP by LMB in NA lakes were corroborated by these were the only lakes where piscivory became consistent within the study period. The observed short lived period of piscivory in LLA and AA lakes indicates that LMB in these lakes only had a size advantage over available fish prey in limited period of time and were unable to maintain this advantage. Therefore the differences in zooplankton abundance caused by both anadromous and landlocked alewives appears to reduce the probabability of LMB reaching piscivory in their first year, which may havea impacts on future growth and survival (Buijse & Houthuijzen 1992; Olson 1996; Ludsin & DeVries 1997). Additionally, such negative consequences can be expected to be greater with the incidence of LLA lakes where growth and increase in TP increase were the lowest.

The changes in food web affiliations of LMB from the three lake types are to some degree expected to be reflected in the proportions of the categorized food items (pelagic or littoral) from the diet analysis. In AA lakes there was agreement between the diets and food web affiliation for the first half of the study period. Both isotope data for food web use and diets showed pelagic decrease and littoral increase. For LLA and NA lakes, the decrease in pelagic and increases in

littoral and fish prey, respectively, amongst the food items of the diets was not evident in food web affiliation. Disagreements between food web affiliation and diet are difficult to pinpoint from our data. Diets only account for the immediate intake while isotopes provide a picture integrated over a longer period (Layman & Post 2008). Some of the disagreement may lie in the unknown food web affiliation of the fish prey occurring in diets and, furthermore, in the temporal resolution of our sampling, leaving gaps that are not accounted for, especially in diet data. Regardless, in concert these two methods add details to the effects of the presence and the life history types of alewives.

Alewives have strong impacts on zooplankton and these impacts differ among alewife life history types. Previous studies have shown that the competition effect from zooplanktivorous fish, reducing zooplankton size and biomass, can impact the timing of ontogenetic shifts in coexisting piscivore fish. We find that the presence of alewife and moreover the life history type of alewife influences the growth and timing of ontogenetic niche shifts in coexisting young-of-the-year largemouth bass. Alewife slows the rate of growth and the transition to piscivory and these effects were greater for landlocked and anadromous alewife. The differences in growth we observed in this study, and what we know about the system, suggests that alewife competition may cause growth related reductions in survival of LMB (Buijse & Houthuijzen 1992; Olson 1996; Ludsin & DeVries 1997). Early size differences are known to persist at later ages (Mittelbach & Persson 1998) and may result in differences in fecundity which typically correlates with as adult size (Wooton 1990). Furthermore, fast growth enables reaching reproductive size at a younger age (Baylis et al. 1993). This might give an advantage in fecundity for LMB in NA lakes over AA lakes and then LLA lakes. However, when reaching piscivory, the growth of predatory fish is positively correlated to planktivore biomass (DeVries & Stein 1992; Olson et al. 1995; Hjelm et al. 2000), which may compensate for reduced survival and fecundity related to slow growth in early life. Thus, planktivore completion can result in adult piscivores populations with few but large specimens

(Werner & Gilliam 1984; Olson 1996). The presences of adult alewives may further reduce survival

by direct predation on the young juvenile bass (Werner 1977; DeVries & Stein 1992). The growth

differences established in this study may be associated with effects on future survival and translate

into differences in fecundity as well as shaping the size structure and abundance of the adult

population. The results presented in this study contribute to our understanding of the interplay in

predator-prey competition and, moreover, underlines the importance of considering intraspecific

variation in competition and ecosystem interactions.

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Ref Type: Journal (Full)

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MS III

Habitat specific avian predation on resident and lake dwelling brown trout (*Salmo trutta*)

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Abstract

Piscivores can substantially reduce prey fish abundances, especially in confined waterbodies such as lakes. In Lake Hald, Denmark, a decline in the number of spawning brown trout during the last 10 years coincided with increases in the numbers of nesting cormorant and heron in adjacent and nearby breeding colonies. The objective of this study was to evaluate the role of cormorant and heron predation in this decline. For this purpose juvenile trout in the tributaries was tagged with passive integrated transponder (PIT) tags from 2008-2010. Subsequently, their fates were followed one year forth from tagging. The tagged trout were assigned to specific habitats by registrations at automated listening stations. These data were subsequently combined with manual scans for tags in cormorant and heron colonies. These two measures provided habitat specific minimum predation estimates. The annual predation from both cormorant and heron was significantly higher in the lake habitat compared with the tributaries. There was no significant difference between cormorant and heron predations within the habitats. In the lake and the tributaries respectively, the average predation was 21,0% and 2.3% from cormorant and 16.2%.and 7.8% from heron. A study following 20 radio tagged trout over a 1½ month period, demonstrated that cormorant and heron , respectively predated 41% and 35% of the radio tagged trout from the lake habitat. This suggests that predation may be much higher than estimated on basis of the PIT experiment. The results indicated that cormorant as well as heron predation on lake dwelling trout is likely to play an important role in the decline of the trout population. Additionally, very low recapture rate of tagged trout in the tributaries suggests that predation is higher than that suggested from cormorants and herons. We suggest the presence other predators may play a substantial role in the tributaries. The spawning activity of the trout population is at a critically low level and we suggest possible management measures to alleviate the predation pressure in the lake as well as the tributaries.

Introduction

Brown trout (Salmo trutta) can take on a wide array of life history strategies involving freshwater residency and migrations as well as anadromy (Jonsson 1985; Jonsson 1989; Klemetsen et al. 2003). Lake Hald, located in the central part of the Jutland peninsular in Denmark, houses an indigenous landlocked brown trout population which for centuries has been sustained by reproduction of lake dwelling (potamodromous) and resident trout in the tributaries. The return of anadromous individuals has been impossible since the 15th century due to a downstream dam (Hansen et al. 1993). However, in spite of the population being landlocked, spring smolt emigrations have been reported until present day. Consequently, at least three different life history strategies are present in this brown trout population; residents, potamodromous and anadromous. Through the 1970's the trout population of Lake Hald was severely affected by poor conditions in both lake and tributaries, resulting in a genetic bottleneck due to low numbers of individuals (Jensen et al. 2005). Following wastewater treatment and restorations of the tributaries in the 1980's the spawning activity of the brown trout showed a dramatic increase up through the 1990's. However, from 1999 to 2010 the spawning activity declined to levels similar to the situation before the initiation of the wastewater treatment (Figure 1). The decline in spawning activity coincided with the arrival of cormorants (*Phalacrocorax carbo sinensis*) to the area and the establishment and growth of a breeding colony on the lake shore (Figure 1 & 2). The spawning activity of the trout population has been estimated by a yearly count of the large spawning redds dug by adult potamodromous trout (counted by the local anglers association) and hence suggest that a part of the explanation of the decline in spawning activity relates to the survival of the lake dwelling part of the population.
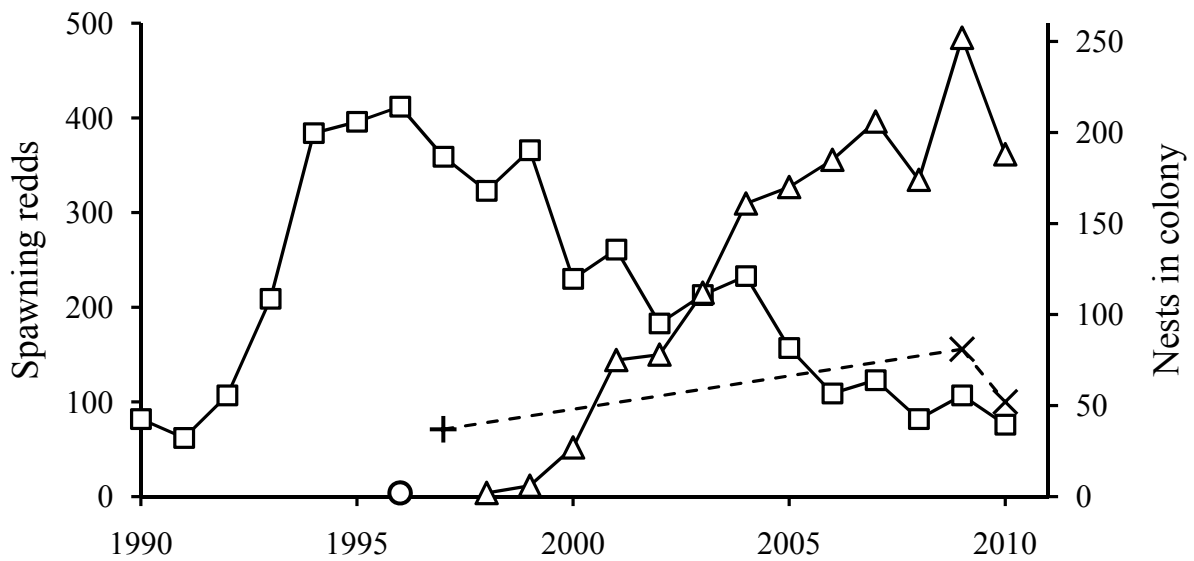
Figure 1: Time series showing the development in the total number of spawning redds (□) in the tributaries of Lake Hald, the number of nests in the cormorant colony at the lake shore (○ and Δ) and in the nearby heron colony(+ and ×). Spawning redds have been counted by the local anglers association. The registration of the first cormorant nests in the coloy (○) was done by Aage Ebbesen. Data on cormorant nest from 2000-2010 (Δ) was kindly provided by Thomas Bregnballe, Aarhus University.. The first count of the heron colony (+) was done by *Dansk Ornitologisk Forening* and years 2009 and 2010 (×) were counted in relation to the current study.

From being locally extinct in Denmark in the 1970's, cormorant numbers have increased dramatically subsequent to a general European protection of this species and many new colonies have since established (Bregnballe 1996). Observations of cormorants foraging at Lake Hald started in 1988 and the number increased through the 1990´s. In 1996 the first nests in the cormorant colony at the lake shore were observed (*personal communication Aage Ebbesen*). The number of nests has been counted once a year in the period 2000-2010 (*Thomas Bregnballe, unpublished data*) (Figure 1). Cormorants are known as skilful underwater predators and there are several examples from lakes in the US where the numbers of foraging double crested cormorants

(*Phalacrocorax auritus*) correlate with the abundances and longevity of sub adult yellow perch (*Perca flavescens*) and walleyes (*Sander vitreus*) (Rudstam et al. 2004; Fielder 2008; Dorr et al. 2010; Fielder 2010). Additionally, commercial landings can be greatly reduced by cormorants as seen in Lake Chiemsee, Bavaria (Klein 2000; Klein 2005). In eutrophic and turbid lakes, cormorants can adapt social fishing behaviour and targeting roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), smelt (*Osmerus eperlanus*) and ruffe *(Osmerus eperlanus)* and, thus, potentially serve as bio manipulators as they primarily target planctivorous species (Dirksen et al. 1995). In contrast to this, in oligotrophic clear water lakes the cormorants appear more as solitary hunters, preying more specifically on ell and trout (Denie 1995). Though Lake Hald is now reckoned as a clear water lake, both social and solitary foraging has regularly been observed and, furthermore, hunting cormorants have been observed in the tributaries, especially in winter (*personal communication Aage Ebbesen*).

The coinciding decline in the potamodromous brown trout population in Lake Hald and the cormorant increase, suggest that the cormorants play a role in the decline. However, there are several other piscivorous predators present at and in Lake Hald. These include a colony of grey heron (*Ardea cinera*) located 7 kilometres from the lake, which likewise has increased through the 1990's (Figure 1). Additionally, otter (*Lutra lutra*) and mink (*Mustela vision*; an invasive species) are also common in the area. Furthermore, several piscivorous fish species are present in the lake, for example pike (*Esox lucius*), burbot (*Lota lota*), eel (*Anguila anguila*) and adult lake trout which can prey on sub-adult trout. Piscivorous fish and mammals are known to reduce the abundances of their fish prey (Heggenes & Borgstrom 1988; He & Kitchell 1990; Findlay et al. 2000; Lindstrom & Hubert 2004).

Passive integrated transponder (PIT) tags been utilized to study individual migration behaviour and e.g. the dynamics and quantification of migrations between habitats (Olsson & Greenberg 2004; Skov et al. 2010). Furthermore, registration of PIT tags in colonies of piscivorous

birds have been used to provide stock and locality specific minimum estimates of predation from piscivorous birds (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Sebring et al. 2010). In the present study, we used PIT tag accumulations in colonies of piscivorous birds in combination with individual migration histories of PIT tagged trout to generate habitat specific predation estimates at Lake Hald. We estimated minimum predation from cormorant and heron on trout that were registered to reside in the tributaries and in the lake. We hypothesise that cormorant predation is substantial in the lake habitat and that this predation plays a causative role in the decline of lake dwelling brown trout.

Methods

This study was conducted in Lake Hald, Denmark (Figure 2), which drains into a branch of the river Gudenaa. Movements of tagged trout in and out of the two major tributaries, Dollerup and Mostgaard, and the lake outlet, Non Moelle, were monitored using PIT-technology (Zydlewski et al. 2001). The lake covers an area of approximately 342 ha and has a maximum depth of 31m. The lake outlet has had a weir and dam at least since the15th century (Hansen et al. 1993), which has made upstream migrations impossible. The major tributaries and the lake have been heavily polluted from several fish farms and from receiving untreated wastewater from a local town until 1985. Subsequently, wastewater discharge was stopped, fish farms in the tributaries were removed and oxygenation of the lake to lock phosphorous in the sediment was implemented. Additionally, restoration of the tributaries, including bypassing of remnant mill ponds, reinstalling spawning gravel in the tributaries was performed (Liboriussen et al. 2007). Hence, since 1985 the lake has been in a clear state until present.
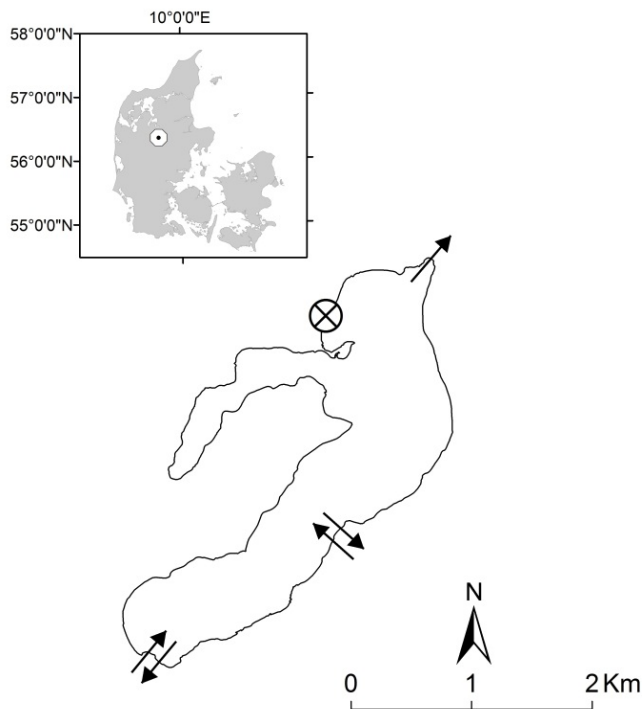
Figure 2: Schematic overview of the location of the research area at Lake Hald. Arrows indicate locations of PIT antennae in the tributaries and the lake outlet and the direction of registered movements. Crossed circle indicate the location of the cormorant colony. Additionally, a heron colony is located 7 km north east from the lake (not shown).

Juvenile trout were caught in the two major tributaries, Dollerup and Mostgaard, in summer and winter for three consecutive years; February 2008 (2008W), June/July 2008 (2008S), January/February 2009 (2009W), January/February 2010 (2010W) and June/July 2010 (2010S). Trout were caught by electrofishing and tagged with PIT tags (Texas Instruments, RI-TRP-RRHP, half duplex, 134 kHz, 23.1 mm long, 3.85 mm diameter, 0.6 g (air)). Before tagging, the trout were anaesthetized (benzocain 0.004 %) until operculum rate became slow and irregular (2–4 min). Trout were measured, weighed and tagged. Only trout with a total length exceeding 120mm were tagged. Tagging was performed by intraperitoneal insertion of the PIT-tag through a small (~5 mm) lateral-ventral incision approximately 10 mm posterior to the pectoral fins. The size of the incision allowed it to be left to heal without suture (Prentice et al. 1990). Additionally, in 2009 radio telemetry was utilized to further investigate the fate of the tagged trout. During the spring smolt migration, twenty trout with lengths >150mm were captured, in a smolt trap in the southernmost tributary, Dollerup,

and tagged with both PIT and radio tags. The fish were placed in a V-shaped surgical table and the transmitter was inserted into the body cavity through a mid-ventral 8–10-mm incision, posterior to the pelvic girdle. The antenna was run through a hole from the body cavity, pierced with a blunt needle. The incision was closed with two to three separate silk sutures. The duration of the operation was between 1 and 2 min. Recovery time was 2–5 min. The transmitters used were ATS internal smolt Model 377, weighing 1.7 g in air with an expected operation time of 35 days. Each transmitter had a unique combination of frequency/pulse-rate, making each tagged fish individually recognizable. The reliability of these tags is very high, and according to the manufacturer, failure rates are less than 1%. This is in accordance with our previous experience in the field and in the lab with this transmitter type. After recovery from tagging procedures of c.10 minutes, the trout were released to the same stretch of stream where they were caught. All tagged fish appeared to be in good health at release. Handling and surgery were performed in accordance with guidelines from the *Danish Animal Experiments Inspectorate*.

The habitat shifts between the tributaries and the lake were quantified by registration of PIT tagged trout through paired cross-stream-antennas (Zydlewski et al. 2001). The PIT system provided a setup with three compartments; the tributaries, the lake and down-stream the lake outlet. A habitat shift between the tributaries and the lake was defined as a trout passing through the two antennas and subsequently not registered at least 30 minutes. The emigration of trout at the lake outlet was quantified by registrations of trout on a single antenna positioned immediately downstream the one-way passage through the millpond spillway. The movement of trout were summarized over a year from tagging and calculated as the relative number of trout tagged for each tagging event that were registered in the three compartments of the PIT setup (Figure 3). As all tagged fish were caught, tagged and released in the tributaries, these served as the source compartment of all movements, and the lake and outlet sequence served as migration sinks in the

one or two-stage migrations. Recaptures on subsequent tagging events in the tributaries were noted and displayed as relative to the number that were registered to reside in tributaries. In the radio telemetry study, trout were tagged and tracked every 2 days over a period of 1½ month in the spring of 2009.

The breeding colonies of great cormorants and grey heron were scanned with a pole mounted PIT tag detector approximately every two weeks during the period of smolt migration, from March till June, and every two months the remainder of the year. The cormorant colony was scanned systematically by dividing it in transects marked with cords, whereas the scanning of the heron colony was less systematic due to dense undergrowth. To minimize the disturbance of the nesting cormorants, only the middle six transects (transect 4-10) were scanned on every scanning event, whereas scanning of the entire colony was done two or three times per year. The number of tags accumulating during the year following each tagging event was used as estimates of the predation for each tagging. Predation estimates were calculated as the percentage of trout from each tagging event that were registered as predated (Table 1). The individual PIT-tag codes registered within the bird colonies in combination with registration records from cross-stream PIT-antennas was used to determine which compartment a trout had been predated from (tributaries, lake or beyond the outlet). For each tagging session, habitat specific minimum predation estimates were calculated as the number of trout predated from a habitat relative to the total number registered in the habitat (Figure 4). To account for the effect of the accumulated tag density on detection efficiency (Ryan et al. 2008), we used the registrations of tags that were known to be present in the bird colonies, from earlier scanning events, to estimate scanning efficiencies for subsequent scans For this a Jolly Seber capture-recapture model was used (Ricker 1975). For scanning efficiency of the cormorant colony only the six central transects, that were scanned most frequently, were used for this estimate. For scanning efficiency of the heron colony, the scanning of the entire colony was

used. The colony specific average scanning efficiencies were used to adjust the minimum predation estimates (Table 1 & Figure 4).

For statistical analysis of predation (in percentages), ArcSin transformation was performed (Ricker 1975). To avoid low power of the statistical test due to low sample size, the explanatory variables included were limited to Bird species and Habitat, thus excluding Year and Tagging season (Winter/Summer). Statistical analysis was done following procedures of Zuur et al. (2009). The initial linear model contained the adjusted predation estimates as the dependent variable, explained by Habitat (tributary/lake) and Bird species (cormorant/heron) and their interaction as independent factors:

Predation Adj. = intercept + Habitat + Bird species + Habitat X Bird species + residual error

This model was fitted using Generalized Least Squares (GLS) model. A variance structure that allowed different variances between cormorants and heron was used in order to fulfil model assumptions. GLS models with and without variance structure, fitted using Restricted Maximum Liklihood (REML), were compared using Akaike information criterion (AIC). Subsequently, model reduction by backwards elimination was performed, using Maximun Likelihood (ML) estimation and a significance level of $p<0.05$ for main effects and $p<0.01$ for interactions as recommended by Zuur et al. (2009). The final model was refitted with REML and subsequently investigated for assumption violations. Model assumptions of residual homogeneity and normality were verified by graphical inspection plots. The statistical analysis were done in R version 2.12.1 (R Development Core Team 2011) using the nlme 3.1-97 package (Pinheiro et al. 2010).

Results

The number of trout that were available for tagging was generally highest in the winter, with exception of except 2010W, whereas the summer tagging numbers were lower (Table 1). The observed minimum predation ratios were adjusted according to the detection efficiency for tag registration in the bird colonies (Table 1); detection efficiency was 0.78 ±0.17 (Mean ± S.D.) in the cormorant colony and 0.35±0.18 (Mean ± S.D.) in the heron colony.

	Tagging		Cormorant minimum			Heron minimum		
Year	W/S	N	Obs. %	Adj. %	(± SD)	Obs. %	Adj. %	(± SD)
2008	W	1021	7.7	9.9	(± 1.6)	3.8	11.1	(± 2.0)
2008	S	410	3.7	4.7	(± 0.8)	2.9	8.5	(± 1.5)
2009	W	1170	6.6	8.4	(± 1.4)	4.8	13.9	(± 2.5)
2010	W	496	4.8	6.2	(± 1.0)	1.0	2.9	(± 0.5)
2010	S	505	2.2	2.8	(± 0.5)	0.0	0.0	(± 0.0)
	Average:		5.0	6.4	(± 2.5)	2.5	7.3	(± 5.1)

Table 1: Overall minimum predation estimates presented as the relative number (per cent) of tags from each tagging event (Naiman et al. 2002) found in cormorant and heron colonies after one year. Estimates are shown as observed values and as adjusted percentages with standard deviations. Adjustments were performed according to detection efficiencies with standard deviations 0.78 (±0.17 SD) and 0.35 (±0.18 SD) for the cormorant colony and heron colony, respectively.

The proportion of trout registered to remain in the tributaries, migrating to the lake and passing the outlet were summarized for a period of one year after each tagging event (Figure 3). Neither the proportion that migrated or was predated (overall or habitat specific) showed any significant correlation with the number of tagged trout (Pearson correlations; N=5, p>0.1). Beyond the lake outlet, cormorant and heron predation was very inconsistent and only trout from the taggings of 2008W and 2010W were found to have been predated. However, as this predation is of no

consequence for the potamodromous and resident population, due to the complete prevention of return migration, it will not be considered further in this paper.
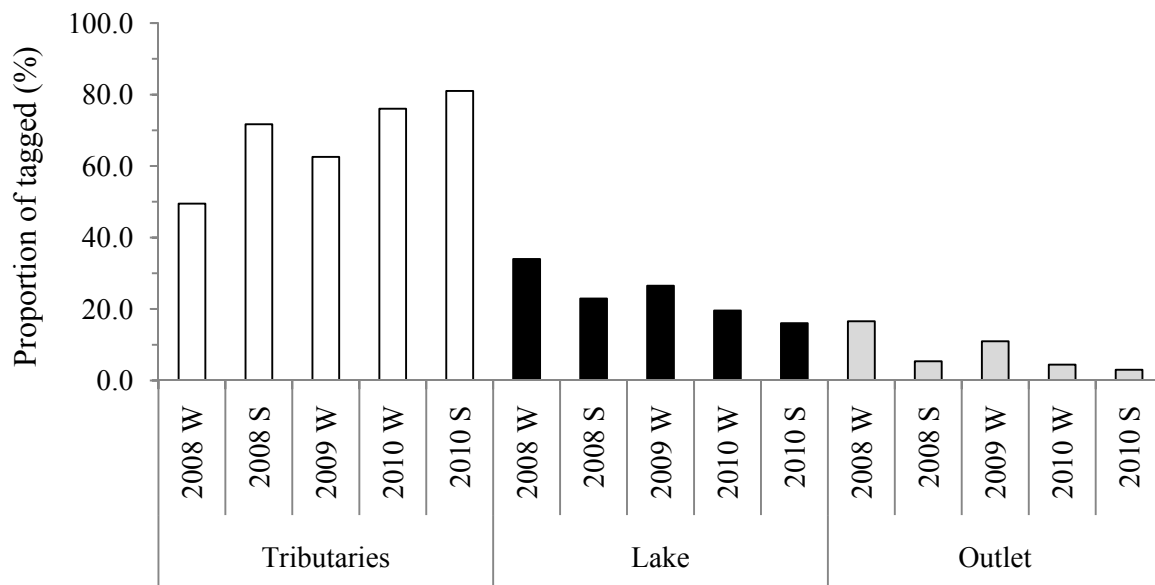
Figure 3: Summary of habitat registrations of trout to habitats one year from tagging. The registrations to the tributaries (white bars), lake (black bars) and the outlet (grey bars) are presented as the relative number (%) of the number tagged at tagging events in winter (Wada et al. 1993) or summer (Sabo et al. 2009) from 2008 to 2010.

The proportions that were predated from the lake and tributary habitats showed a consistent pattern. There was a significantly higher predation in the lake habitat compared with the tributaries in both cormorants and heron (Figure 4). Neither the interaction of "Habitat X Bird species" (GLS, p=0.15) nor the effect of "Bird species" (GLS, p=0.87) were found to be statistical significant and were consequently eliminated from the model. Thus, the final model contained only "Habitat", which showed a statistical significant predation difference between the tributaries and the lake (GLS, $F_{(1,18)}=56.92$, p<0.0001). In summary, the model indicates that the average adjusted predation within each habitat was not significantly different between cormorant and heron, but also

that predation was significantly higher in the lake compared to the tributaries for both the heron and cormorant colonies.
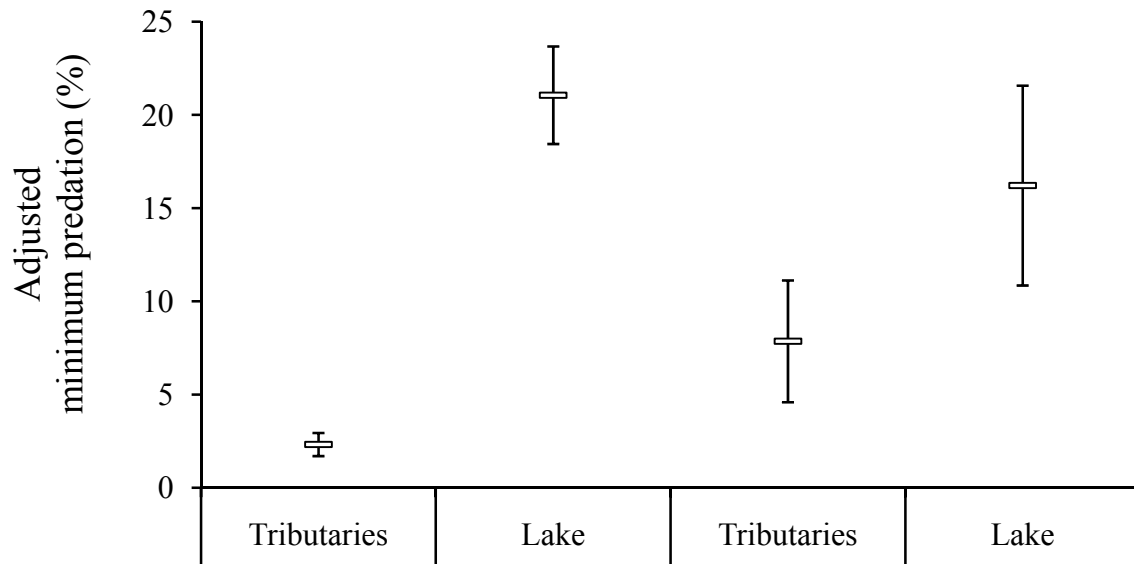
Figure 4: Annual average minimum predation for cormorant and heron in the lake and the tributaries. Predation estimates are presented as an average of five taggings. Error bars represent the standard error of the mean.

PIT tags have additionally been found inside pike and large cannibalistic brown trout caught by anglers in the lake. Furthermore, a tag was registered on the brink of the stream in mammalian defecates, presumably from mink or otter.

Recapture proportions at subsequent tagging events decreased rapidly within one and a half year from tagging and were generally much lower than what was registered to remain in the tributaries (Figure 5). The recaptures of trout that was registered to remain in the tributaries (Figure 3) were 5.6 - 33.3% half a year after tagging, 1.3 - 5.7% after one year and 0.14 - 0.34% after one and a half year. Thus, losses over time appeared to be quite substantial in the tributaries, but especially the half year recaptures suggest unusually high losses for the 2010W tagging (Figure 5).
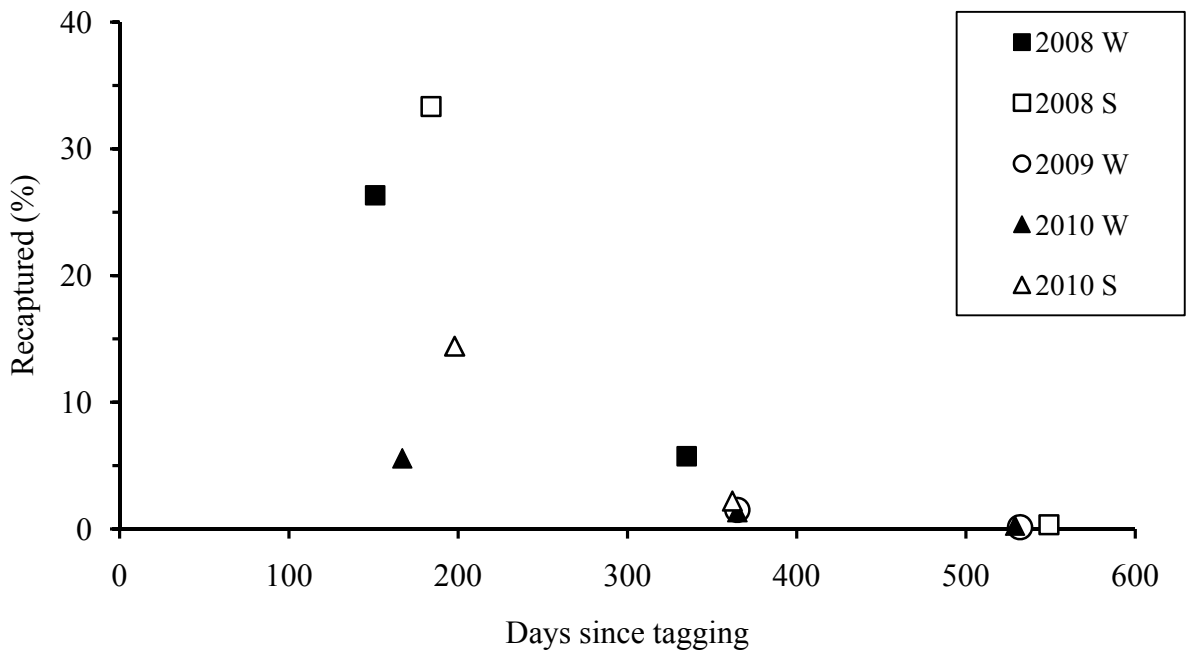
Figure 5: Recaptures from summer taggings and winter taggings approximately a half year, one year and one and a half year after tagging. Recaptures are presented as percentages of the number of tagged trout that were registered to remain in the tributaries from tagging events from 2008-2010 in winter (Wada et al. 1993) and summer (Sabo et al. 2009).

The radio tagging study lasted for 1½ month, from mid-April to the end of May 2009. Out of 20 radio tagged smolt, 17 entered the lake. From those that entered the lake, 6% exited through the lake outlet, 41% were found in the cormorant colony, 35% were found in the heron colony and 18% were last registered in the lake. Further, the radio telemetry study showed that trout were generally found in shallow water alongside the lake shore.

Discussion

In this study we evaluated the potential role of cormorant predation in the decline of the brown trout population of Lake Hald. We showed that the annual predation pressure from heron and cormorant on brown trout in the lake can be quite substantial. Our results illustrated that the minimum

predation from cormorants and heron was significantly higher in the lake habitat than in the tributaries and further that predation inflicted from these bird colonies were of similar magnitudes within habitats.

The adjusted predation estimates per tagging event were on average 6.4% for cormorant and 7.3% for heron. These estimates do not appear conspicuously high. However, in the present study we focused primarily on the habitat specific predation. For trout registered to the lake, cormorants alone accounted for an average predation of 21.0%. Similarly, high predation estimates for double crested cormorant, 22.9%, have been found on sub yearling Chinook salmon (*Oncorhynchus tshawytshca*) from the lower Columbia River (Sebring et al. 2010) by using PIT accumulation in colonies. This population contains both a river resident and an anadromous life history strategy (Narum et al. 2004). Sebring et al. (2010) attributes the high predation vulnerability of this particular population to having this resident strategy, which means that a greater number of individuals spend longer time in the area where predation occurs, relative to migrating salmonid in the same study for which predation was 1.30 - 2.96%. This suggests that salmonids populations with life history strategies residing high predation areas, like Lake Hald and the lower part of the Columbia River, are more vulnerable to cormorant predation, compared with migratory strategies. The predation estimates for cormorants found in the current study and those from Sebring et al. (2010) are the highest estimates we have found reported for estimation of predation using PIT technology. This confirms our hypothesis that cormorant predation in the lake was high. Interestingly, the heron predation averaged 16.2% in the lake and was not significantly lower than the cormorants. Heron predation of 8-10.8% have been reported for small fish farm ponds (Draulans 1988; Lekuona 2002) and our estimates might seem high since heron predation is restricted to the lake shore as they can only capture prey within 20 cm below the surface (Geiger 1983; Fischbacher 1983) and will only forage in water depths of up to c. 40 cm (Fischbacher 1983). However, our

radio telemetry study showed that trout in general were tracked along the lake shore and within the potential reach of herons, thus explaining their high predation success on trout in the lake. The predation from cormorants and herons may in fact be considerably higher. The predation on radio tagged smolt in the lake was as high as 41% from cormorants and 35% from heron over a 1½ month period. Furthermore, PIT tags from predated trout could be expelled outside the colonies and hence the estimates account only for a minimum amount. Regardless, the herons and cormorants collectively accounts for a substantial minimum mortality of trout in the lake.

Besides cormorant and heron predation in the lake, tagged trout was on a few occasions registered to be predated by pike and larger trout. Predation from piscivorous fish is not quantified in this study, and it may contribute considerable to the total trout mortality. Predation losses of trout have been found ranging from 77.0 - 81.5%, presumably from pike, but also with potential contribution from mink and herons (Olsson et al. 2001). Predation on salmon (*Salmo salar*) and trout smolts passing a Danish lake have been reported as high as 56% from piscivorous fishes and 31% from various piscivorous birds (Jepsen et al. 1998).

Our adjusted estimates of the minimum predation from herons in the tributaries were on average 7.9%. Of similar magnitude predation from grey heron has been estimated to 6.3% on trout in German streams (Geiger 1984), suggesting that the heron predation in the tributaries is not unusual high. We have found no literature quantifying cormorant predation in small streams as the tributaries in the present study. This may imply that predation from cormorant in small streams is rather limited or that it has not been investigated in detail. Channels are thought to be too narrow and shallow for cormorants to hunt efficiently (Rutscke 1998). However, we estimated adjusted cormorant predation in the tributaries to average 2.3%. This estimate verifies that cormorants forage

in the lower and wider stretches of the tributaries, which has been observed by locals (*personal communication Aage Ebbesen*). However, this predation appears to be relatively low.

Uncertainties remain about trout losses of trout from the tributaries. The low number of recaptures suggests that substantially more trout are removed from the tributaries than accounted for by the heron and cormorant predation. The recaptures , all < 6%, fall far below the annual survival previously reported for tributaries; e.g. survival for stocked salmon, 15-33% for age 1+ and 30% for age 2+, combined winter and summer survival (Letcher et al. 2002), and 13 % (±11 s.d) for 1+ trout (Egglishaw & Shackley 1977). Our survival estimates may be underestimated and/or there may be losses by predation. Besides predation from herons, both mink and otter are present in the area. We have no quantitative data on this except for one tag that was found in defecates, presumably from one of these two mammals. Although the magnitude of this predation is unknown in this study, the presence of these predators harbours potential losses for both juvenile trout as well as for spawning adult trout in the tributaries. Radio telemetry has shown river predation of 34% on brown trout a month after release, which most likely was caused by otter or mink (Aarestrup et al. 2005). The preferred prey of otters has been shown to be sub adult brown trout (Kortan et al. 2010), otherwise cyprinids if these are the dominant available prey (Jacobsen 2005). Salmonids occur most frequently in the diets of otters during autumn and winter (Jenkins et al. 1979; Wise et al. 1981) and consequently they may be targeting trout parr as well as spawning adults. Mink generally take less fish than otters as they prefer birds and mammals (Day & Linn 1972; Akande 1972; Dunstone & Birks 1987). However, in the winter season when the preferred terrestrial prey becomes scarce, their preference changes towards fish (Wise et al. 1981). In Norwegian streams, during periods where mink were present, the losses of stocked salmon and trout have been reported as high as 87% per month and in smaller streams 80% within few days (Heggenes & Borgstrom 1988). This, however, might be an extreme case, and more modest estimates of predation have been reported for mink, 8%

for cutthroat trout (*Oncorhynchus clarkii*) and 28% of brook trout (*Salvelinus fontinalis*) over a 5½ month period (Lindstrom & Hubert 2004). Additionally, adult salmonids in streams may be preyed upon by both otters (Carss et al. 1990) and mink (*personal communication Lene Jacobsen*).

Overall the predation from cormorant and heron in the tributaries was not unusually high in the current study compared with other studies. Heron and cormorants definitely take a share from the tributaries, but they are not expected to be the only predators to cause trout mortality in this habitat. In streams, the total predation from mink, otter, piscivorous fish and birds can produce mortalities in the range of 23-42% on juvenile salmonids (Olsson et al. 2001) and sometimes as high as 50-90% (Wooton 1990). The extent of the predation from other predators in the tributaries will remain unanswered until investigated further. There may, however, be indications of high alternative predation in the tributaries in the winter 2009/2010 (2010W). By Danish standards, the winter this year was very cold (Danish Meteorological Institute), resulting in a long lasting ice cover on the lake. This may have caused the tributaries to be the only foraging sites available for the piscivorous birds and mammals in the area (ex. mink, otter, heron and cormorant). This could potentially have led to increased predation in the tributaries, which could explain both the low number of trout available for tagging during winter and the low proportion of tagged trout leaving the tributaries as well as the low recapture rate from this tagging.

The estimates of heron predation for the taggings of 2010 stand out from the rest of the years. The predation from heron was almost absent from the winter tagging and totally absent from the summer tagging. This observation may comply with a numeric response to available prey (Peterman & Gatto 1978). The lower number of trout to prey on may not have attracted the herons to the same extent as in 2008 and 2009. However, the low predation may also relate to the low number of nests in the heron colony, suggesting low number of foraging heron this year. The absence of heron predation on the summer tagging 2010 may also be an effect of the herons leaving

their nests during July, whereby the risk of being predated and transported to the colony is low. While the trout emigration from the tributaries for the winter tagging 2010 was somewhat lower than the two previous winter taggings, the recapture rate half a year after tagging was the lowest registered in this study. The losses in the tributaries in 2010 were not believed to be attributable to herons and cormorants alone, thus giving additional suggesting the presence of other predators or increased natural mortality.

The effect of cormorant (*Phalacrocorax auritu*s) predation on local lake fisheries has been well documented (Rudstam et al. 2004; Fielder 2008; Coleman 2009; Dorr et al. 2010; Fielder 2010). Cormorant populations have been linked to declines of several fish populations; yellow perch (*Perca flavescens*) in Lake Huron, Michigan (Dorr et al. 2010), and yellow perch and walleye (*Sander vitreus*) in Oneida Lake, New York (Rudstam et al. 2004). Here the cormorant predation on sub adult fish was linked to decrease in recruitment to the adult fish populations (Rudstam et al. 2004). Similar to these examples, a decrease of the trout population and a concurrent increase of the cormorant population were observed in Lake Hald. Considering that cormorants were the latest arriving predator to the area and the rapid increase to a high number of nesting birds, it is likely that the arrival of the cormorants to the area has been the deciding weight on the scale, resulting in the decrease of the trout population of Lake Hald. Many resources have been invested in restoration of the area and in keeping the lake in the clear water state (Liboriussen et al. 2007). Both birds and trout are important to the local area. Trout, however, appears to be unable to maintain a thriving population under the current conditions. The decline may pose serious consequences on the genetic variability and hence the future adaptability of the population (Hansen et al. 2000). The trout population has already suffered a genetic bottleneck from the period before the restoration efforts at the lake (Jensen et al. 2005) and the registered spawning activity suggest that it has fallen back to this level. Therefore, we advocate that management efforts to increase survival of brown trout

should be considered. Future management efforts could include actively managing the size of the cormorant colony or reducing cormorant foraging by harassment as a measure of predation control. Examples from the U.S. illustrate the effect of alleviating the predation pressure from double crested cormorant (Coleman 2009; Dorr et al. 2010; Fielder 2010). The implementation of harassment programmes, reducing double crested cormorant foraging by 40% (Coleman 2009) and 90% (Dorr et al. 2010) was followed by immediate increases in the recruitment to lake fish populations. Potentially such an approach would also reduce foraging of herons. Furthermore, the eradication of the mink in the area could be intensified, thereby minimizing the predation from this invasive species in the tributaries.

In this study, the applied approach, combining movement records from PIT data with predation data, allowed assignment to the specific habitat where a tagged fish was predated. Although not accounting for all the trout losses, our results give a quantitative indication of habitat specific minimum predation pressures from cormorants and heron. This may help to direct management actions not only the trout population in Lake Hald, but also other valuable fish populations that find themselves in a similar situation. The trout population has reached critical numbers and we suggest that reducing predation by management implementations could be a solution.

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MS IV

Field based evaluation of the effect of 23 mm passive integrated transponder (PIT) tags on the length-mass relationship in wild juvenile brown trout (*Salmo trutta*)

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Abstract

This study evaluates the effect of surgically implanted 23 mm passive integrated transponder (PIT) tags on the length to body mass relationship of 403 juvenile wild brown trout (*Salmo trutta* L.) in the field. At the time of tagging the trout had a total length (L_T) from 120-184mm) and average tag-to-body-mass ratio of 2.69 ± 0.74 % (Mean ± SD). The effect of being tagged with 23mm PIT tags under natural conditions was evaluated for time periods of 97, 143, 192 and 328 days. The length to body mass relationship was compared between tagged and concurrently captured untagged trout of comparable sizes. The effect of treatment (tagged/untagged) and period, with log-length as covariate, on log-mass was analysed with an ANCOVA (GLM) approach. We found no effect on the length to body mass relationship from being tagged, indicating that tagged and untagged fish had managed equally well in the period leading up to the concurrent capture. However, we advocate more research on the effects of tagging under field conditions. Especially long term studies on survival and growth covering life stages from juvenile to adulthood, and studies on whether tagging affects vulnerability to predation.

Keywords; Body condition, Weight–length relationships, Tagging-effects, tag-to-body-mass ratio, Tagging-size, Telemetry, 23mm PIT tag.

Introduction

Telemetry is a powerful method for gaining insights into movements, distributions, migrations, home ranges and activity patterns of fish species (Cooke *et al.* 2004). For these observations to be valid the basic assumption is that capture, handling and tagging do not adversely affect the tagged individuals (Cooke *et al.* 2008). One branch of telemetry involves the use of passive integrated transponder (PIT) tags. These tags are a versatile tool in fisheries management (e.g. Aarestrup *et al.* 2003) and their use can be modified for behavioural studies of migration patterns (e.g. Skov *et al.* 2008; Svendsen *et al.* 2009); spatial preferences during migration (Svendsen *et al.* 2007); difference in habitat use (Teixeria & Cortes 2007); species interactions (Hirsh & Fisher 2008); and estimation of minimum predation (Antolos *et al.* 2005). PIT tags are small, relatively inexpensive and with potentially indefinite operational times, as long as they remain intact and, furthermore, since they are some of the smallest tags in use, they are also considered to have minimal effects on growth and survival (Zydlewski *et al.* 2003).

Handling during capture and tagging of fish, such as anaesthesia and tagging procedure, may have adverse effects (Jepsen *et al*. 2002; Thorsteinsson 2002) and must obviously be performed in a manner that minimizes such effects. If tagging affects the performance of a fish this can lead to reduced survival and growth (Jepsen & Aarestrup 1999; Koed & Thorstad 2001). Setting the limits for no effect of tagging depend on the species that is tagged (Navarro *et al.* 2006; Stakenas *et al.* 2009) and on the tag size relative to body-size or fish length. If the size of the fish is too small, relative to PIT tag size, survival and growth are reduced (e.g. Bateman & Gresswell 2006; Acolas *et al.* 2007), whereas no apparent negative effects are found on larger juvenile salmonids (Zydlewski *et al.* 2003; Ombredane *et al.* 1998).

PIT tags come in a variety of sizes and often the smaller tags (8-12 mm) are preferred as they facilitate tagging of smaller individuals. For salmonids, the majority of studies on tag-induced

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effects are based on the 11.5 and 12 mm tags (e.g. Ombredane *et al*. 1998; Navarro *et al.2006*: Acolas *et al*. 2007; Knudsen *et al*. 2009; Stakenas *et al*. 2009). Unfortunately, these tags have a rather short detection range. The larger tags, such as the 23 mm, are advantageous in studies where a larger detection range is needed, i.e. when migration behaviour is monitored by cross stream antennas (e.g. Skov *et al*. 2008; Svendsen *et al*. 2009). Adverse effects of implanting the larger PIT tags have generally been evaluated in laboratory experiments (e.g. Zydlewski *et al*. 2003; Bateman & Gresswell 2006). Test of possible tagging effects under laboratory conditions fail to reveal decreased competitive performance, predator avoidance, etc. Thus, evaluation of long-term effects of handling, tagging and carrying a transmitter is best studied when the fish remain in its natural environment. Here, negative effects imposed on the tagged fish leading to a reduced performance, should over longer periods influence growth and survival (Jepsen & Aarestrup, 1999).

The length-mass relationship, often referred to as body condition, is frequently used in ecological studies, and on a variety of species, where it has been correlated to reproductive investment, survivorship, habitat use (Green 2001) and quality of habitat (Amara *et al*. 2007). In herring, *Clupea harengus* L., body condition (i.e. Fulton's K) is correlated to the feeding success and it relates to the growth in the immediate past (Óskarsson 2008). Additionally, body condition correlates positively to survival time under stress in cutthroat trout, *Oncorhynchus clarki henshawi* (Richardson), (i.e. thermal stress) (Robinson *et al*. 2008). Hence influences which negatively affect the performance of a fish can be expected to influence body condition indices as well as growth. Accordingly, these measures can be used as relative proxies for individual performance in the period leading up to its capture/recapture. However, body condition indices may only be compared between groups of same reproductive status (Óskarsson 2008) and of similar size range (De Robbertis & Williams 2008). Body condition has been used for field evaluation of the effect of PIT tagging (23mm tags) of cyprinids, where no effect of tagging was found (Skov *et al*. 2005)

In the present field study the effect of tagging was assessed in juvenile brown trout (*Salmo trutta* L.) tagged with 23 mm PIT tags. Relative body condition was used as a proxy for individual performance, which was used to compare tagged and untagged trout caught simultaneously.

Materials and Methods

The study was carried out at Lake Hald in the central part of the Jutland peninsula, Denmark. This lake holds a landlocked population of brown trout, which use the several tributaries as spawning grounds. Juvenile trout for this study were caught on several occasions in the largest tributary running into the lake, the Dollerup tributary (February/March 2008, July 2008 and Jan/February 2009). Recaptures were done by electrofishing in January/February 2009 as well as by fyke net trapping in April 2009 and May 2009. At these sampling occasions a number of tagged and untagged fish were concurrently caught, which allowed comparison of body condition between tagged and untagged trout, in terms of body condition. The time from tagging until recapture resulted in four time periods, presented according to days since tagging, ordered increasingly from A, B, C to D, along with concurrently captured untagged trout (Table 1).

Tagging procedures

Upon capture trout were anaesthetized (benzocaine 0.004 %) and hereafter total length (L_T) and wet body mass (M) were measured. Subsequently, if L_T exceeded 120mm, they were tagged with PIT tags (Texas Instruments, RI-TRP-RRHP, half duplex, 134 kHz, 23.1 mm long, 3.85 mm diameter, 0.6 g (air)), which was performed by intraperitoneal insertion through a small lateral-ventral incision (c. 5 mm) approximately 10 mm posterior to the pectoral fins. The incision was left to heal without suture (Prentice, Flagg & McCutcheon, 1990). If previously tagged, their PIT tag was registered, fish were measured and weighed and the tagging incisions were inspected for abnormalities associated with tagging. After recovery of 5-10 minutes, the trout were released to the

same stretch of the tributary from where they were caught. Unlike the normal procedure, the individuals recaptured after period C were not weighed at tagging, making tag-to-body-mass ratio impossible to calculate for this group. Handling and surgery were performed by an experienced fish surgeon in accordance to the guidelines described in permission (2005/561-987) from the *Danish Ministry of Justice*.

Period	Measurements	Tagged			Untagged		
		Mean	*Std. Dev.*	*N*	*Mean*	*Std. Dev.*	*N*
A	**L_T (mm)**	146.9	15.3	44	138.3	14.0	50
Fyke net trap	**M (g)**	28.9	10.8	44	23.9	8.4	50
April 2009	**Tagged (days)**	97.2	8.4	44	-	-	-
B	**L_T (mm)**	166.3	15.0	16	157.8	12.4	21
Fyke net trap	**M (g)**	45.3	12.2	16	37.6	8.6	21
May/Jun 2009	**Tagged (days)**	142.5	20.4	16	-	-	-
C	**L_T (mm)**	148.5	14.4	98	140.8	15.5	117
Electrofishing	**M (g)**	30.7	11.2	98	26.4	9.9	117
Jan/Feb. 2009	**Tagged (days)**	191.8	11.9	98	-	-	-
D	**L_T (mm)**	199.5	23.0	22	191.9	22.2	35
Electrofishing	**M (g)**	80.0	29.7	22	70.1	25.6	35
Jan/Feb. 2009	**Tagged (days)**	328.0	14.8	22	-	-	-

Table 1: Data from tagged trout recaptured after four duration periods subsequent to tagging, **A**, **B**, **C** and **D**, and from untagged trout caught concurrently. Presented are measurements of total length (L_T *(mm)*), body mass (*M (g)*) and the mean number of days the recaptured fish had carried a PIT tag.

Data analysis

Considerations regarding the analysis of mass-length relationships were made according to

Green (2001) in combination with the advised caution in the use of allometric models, in relation to

comparing groups of fish over a broad size range (De Robbertis & Williams 2008). The effect of

tagging on the log-M was analysed by an analysis of covariance (ANCOVA, GLM approach). Log-

M was entered as the dependent variable with treatment (tagged/untagged) and period (A, B, C and

D) as fixed factors and Log –L_T as covariate. All interaction terms were included in the analysis.

PASW® Statistics 18 was used for statistical analysis (SPSS Inc., *http://www.spss.com*).

The tag-to-body-mass ratios at tagging were calculated for individuals in recapture period A, B

and D, not including C since there were no M at tagging for this group. Tag-to-body-mass ratio was

calculated as: ((tag-mass / M) x 100 %)

Results

Regressions for tagged and untagged trout ($R^2 > 0.90$), representing the four periods of carrying PIT

tags, are graphically illustrated in Figure 1 (A, B, C and D). The GLM explained 96.9% of the

variance (adjusted R^2). No significant effect of treatment (tagged/untagged) was demonstrated ($F_{1, 402} = 0.489$; $p = 0.485$). There was a significant effect of log-L_T on log-M ($F_{1, 402} = 5341.20$; $p < 0.001$), as would be expected with increasing fish sizes. Furthermore, there was a significant effect

of period on log-M ($F_{3, 402} = 8.652$; $p < 0.001$), showing that fish sizes between periods were

different. None of the interaction terms were significant (all $p > 0.172$) and hence no difference

between tagged or untagged fish was evident in the body conditions illustrated by the relationship

of log-M on log-L_T. At tagging, the recaptured individuals had mean tag-to-body-mass ratio of 2.69

± 0.74% (Mean ± St.Dev.), ranging from a minimum of 1.02% to a maximum of 4.55%. Already

after the shortest recapture period in this study (97.2 ± 8.4 days; period A), tagging incisions were
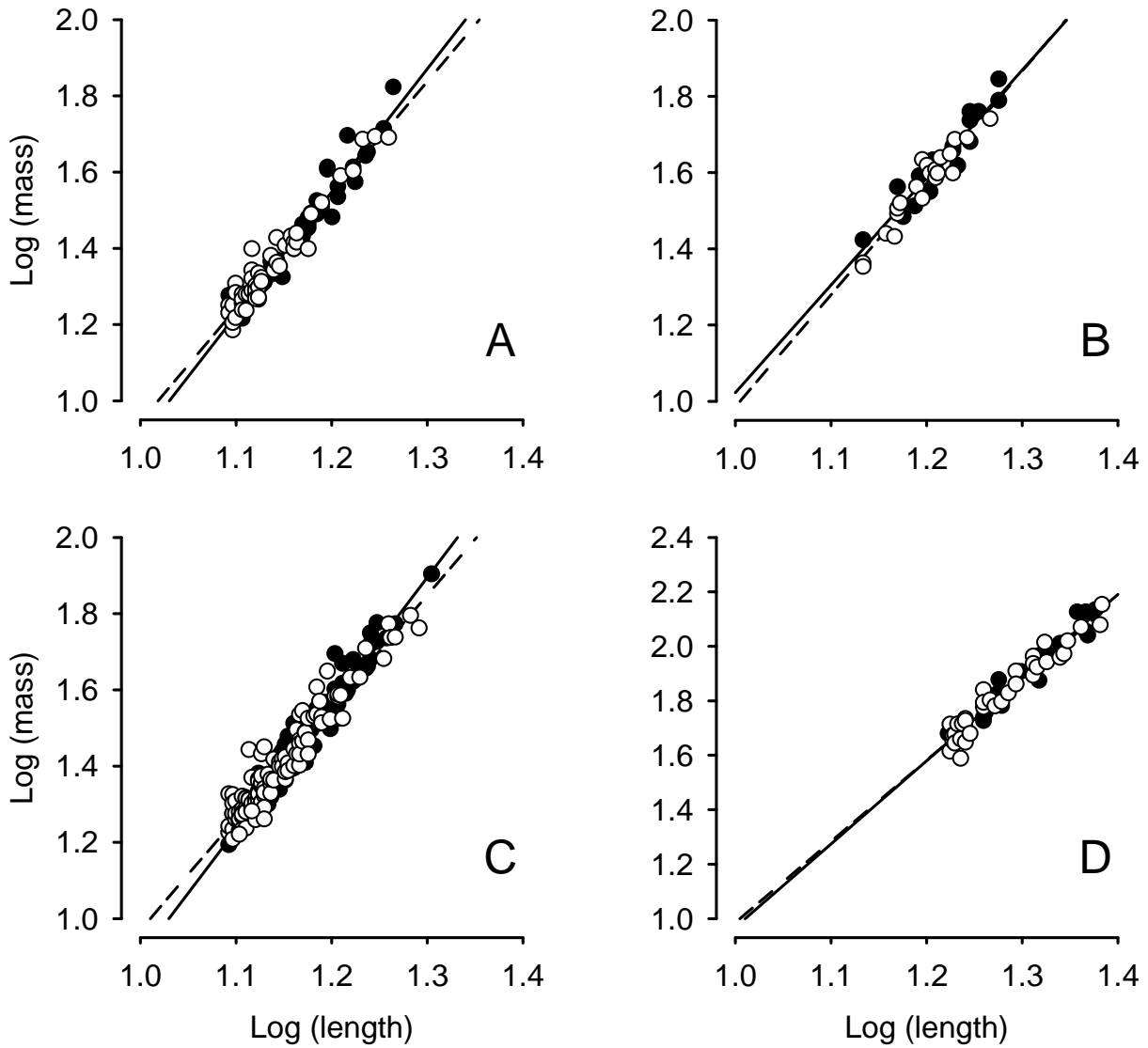
virtually traceless and visible scarring was rare.

Figure 1: Regressions of log-M on log-L_T for the duration periods **A**, **B, C** and **D**. The recaptured (tagged) group are illustrated by closed circles and the reference group (untagged) by open circles, the regressions are shown by solid and broken lines respectively ($R^2 > 0.903$).

Discussion

We found no differences between tagged and untagged trout in any of the time periods of the present study. This indicates that the long-term performance of the fish was not adversely affected from the tagging and handling procedures and from carrying a PIT tag. The tagged and untagged fish compared in the present field study were all in the same life stage and sizes and it was assumed that the tagged and untagged individuals in the groups had experienced the same or very similar environmental stressors and conditions in the time period prior to the concurrent captures.

The 2 % (air) tag-to body-mass rule (Winter 1983) is often used for of fish tagging to avoid adverse effects of tagging. However, using higher ratios than the 2% does not necessarily cause adverse effects and it depends on organism and study objective as well as tag and tagging methods (Jepsen *et al*. 2004). For example, evaluations of tagging effects on Atlantic salmon (*Salmo salar* L.) have neither shown effect on swimming capability at ratios of 6-12 % (Brown *et al.* 1999) nor on behaviour at tag-to-body-mass ratios from 2.4 - 4.3 % (Connors *et al.* 2002). Acolas *et al.* (2007) found that survival in brown trout, with fork lengths (F_L) down to 41 mm and tagged with 11.5 mm PIT tags, was positively correlated to body length over a period of 27 days and there was 99 % survival at body lengths $\geq$ 57 mm (F_L). In accordance with this, brown trout from 55 to 127 mm (F_L) tagged with 11 mm PIT tags show no tag induced effect on growth or survival over a period of seven months in their natural habitat (Ombredane *et al.*1998). The length limit of Acolas *et al.* (2007) was equivalent to a tag-to-body-mass ratio $\leq$ 3.4 %. This, along with the results presented in the current study, an average tag-to-body-mass ratio 2.69 $\pm$ 0.74 %, suggests that breaking the 2 % rule can be justified in intraperitoneal tagging of juvenile salmonids.

Laboratory findings on juvenile rainbow trout (F_L: 73-97 mm), tagged with 23 mm PIT tags, have shown negative effects on survival and growth 10-20 days after tagging (Bateman & Gresswell 2006). This, however, was compensated for within 30 days and was concluded to be an

apparent effect of tagging method and the tag to fish size ratio. It was further concluded that tagging salmonids of F_L < 90 mm with the 23 mm PIT tag would be associated with increased mortality. A particularly thorough study, with laboratory and field evaluation, primarily on rainbow trout (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*) (F_L: 100-150 mm), addresses the effects of different sizes of PIT tags (Zydlewski *et al.* 2003). They found no effect on survival or growth in juveniles with F_L > 100 mm tagged with various PIT tag sizes (12 mm, 20 mm, and 23 mm) over a period of seven months. We used a minimum length at tagging of L_T>120 mm for tagging with 23 mm PIT tags. Despite the difference in length measure (L_T and F_L), our minimum length for tagging is well above a F_L<90mm as suggested by Bateman & Gresswell (2006) and within the size range where Zydlewski *et al.* (2003) finds no effects. Hence, our field results are in good agreement with the results from two above studies. Though the recommended tag-to-body-mass ratio (in air) of smaller than 2 % (Winter 1983) was exceeded, a T_L >120mm and a tag-to-body-mass ratio around 2.69 ± 0.74 % appeared acceptable for brown trout. Of course we can only speak for the individuals that were recaptured.

Studies with tag dummies have shown quick resumption of normal behaviour and no adverse effects on swimming performance, using tag-to-body-mass ratios of c. 2.2% in juvenile salmon (Moore *et al.* 1990). Further, tagging is not associated with decreases in predator escape response, in blueback herring (*Alosa aestivalis*, Mitchill) (Dunning & Ross 2010), nor does it increase predation in brown trout, using tag-to-body-mass ratio of 1.7–5% (Jepsen *et al.* 2008b). This suggests that tagging does not lead to inferior performance and increased predation. Using tag-to-body-mass ratios of c. 2.4% and subsequently releasing brown trout to the field, had no effect on survival, but did, however, show reductions of growth five months after release (Jepsen *et al.* 2008a). This may have have consequences in the longer term, which has been indicated by negative

effects on size and fecundity in PIT tagged hatchery reared Chinook salmon (*Oncorhynchus tshawytscha*, Walbaum) returning as adults (Knudsen *et al.* 2009).

Most studies on tag effects fish are followed over relatively short periods, covering only a single life stage, our study included, and relating mostly to grow and survival. The effects of tagging over periods that cover different life stages (ex. from young to adulthood) as well as the influence on vulnerability to predation have received little attention and need to be addressed. Addtioanllay, most studies on tagging effects have been done in laboratory settings, which calls for more field based studies that covers more species, tag types and sizes of fish.

In conclusion, the presented results indicate that performance in brown trout $L_T > 120$ mm tagged intraperitoneally with 23 mm PIT tags were not adversely affected on the length-mass relationship, suggesting that the used combination of tags and fish sizes results in behaviour and survival that are representative of the untagged population. We advocate more that more field studies and laboratory studies on adverse effects on tagging and that these studies should cover the entire life span.

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Dansk Resumé

Denne afhandling omhandler livsstrategier hos ferskvandsfisk. I den forbindelse er der blevet foretaget undersøgelser af livsstrategier hos ørredbestanden i Hald Sø (Danmark) samt af samspillet mellem ørredaborre (largemouth bass) og flodsild (alewives), som udviser to forskellige livsstrategier i Connecticut (USA). En dansk ørred kan have op til flere livsstrategier, alt efter hvilke levesteder de udnytter, eksempelvis bækørred, søørred og havørred. Bækørred opholder sig hele livet i bække eller åer mens havørred vandrer ud i havet i perioder af livet, men vender tilbage til bækken for at gyde. Hald Sø er kendt for en god bestand af søørreder. Hald sø er dog et lukket system, hvor havørreder der forlader systemet ikke kan vende tilbage pga. en opstemning ved søens udløb. Den tredje livsstrategi, søørred, er mere sjælden, men her vandrer ørreden bort fra bækken og tager ophold i en ferskvandssø for at vokse sig stor inden den vender tilbage til bækken for at gyde. Dette studium omhandlede de tre ovenfornævnte livstrategier, som er at finde hos ørred bestanden i Hald Sø. Hos flodsild er livstrategierne ligeledes udtrykt ved migrationsforskelle. Naturlige - eller menneskeskabte forhindringer gør, at flodsild forhindres i at vandre til havet, som de ellers ville gøre. Således er der opstået bestande af flodsild som gennemfører hele deres livscyklus i søer. De bestande af flodsild som ikke bliver forhindret i at vandre, bruger havet som opvækstområde og søer til gydeområde.

Gennem deres liv, udfører mange fisk (og andre dyr) skift mellem flere levesteder, for til enhver tid at søge de optimale forhold i forhold til fødesøgning og formering samt at for at undgå at blive spist. I sidste ende har disse skift til formål at øge den samlede reproduktionssucces for den givne fiskebestand. Hos laksefisk kan man finde en del af forklaringen på hvorfor nogle individer vandrer og andre bliver residente i deres opvækstvandløb, i vækstpotentialet for det givne vandløb. Det vil sige, at føde forholdene skal passe til fiskenes fødebehov, hvilket varierer mellem livsstrategier. Opfyldes fødebehovet ikke, øges sandsynligheden for at en fisk vandrer. Laksefisk

som vandrer er karakteriseret ved at være mere dominante, have hurtigere vækst samt at have et højt stofskifte og dermed et større fødebehov i forhold til residente fisk. Dette er en fordel når der er rigeligt med føde i vandløbet. Derimod, hvis føden er begrænset, er det disse fisk som mærker sulten først. Vandløb har ofte en relativt begrænset fødemængde, derfor vandrer de fisk som på sigt, grundet deres stofskifte, ikke kan opretholde tilstrækkelig vækst under det givne fødeudbud. Ørreder som vandrer, forlader generelt deres opvækstområde som ungfisk i foråret, dette fænomen kaldes "smolt migrationen". "Beslutningen" om at vandre træffes allerede flere måneder i forvejen og er afhængig af at individet har opnået tilstrækkelig vækst i de foregående vækstsæsoner. Efter at "beslutningen" er truffet, styres vandringen og relaterede fysiologiske tilpasninger (smoltifikation) af faktorer såsom dagslængde forøgelse, temperaturstigning og vandføring.

Der findes som beskrevet ovenfor en del viden om hvorfor nogle individer af ørreder vandrer og andre bliver tilbage. Til gengæld findes der ikke megen viden om hvor nogle ørreder vandrer i havet (havørreder) mens andre tager ophold i søerne (søørreder). I den forbindelse blev nogle af de underliggende fysiologiske forskelle mellem bækørred, søørred og havørred undersøgt hos ørredbetenden i Hald Sø. Der blev indsamlet blodprøver og gællevævfra ørreder med forskellige livsstrategier. Endvidere, blev dermålt længde og vægt på disse fisk. Disse data blev brugt til at undersøge forskelle mellem bækørreder, søørreder og havørreder, ud fra en række fysiologiske og fysiske indikatorer for næringsstatus, stress, smoltifikation og vævsskade. Generelt kunne det ses at søørreder og havørreder ret ens på mange af de målte indikatorer. I forhold til de stationære bækørreder, viste begge de vandrende grupper indikationer for at være smolificeret samt indikation for at have lavere næringsstatus. Dette kunne tyde på at søørreder og havørreder havde været begrænset af føde i bækken, og derfor vandrer. Alternativt kunne en stor del af deres energireserver være blevet brugt i forbindelse med smoltifikationsprocessen. Der blev dog fundet en vigtig forskel mellem sø- og havørreder, som formodentlig er en vigtig brik i forklaringen på

hvorfor nogle bliver søørreder og andre havørreder. Sammenlignet med havørred, viste søørreder tegn på at have et lavere fedtindhold og dermed mindre energireserver. De mindre energireserver i forhold til ørreder som vandrer videre mod havet, kan være en forklaring hvorfor søørreder stopper vandringen tidligere, da denne vandring er forbundet energiomkostninger.

For at undersøge hvordan ørrederne i Hald Sø vandrede og dermed deres fastslå deres livsstrategier, blev ørrederne mærket med såkaldte PIT-mærker. PIT-mærker er en slags elektroniske mærker, som placeres i bughulen af fiskene. PIT-mærker kendes også fra dyrlægens mærkning af hunde og katte, og er blandt andet kendetegnet ved, at hvert mærke har sin egen unikke kode. Således kan man efter mærkningen genkende hver enkelt ørred og herunder observere individuelle vandringsmønstre ind og ud af søen. Dette sker vha. dataloggere som blev opstillet i samarbejde med lodsejere og Skov- og Naturstyrelsen. Disse var placeret i tilløbene fra Dollerup Møllebæk og Mostgård Bæk samt i udløbet ved Non Mølle. I forbindelse med brugen af PIT-mærkning blev det samtidig undersøgt om mærkningen skulle have en utilsigtet negativ indflydelse på ørredernes ve og vel. Fisken ve og vel måles ofte på deres konditionsfaktor, som er et mål for vægten i forhold til længden. En høj konditionsfaktor betyder at fisken er relativ fed i forhold til en given længde og indikerer at en fisk har klaret sig bedre end en med relativ lavere konditionsfaktor. Dette forhold mellem længde og vægt blev brugt til at sammenligne PIT-mærkede ørreder, som blev genfanget, med umærkede ørreder fanget ved samme lejlighed. Her blev der ikke fundet nogen forskelle i konditionsfaktor mellem de to grupper af fisk, hvilket viste at de PIT- mærkede fisk havde klaret sig ligeså godt som dem uden PIT-mærker. De mærkede fisk så altså ikke umiddelbart ud til at være blevet påvirket negativt af mærkningen.

I Hald Sø er der gennem de senere år observeret en markant tilbagegang i fangsterne af søørred samt i antallet af gydebanker i søens tilløb. Det er muligt, at tilbagegangen i bestanden er relateret til en nærliggende og støt voksende skarvkoloni, som er etableret gennem de senere år,

samt til en fiskehejrekoloni et stykke derfra. Derfor blev der i dette studium kigget på hvor mange

ørreder som skarv og fiskehejre spiser fra bækkene og søen. Omfanget af fuglenes prædation på

ørredbestanden blev undersøgt ved at scanne skarv- og fiskehejrekolonierne for de førnævnte PIT-

mærker, som efter en tur gennem fuglens maver ender på jorden under rederne. De fundne mærker

kan præcist tilbageføres til individuelle fisk og deres vandringsmønstre, hvilket gjorde det muligt, at

se om en fisk var blevet spist fra bæk eller sø. I løbet af et år blev 21,2 % af ørreder i søen spist af

skarv og 16,2 % af fiskehejre. I alt blev 37,2 % af ørrederne i søen således spist af skarv og

fiskehejre. Dette er minimumsestimater, dvs. andelen af spiste ørreder kan i realiteten være noget

højere, da det ikke kan forventes at alle ørreder som bliver spist ender under fuglenes reder. F.eks.

kan skarv og fiskehejre have gylpet mærkede fisk op, eller have haft afføring over et stort område,

udenfor det som bliver scannet. Radiotelemetri blev benyttet til at lave supplerende undersøgelser af

omfanget af prædationen fra skarv og hejre. I foråret 2009 blev 20 ørreder mærket med

radiosendere og deres bevægelser blev derefter fulgt i 3-4 uger. Radiotelemetrien viste at 41 % af

ørrederne som vandrede ud i søen endte i skarvkolonien og at 35 % endte i fiskehejrekolonien.

Dette supplerede PIT-mærke data og indikerede, som forventet, at prædationen er noget højere end

anslået ud fra PIT-mærke undersøgelsen. Undersøgelsen peger således på, at skarv og fiskehejre gør

et betydeligt indhug i ørredbestanden ved Hald Sø, og at det er sandsynligt, at udvikling af

skarvbestanden ved søen har været stærkt medvirkende til nedgangen af søørrederne. Mens skarv og

hejre tager for sig af retterne i søen, så er ørrederne mindre udsat i bækkene hvor den årlige

prædation i bækkene var 2,3 % fra skarv og 7,8 % fra fiskehejre, altså noget laver end den

tilsvarende prædation fundet i søen. Der blev ved en efterfølgende undersøgelse af bækkene fundet

færre PIT-mærkede ørreder end forventet, hvis kun skarv og hejre skulle stå for prædationen. Dette

kunne indikere, at der er andre fiskespisende rovdyr som tager ørrederne i bækkene. Der er

konstateret en bestand af både mink og odder i området ved Hald Sø, og det er kendt fra andre

undersøgelser at disse to arter kan gøre store indhug i ørredbestande. Ørreden er generelt er en vigtig art for sportsfiskerne i Danmark. Samlet set har dette studium tilføjet betydelig ny viden om biologien hos søørreder, hvilket har forbedret mulighederne for at lave for at lave målrettet forvaltning af disse bestande.

Den del af dette studium som foregik i Connecticut (USA), omhandlede hvordan livsstrategier hos flodsild har forskellig betydning for opvæksten hos sameksisterende ørredaborre. Flodsild er en fisk som er specialiseret i at æde dyreplankton og findes i Connecticut-området med to forskellige livstrategier, en vandrede form og en ikke-vandrende form. I søer hvor der findes ikke-vandrende flodsild, er dyreplanktonet græsset ned året rundt, så der kun er små zooplanktonarter tilstede. I søer hvor der er vandrende flodsild, og disse derfor kun tilstede i søen en del af året, er der mange store dyreplanktonarter i det tidlige forår. Disse bliver græsset ned henover foråret og den tidlige sommer, når de vandrende flosild ankommer fra havet i det tidlige forår for at gyde i søerne. Fiskeyngel fra næsten alle fiskearter er i starten af deres liv afhængige af dyreplankton, for hurtigt at kunne vokse sig store og derved minimere risikoen for at blive spist. Man kan således forestille sig at der i søer, med ikke-vandrende flodsild, er så hård fødekonkurrence om dyreplankton, at andre fiskearter klarer sig dårligere end i søer med vandrende flodsild. På den baggrund blev det undersøgt hvordan de to livstrategier hos flodsildene påvirker den tidlige opvækst hos ørredaborre. Som voksne fisk er ørredaborre er en rovfisk og ligger i toppen af fødekæden, og de skulle gerne nå en størrelse hvor de kan spise andre fisk i løbet af den første vækstesæson. Ynglen fra ørredaborre, klækkes i det sene forår og kan have det svært hvis konkurrencen om føden er hård. Dette har betydning for ørredaborre, eftersom forsinkelser i deres vækst mindsker sandsynligheden for, at de kan opnå en størrelse det første år hvor de er store nok til at kunne lave det endelige fødeskift til fisk. Dette er et vigtigt fødeskift, da det både øger den videre vækst samt sandsynligheden for at overleve den første vinter. Undersøgelsen viste, at ørredaborre

klarede sig bedst i søer hvor der slet ingen flodsild var. Her var væksten hos ørredaborre så høj at de

opnåede det vigtige fødeskift til fisk inden deres første vinter. Uanset om det var vandrende eller

ikke-vandrede flodsild som fandtes i søerne, medførte det at ørredaborre voksede langsomt og de

opnåede ikke fødeskiftet til fisk i løbet af første år. Når der var flodsild tilstede trivedes

ørredaborren bedst i de søer hvor flodsildene kunne vandre, sammenlignet med søer hvor de ikke

kunne vandre. Dette viste sig ved, at ørredaborre i søer med ikke-vandrende flodsild var mere

forsinket i vækst og fødeskift end dem i søer med vandrende flodsild. Undersøgelsen illustrer, at

fiskearter påvirker hinanden og, som svar på undersøgelsens primærer spørgsmål, at forskellige

livsstrategier hos den ene art kan have forskellige konsekvenser for en anden art. Altså, livstrategi

er en vigtig faktor i samspillet mellem arter. Ørredaborre har stor rekreativ og kommerciel

betydning for fiskerne i Connecticut. Den viden som er blevet tilvejebragt ved denne undersøgelse

har givet en bedre forståelse for, hvilke biologiske forhold der bestemmer om der er mange eller få

fisk at fange. Dette er således et godt eksempel på, at forståelsen af de biologiske forhold er central i

forbindelse med forvaltningen af fiskebestande.