BEHAVIOURAL CAUSES AND CONSEQUENCES OF SEXUAL SIZE DIMORPHISM IN AN APEX PREDATOR SPECIES

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Behavioural causes and consequences of sexual size dimorphism in an apex predator species

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ABSTRACT

Individual differences within populations in a range of phenotypic traits are hypothesised to have important ecological and evolutionary implications. Variation in individual growth rates that result in corresponding variations in body sizes, including size dimorphism, is a particularly widespread feature of many animal populations. The increasing characterisation of consistent individual behavioural variations, unrelated to age or sex, is equally considered to have important fitness consequences. Our understanding of behavioural causes of size dimorphism remains weak, and few studies have investigated the relationship between individual behavioural consistency and growth variations in size dimorphic populations. The overall aim of this thesis is to identify the behavioural drivers that underpin observed growth variations and result in size dimorphism by using pike (*Esox lucius*) as a model species.

The results show that early life growth is an important driver of sexual size dimorphism in this species. A subsequent focus on the juvenile life stages revealed that individual differences in movement and dispersal tendencies were related to growth and body size in wild pike. The findings indicate that intraspecific interactions such as size-dependent interference competition during the first year of life plays a key role in maintaining intraspecific size variation and size dimorphism in the wild population. Experimental work revealed the occurrence of a behavioural syndrome, where the rank order differences in the foraging behaviour between individuals were maintained across time and risk situation. This suggests that individual competitive ability is underpinned by a variation in boldness to forage under risk. The importance of a heterogeneous environment and presence of intraspecific competition pressure for driving habitat and resource segregation, and subsequently sexual size dimorphism, is discussed.

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I confirm that the thesis is my own work with the following exception:

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Chapter 1

General introduction

1.1 INTRASPECIFIC PHENOTYPIC VARIATIONS: CAUSES AND CONSEQUENCES

Individual phenotypic variation is a prerequisite for natural selection on any trait within a population (Darwin 1859). At the population level, phenotypic variation is diverse, ranging from morphology to behaviour, and along continua of increasingly discrete variation (Magurran 1993; Bolnick et al. 2003). Furthermore, various phenotypic traits are often interlinked and impacted by each other (Magurran 1993). In comparison to the occurrence of discrete phenotypes in a population, for example, polymorphism and alternative behavioural strategies (Maynard-Smith 1982; West-Eberhard 1989; Smith & Skulason 1996), less discrete and continuous individual variation has been considered as noise around either an adaptive mean or an optimal response, with the average of an individual often considered sufficient to describe a population (Ringler 1983; Lomnicki 1988).

Recently, there has been increasing interest in describing these differences between individuals in populations, with a particular increase in studies examining the consistency of individual differences in behaviours (e.g. Bolnick et al. 2003, 2011; Sih et al. 2004a; Dall et al. 2004; Reale et al. 2010). It is hypothesised that individual behavioural differences are associated with differences in the state (e.g. age, size or morphology, energy reserves) that are relevant for individual’s behavioural choices that are related to fitness (Houston & McNamara 1999; Clark & Mangel 2000). Among states, intra-population variation in body size, including size dimorphism that may occur within or between the sexes, is particularly evident in a number of animal species (Uchmanski 1985; Blanckenhorn

2005). Early life growth trajectories may drive the behavioural repertoire later in life through the association between individual behaviour, growth and body size (McNamara & Houston 1986). Thus, an understanding of the relationship between individual behaviour and size variation constitutes a key factor in elucidating the processes influencing the development of size dimorphism in a population.

In this introductory chapter, the ecological importance of body size and sexual size dimorphism are explained, with identification of the factors underpinning variation in growth. This is followed by an overview of the widespread occurrence of consistent behavioural variation, with a focus on personality traits and individual niche use, and subsequently, the theory of state-dependent behaviours (*cf.* Section 1.3). The use of pike *Esox lucius* L. as a model species to test hypotheses to identify the behavioural variation underpinning body size dimorphism is then explained. Finally, the aims, objectives, and structure of the thesis are outlined.

1.1.1 Importance of body size at the individual level

Variation in individual growth rates that result in corresponding variations in body sizes is a widespread feature of many animal populations (Uchmanski 1985; Sebens 1987; Huston & DeAngelis 1987; Persson & De Roos 2007), including captive cohorts reared in equal and controlled conditions (Stamps 2007). The body size of an individual is one of the most important traits in many species given its substantial effects on ecological interactions and key life history processes (De Roos et al. 2003; Persson & De Roos 2007). These include, for example, metabolic requirements, food choice, foraging rate, growth rate, ontogeny and reproductive traits (Werner & Gilliam 1984; Sebens 1987; Cohen et al. 1993; De Roos et al. 2003; Brown et al. 2004; Kingsolver & Pfennig 2007). Larger individuals within populations can often handle larger food items through their higher gape size and/or bite force and so are likely to successfully capture more prey or more energetically beneficial prey types (Werner & Gilliam 1984; Nilsson & Brönmark 2000; Galarowicz & Wahl 2005; Woodward & Warren 2007).

Consequently, for many species, predation vulnerability is associated with body size, both of the prey and its potential predator (Werner & Gilliam 1984; Polis 1988; Paradis et al. 1996; Claessen et al. 2000).

The competitive ability of an individual is often also influenced by its body size, and particularly how body size changes with ontogeny (Balon 1993). The ability to compete is defined as the capacity of an individual to share limited resources to depletion and have positive growth at low food densities (Werner & Hall 1988; Werner 1994). In turn, predation, predator avoidance and competition regulate intra- and interspecific interactions, population dynamics, and thus shape community structure within food webs (De Roos et al. 2003; Cohen et al. 2003). Furthermore, size variations may affect important ecological processes such as cohort survivorship (Rose et al. 1999), extinction risk (Kendall & Fox 2002; Pfister & Stevens 2003), and migration (Chapman et al. 2011). Although body size is clearly a key factor in the ecology of species and populations, individual variations in body size have been largely ignored in theoretical and empirical research (Lomnicki 1988; Peacor & Pfister 2006). Such an approach is ultimately inconsistent with a Darwinian view that stresses the importance of variation among individuals (Persson & De Roos 2007). Thus, this focus on population means that rarely considers individual variation limits the ecological utility of using these traits in studies and inhibits understanding of the underlying processes and mechanisms that cause the variation.

1.1.2 Sexual size dimorphism

A common and distinct type of size variation in individuals within populations is sexual size dimorphism, referred to hereafter as SSD (Shine 1989). In species where this is apparent, either one of the sexes is generally larger in body length or mass (inter-SSD) and/ or two morphs of different sizes exist within one or both of the sexes (intra-SSD) (Blanckenhorn 2005). Most animal populations tend to show some degree of SSD, but its direction (female or male-biased) varies between taxa, while its degree (the size of the divergence) may also vary among populations of the same species (Arak

1988). The degree of inter-SSD is believed to increase when males are the larger sex and decrease when females are the larger sex (Rensch’s rule: (Rensch 1959; Fairbairn 1997).

Female-biased SSD is the common pattern among invertebrates and cold-blooded vertebrates, whereas males are the larger sex in most birds and mammals (Andersson 1994a; Abouheif & Fairbairn 1997). In cold-blooded organisms, clutch size and, in some instances also egg or offspring size, increase with the body size of females (Shine 1988; Roff 1992; Stearns 1992; Preziosi et al. 1996). This strong selection for fecundity in females is therefore a likely reason why female invertebrates and cold-blooded vertebrates attain larger body sizes than males (Ghiselin 1974; Salthe & Mecham 1974; Andersson 1994b; Legrand & Morse 2000). In warm-blooded species, it has been suggested that fecundity selection may not be as strong. This is because larger females do not necessarily produce more offspring, although these tend to be better quality offspring (Cluttonbrock et al. 1982, 1988). By contrast, male size is affected by sexual selection where larger sized males tend to have a reproductive advantage in obtaining mates in female-choice strategies or male-male competitions (Andersson 1994b). This has been found to be the case in most animal taxa ranging from insects (e.g. Blanckenhorn 2007) and spiders (Legrand & Morse 2000) to higher vertebrates (cf. Fairbairn et al. 2007).

While evidence for selection favouring larger body sizes in both females and males is well-documented (e.g. Thornhill et al. 1983; Simmons 1986; Shine 1990; Schutz & Taborsky 2005; Clutton-Brock & McAuliffe 2009), the possible advantages of small body sizes are rarely mentioned (Bisazza & Marin 1995; Blanckenhorn 2000). Within males, size dimorphism is often linked to a difference in reproductive tactics, for example, large fighters and small sneakers (Taborsky 1999). The small-sized individuals have long been considered to ‘make the best of a bad job’ because they are assumed to have minimal opportunity to reproduce due to their lower ability to fight than larger individuals, thus causing reduced fitness. However, evidence for equal fitness through frequency-dependent selection has been documented, which explains why the size divergence is maintained through time (Maynard-Smith 1982; Gross 1985).

SSD has been studied most extensively in invertebrates, particularly in insects and spiders (Fairbairn et al. 2007). Among vertebrates, mammals and birds are the most studied, while lower vertebrates with indeterminate growth, where intra-SSD is particularly common, have been less studied (Taborsky 1999; Fairbairn et al. 2007). Animals that grow throughout their lives experience a trade-off in resource allocation between growth and reproduction (Stearns 1992; Heino & Kaitala 1999). Fecundity usually increases with body size in animals with indeterminate growth and so a trade-off between current and future reproduction also exists (Heino & Kaitala 1999). Although SSD is frequently associated with differences in age at maturity, survival, longevity, habitat use and diet (Fairbairn et al. 2007), the mechanisms that give rise to SSD in general are particularly poorly understood in vertebrates, in contrast to the behavioural consequences in adults (John-Alder & Cox 2007). While studies of SSD have tended to focus on the adult phase of the life-cycle, the influence of early life history on the formation of intra-SSD is usually overlooked (Fairbairn et al. 2007).

1.1.3 Growth rate

The SSD of a given species is largely determined by differences between and/or within the sexes in development time and/or growth rate (Blanckenhorn 2005). As with the plethora of evidence for the advantages of larger size, it is assumed that life history strategies that maximise growth should be advantageous, at least until reproductive maturity (*cf.* Arendt 1997). For example, fast growth ensures a size advantage throughout ontogeny and acts as a defence mechanism against size-dependent predation pressure (Arendt 1997). However, even among individuals of the same age, growth variations seem to be the rule rather than the exception, especially in species with indeterminate growth (Huston & DeAngelis 1987; Wiegmann et al. 1997; Pfister 2003; Kestemont et al. 2003; Campeas et al. 2009; Baras & Lucas 2010).

As intra-population variation in growth often occurs in equal rearing conditions or environments, factors intrinsic to the individual, such as behavioural traits (which may be underpinned by genetics), may play a key role for individual growth (Peacor & Pfister 2006; Stamps 2007). For example, a differentiation in boldness during foraging may relate to a consistent difference in resource acquisition resulting in consistent differences in growth (Biro & Stamps 2008). This may explain why the degree of intra-population variation in body size often increases through time as the larger individuals experience faster growth (Ricker 1958). Increased intraspecific competition may cause the individuals to diverge further depending on their intrinsic propensities (Magurran 1993). Similarly, resource partitioning, whereby individuals in a population use different habitats and consume different food resources, reduces competition (Bolnick et al. 2003). This may increase any initial differences in growth and/or morphology, and lead to size dimorphism within the population. Indeed, a variation in foraging ability in juveniles may have a strong influence on growth and development and thus the development of SSD (Blanckenhorn 2005).

1.2 CONSISTENT INDIVIDUAL BEHAVIOURAL VARIATION

Behaviour was long regarded as a highly plastic phenotypic trait as it seemingly responds quickly to temporal changes in the environment, context type (e.g. feeding or mating), or with the experience of the individual (e.g. Hazlett 1995). Studies of behavioural trade-offs, with a focus on foraging and predator avoidance, also showed that animals have the ability to compromise between activities (Dill 1987; Lima & Dill 1990). The importance of motivational state, for example hunger or reproductive status, affected the trade-off between foraging or reproductive activity and predator avoidance (Colgan 1993).

Behaviour has often been dealt with in discrete categories (e.g. game theory models), describing alternative behavioural strategies/tactics rather than continuous variables (e.g. hawk/dove, Maynard-Smith 1982; Sih & Bell 2008). Recently, new interest in individual behavioural differences has been evoked, with a focus on within-population variation in niche use, so called individual specialisation (Bolnick et al. 2003), and consistent individual differences in behaviour over time or across contexts, defined as personality or behavioural syndromes (Gosling 2001; Sih et al. 2004b). In the past decade, the definition of personality has been debated vigorously in behavioural ecology (Reale et al. 2007, 2010). In this thesis, personality is defined as the presence of behavioural differences between individuals that are consistent over time and can involve any type of behaviour. This is close to the notion of behavioural syndromes, which addresses the study of correlations at the population level either between behavioural traits across situations or contexts (Sih et al. 2004; Reale et al. 2010). A context is a functional behavioural category (e.g. feeding, mating, predator avoidance or dispersal), and a situation is the set of conditions at a particular time which can involve different levels along an environmental gradient (e.g. foraging behaviours in different habitats) (Sih et al. 2004a, b; Bell & Sih 2007). Behaviours that covary across situations are further defined as a context-specific behavioural syndrome, while a covariation across contexts is known as a context-general behavioural syndrome (Coleman & Wilson 1998; Sih et al. 2004a; Reale et al. 2007).

In 1994, Wilson et al. first brought attention to the low level of understanding of the taxonomic distribution of the shy-bold continuum, which was then restricted to primates and a few other species including cats, rats, canids and quails. The question on why humans vary in their propensity to take risks and whether similar variation exists in other species were posed (Wilson et al. 1994). Since then, a great interest in this field has been shown, with a tenfold increase in publications on the subject of personality and behavioural syndromes (Reale et al. 2010). Subsequently, a plethora of evidence from a variety of species has showed that rather than individuals being flexible in their behaviour, individuals behave differently in a consistent manner, i.e. individuals have consistent behaviours (Sih et al. 2004a; Bell et al. 2009).

Whilst individuals may adjust their behaviour to give appropriate responses in different situations, they still show a consistent level of response relative to the responses of other individuals (Dingemanse et al. 2009). Furthermore, individual behaviour has been found to be heritable (Boake 1994; Stirling et al. 2002; van Oers et al. 2005; Kolliker 2005) and related to fitness (Smith & Blumstein 2008). Similarly, many animal species exhibit within-population variation in resource use (specialism), where individuals use a significantly narrower set of resources than the population average, unrelated to age (Polis 1984), sex (Shine 1989), or morph (Bolnick et al. 2003). Such individual specialisation is thought to arise due to resource partitioning, which then reduces intra and/or interspecific competition, benefiting the coexistence of species (Barbault & Stearns 1991). Since the review by Bolnick et al. (2003) on individual specialisation, the number of studies demonstrating its taxonomic prevalence has increased rapidly (Matthews & Mazumder 2004; Svanbäck & Bolnick 2005; Quevedo et al. 2009; Jaeger et al. 2010; Araújo et al. 2011). Studies linking personality traits with individual variation in resource use are, however, lacking, with the two fields (personality and individual specialisation) largely treated separately.

Why individuals would behave consistently and specialise on certain resources is difficult as behavioural plasticity and individual generality in niche use would enable individuals to produce appropriate responses and use alternative resources during changing conditions. One suggested explanation involves the high cost of plasticity, as it requires constant information gathering and processing of the environment (DeWitt et al. 1998; Dall et al. 2004). Behavioural consistency might also develop due to morphological and physiological limits on the individual, suggesting that the variation is adaptive (Hazlett 1995; Dall et al. 2004). Individual behavioural variation may facilitate divergence in other phenotypic characters, such as morphology (Robinson & Wilson 1994; Imre 2002), and even be involved in rapid speciation (Bolnick et al. 2003), leading to increased fitness of certain behavioural phenotypes.

1.3 STATE-DEPENDENT BEHAVIOUR

Theoretical explanations for the maintenance of individual differences in behaviour have focused on state-dependency (Dingemanse & Wolf 2010). The state of an animal refers to features that are relevant during behavioural decisions in order to increase fitness (Wolf & Weissing 2010). This definition follows the use of state in life-history theory (Stearns 1992) and evolutionary game theory (Maynard-Smith 1982). States of an animal therefore include physiological, morphological and environmental characteristics, ranging from, for example, age, sex, size, experience, fighting ability, energy reserves, and metabolic rate to the type of environment (Houston & McNamara 1999; Dingemanse & Wolf 2010). State-dependent models are based on the assumption that there is a balance between the costs and benefits of a behavioural action at a given state, and therefore the model predicts that the consistent variation in behaviour between individuals relates to differences in their state (Houston & McNamara 1999; Dall et al. 2004; McElreath & Strimling 2006).

The fitness consequences of behavioural decisions of individuals therefore depend on their individual state. For example, individuals with higher vigour are likely to face lower predation risk as they are better at fleeing than less vigorous individuals. The stability of different states varies, ranging from stable states such as sex or absolute body size to less labile states like energy reserves and experience. States considered labile may still lead to consistent individual behavioural differences through feedbacks between initial state and behaviour which act to stabilise initial differences among individuals over time. An example of this is provided by the positive feedback between performance and experience, where individuals often perform better with increased experience (Rosenzweig & Bennett 1996; Brown & Laland 2003). However, with positive feedbacks between state and behaviour, it is uncertain whether the behavioural difference precedes or follows the difference in state. For example, success during initial social interactions may enhance status, allowing an individual to become dominant, and consequently, secure more food and grow faster (Magurran 1993). In minnow (*Phoxinus phoxinus* L.), both body size and prior residency determined the outcome of contests for feeding sites (Pitcher et al. 1986). In juvenile Atlantic salmon (Salmo salar L.), a correlation between dominance and size emerges only as the fish become older (Huntingford et al. 1990). Longevity and life expectancy may also influence behaviour, shown, for example, in black goby (*Gobius niger* L.), where young males significantly decreased their nest building and spawning activity in the presence of the predator, cod (*Gadus morhua* L.), whereas older males ignored the predator and continued to spawn as normal (Magnhagen 1990).

Wolf & Weissing (2010) called for more empirical studies to explicitly test predictions derived from state-dependent personality models, stressing the need to study more and different states and behaviours. In addition, an integration of ecology through investigating how key ecological variables are related to the presence/absence and structure of consistent individual behaviour in natural populations is needed (Wolf & Weissing 2010). As well as the focus on body size, this thesis will investigate behaviours related to age, sex and environmental type.

1.3.1 The relationship between growth-mortality tradeoffs and personality traits

Consistent individual differences in growth rate have been observed in many vertebrate populations, even when animals are raised alone with food *ad libitum* in the absence of predators, competitors and parasites (Ragland & Carter 2004; Martins et al. 2005; Baras & Lucas 2010). This indicates that consistent differences in growth are not simply a result of variation in social or environmental factors. According to Stamps (2007), the explanation for individual consistency in behaviours that contribute to growth-mortality trade-offs (e.g. risk-taking to feed or aggression to defend feeding territories) lies in concurrent consistent individual differences in growth rates. Therefore, more aggressive or bolder individuals will gain more food and grow faster, unless the context is unfavourable, for example, during predator presence, bolder individuals may be predated upon. A growth-mortality perspective argues that behaviours need not be positively related to one another across individuals, rather it depends on the effect of the behaviour on growth/mortality. For example, exploration (i.e. the time taken to explore a novel environment) requires time and energy that could have been used to forage and/ or grow. Exploration or predator inspection is assumed to provide information that may increase growth, survivorship, or both, in the future (Naef-Daenzer 2000; Whishaw et al. 2006).

The growth-mortality approach predicts that consistent differences in growth rates between individuals in a population will be accompanied by consistent individual differences in behavioural traits that contribute to growth-mortality tradeoffs. Since Wilson et al. (1993) first found no relationship between boldness and growth rate (albeit here none of the fish grew during the experiments), more studies have been completed, but with varying results. In farmed fish of the Salmonidae family that have been artificially selected for fast growth, it has been found that the fish take increased risks as their foraging rates increase (Huntingford & Adams 2005). Biro et al. (2004, 2006) found in captive rainbow trout (*Oncorhynchus mykiss* Mitchell), those fish selected for high growth rates took greater risks while foraging, grew faster, and survived at a lower rate in the presence of predators than a wild strain of fish under the same conditions.

1.4 APEX PREDATOR AS A MODEL SPECIES TO RESEARCH SSD

In a review article on SSD, Blanckenhorn (2005) called for case studies of appropriate model species to test multiple hypotheses in order to disentangle the causes generating intra- and inter-SSD and its consequences for their behaviour and ecology. The purpose of the thesis is to achieve this by integrating experimental work and field studies of wild populations. A recently published book reviewing studies in SSD highlighted the paucity of studies on fishes, as they were the only vertebrate group excluded (Fairbairn et al. 2007). Consequently, the use of pike as the model species in the thesis provides both a fish case study in SSD and also one using an apex predator species.

Pike has a wide distribution in fresh- and brackish waters in Eurasia and North America (Raat 1988; Crossman 1996) where it plays an important role in structuring prey communities including its own species through cannibalism and competition (Casselman & Lewis 1996; Craig 1996, 2008). Its broad distribution and important role in the fish community has resulted in a great number of studies of pike biology (Raat 1988; Craig 1996, 2008). Their populations also play a major role in recreational and commercial fisheries in many countries (Nilsson et al. 2008; Arlinghaus et al. 2009). They are an excellent model organism for investigating the development of intra and inter-SSD as they demonstrate considerable variation in growth rates during the juvenile life phase (Mann & Beaumont 1990; Ivanova & Svirskay 1995; Bry et al. 1995; Craig 1996), suggesting that early life strategies may play a key role in the development of their dimorphism (Raat 1988; Koli 1990; Mann & Beaumont 1990; Knight 2006; Vehanen et al. 2006). However, the degree of the size dimorphism varies greatly among adult pike populations (Lorenzoni et al. 2002; Persson et al. 2006). As in most species, the direction of SSD is female-biased (Raat 1988) and, as with many other fishes, they exhibit indeterminate growth, i.e. they continue to grow indefinitely, albeit at a decreasing rate following sexual maturity (Parker 1992). Life expectancy of pike varies inversely with growth rate, which is dependent on latitude (Casselman 1996). For example, Frost & Kipling (1967) report life expectancies of 17 years in Lake Windermere (UK), and a maximum age of 25 years have been recorded in the upper Saskatchewan River (Canada) (Miller & Kennedy 1948). Females generally live longer than males (Casselman 1996).

Pike is also an iteroparous species, reproducing multiple times during its life, with age and size at maturity depending on the latitude and habitats characteristics where it is found (Raat 1988). Maturity has been reported as early as during ages 1 to 2 years at 31 and 45 cm respectively in fast-growing populations, whereas this may not be until 4 years of age at 45 cm in slow-growing populations from more northern latitudes (Raat 1988). They spawn in vegetated shallow water in spring when the water temperature increases, but this again depends on latitude (Raat 1988; Koli 1990). These spawning areas are typically in river tributaries, shallow pools or bays, flooded wetlands, marshes or grasslands (Bry 1996) and individual pike often return to spawning grounds they have previously used, showing strong fidelity (Vehanen et al. 2006). Pike undertake polygamous mating, with a female commonly accompanied by a few males onto the spawning areas (Raat 1988; Knight 2006). It has also been postulated that alternative reproductive tactics are employed by small male pike in order to obtain fertilisations as a consequence of their disadvantages during size-dependent selection by females (Fabricus & Gustafson 1958; Knight 2006). Fabricus and Gustafsson (1958) studied the spawning behaviour of pike in experimental tanks and observed that, while a couple was spawning, another smaller male sometimes made an attempt at attending the female, suggesting that sneaking may occur in pike. Furthermore, protandry (early arrival on the spawning site by males) a strategy that is thought to maximise the chance of being present when a gravid female arrives (Morbey & Ydenberg 2001), has been reported in pike, with small males arriving as early as December at the spawning ground (Knight 2006). Following spawning, pike leave the spawning site and do not exhibit parental care of their offspring (Raat 1988).

After hatching of the fertilised eggs, which is temperature-dependent (e.g. 10°C in 12 days), the embryo stay attached to the vegetation through adhesive papillae in the head for 9-10 days (Frost & Kipling 1967; Raat 1988; Braum et al. 1996). Active feeding starts once the larvae is able to open its mouth, and prior to complete absorption of the yolk, when the larvae are 11-14 mm long (Billard 1996). Diet shifts take place as the pike larvae grow, from zooplankton, macro-invertebrates to fish larvae (Frost 1954; Raat 1988; Bry et al. 1995). During the first months of life mortality rates are substantial with 1% survival being reported from egg to fry at 12 weeks of life (Kipling & Frost 1970; Fago 1977). Juveniles are highly vulnerable to predation from both invertebrates (LeLouarn & Cloarec 1997) and vertebrates, including intraspecific predation (cannibalism) from both the same cohort and from older conspecifics (Kipling & Frost 1970; Mann 1980). Cannibalism among pike larvae has been found to start as early as 20 days after hatching at a body length of 18.7 mm (Ziliukiene & Ziliukas 2006). Indeed, cannibalism has been suggested to be the proximate cause of bimodal size distributions in some fish species (Claessen et al. 2000). The agonistic and cannibalistic behaviours of pike highlight the importance of size and fast growth in order to avoid being a victim to a conspecific attack. Size-dependent avoidance behaviour therefore occurs in pike, which remain solitary throughout their lives showing an ideal free-distribution (Skov & Koed 2004; Haugen et al. 2006).

Although, pike is often described as an ambush predator with low swimming activity (Raat 1988; Eklöv & Diehl 1994; Grimm & Klinge 1996; Kobler et al. 2008), several studies have noted high inter-individual variation in spatial and foraging behaviour (Beaudoin et al. 1999; Masters et al. 2005; Vehanen et al. 2006; Andersen et al. 2008) and presumed the occurrence of behavioural types (Jepsen et al. 2001; Kobler et al. 2009). In comparison to adult pike, studies on behavioural variations during the juvenile phase, when growth rates are the fastest, are rare, particularly in the wild.

1.5 THESIS OBJECTIVES

The overall aim of this thesis is to identify the behavioural drivers that underpin observed growth variations and result in size dimorphism. Using pike as the model species, it will be tested whether in situ measurements of population processes such as movement, dispersal, habitat and resource use can explain individual growth and size variations. Individual growth history will be analysed to characterise relationships between behavioural and life history traits including body size. Furthermore, through a series of experimental studies, an assessment of whether early life history is correlated to personality traits or the occurrence of a behavioural syndrome will be made. Correspondingly, the research objectives are to:

1. Identify the effects of early growth variations on life-time body size in pike and assess sex-related differences in growth trajectories;
2. Test whether in situ juvenile individual variation in movement is correlated to trophic niche, growth rate and body size;
3. Assess whether in riverine juvenile pike, intraspecific variation in trophic niche and body size are correlated to habitat and dispersal characteristics, and whether a difference in dispersal (or habitat shift) affects subsequent growth;
4. Test whether consistent differences in individual foraging behaviour across time and risk situations of juvenile pike relates to growth or size variations; and
5. Identify whether a context-general behavioural syndrome of juvenile pike is growth- or size dependent, thus explaining the development of size dimorphism.

Correspondingly, testable hypotheses will be provided in each of the relevant chapter introductions following descriptions of the specific research topic.

1.6 REFERENCES

Abouheif, E. & Fairbairn, D. J. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *American Naturalist*, 149, 540-562.

Andersen, M., Jacobsen, L., Gronkjaer, P. & Skov, C. 2008. Turbidity increases behavioural diversity in northern pike, Esox lucius L., during early summer. *Fisheries Management and Ecology*, 15, 377-383.

Andersson, S. 1994a. Costs of sexual advertising in the lekking jackson widowbird. *Condor*, 96, 1-10.

Andersson, M. 1994b. *Sexual selection.* Princeton, N.J.: Princeton University Press.

Arak, A. 1988. Sexual dimorphism in body size - a model and a test. *Evolution*, 42, 820-825.

Araújo, M. S., Bolnick, D. I. & Layman, C. A. 2011. The ecological causes of individual specialisation. *Ecology Letters*, 14, 948-958.

Arendt, J. D. 1997. Adaptive intrinsic growth rates: An integration across taxa. *Quarterly Review of Biology*, 72, 149-177.

Arlinghaus, R., Klefoth, T., Cooke, S. J., Gingerich, A. & Suski, C. 2009. Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). *Fisheries Research*, 97, 223-233.

Balon, E. 1993. Dynamics of biodiversity and mechanisms of change - a plea for balanced attention to form creation and extinction. *Biological Conservation*, 66, 5-16.

Baras, E. & Lucas, M. 2010. Individual growth trajectories of sibling *Brycon moorei* raised in isolation since egg stage, and their relationship with aggressive behaviour. *Journal of Fish Biology*, 77, 985-997.

Barbault, R. & Stearns, S. 1991. Towards an evolutionary ecology linking species interactions, life-history strategies and community dynamics - an introduction. *Acta Oecologica-International Journal of Ecology*, 12, 3-10.

Beaudoin, C. P., Tonn, W. M., Prepas, E. E. & Wassenaar, L. I. 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. *Oecologia*, 120, 386-396.

Bell, A. M., Hankison, S. J. & Laskowski, K. L. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77, 771-783.

Billard, R. 1996. Reproduction of pike: gametogenesis, gamete biology and early development. In: *Pike biology and exploitation*, (Ed. by J. Craig), pp. 13-43. London: Chapman & Hall.

Biro, P. A. & Stamps, J. A. 2008. Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23, 361-368.

Biro, P. A., Abrahams, M. V., Post, J. R. & Parkinson, E. A. 2004. Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society B: Biological Sciences*, 271, 2233-2237.

Biro, P. A., Abrahams, M. V., Post, J. R. & Parkinson, E. A. 2006. Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *Journal of Animal Ecology*, 75, 1165-1171.

Bisazza, A. & Marin, G. 1995. Sexual selection and sexual size dimorphism in the eastern mosquitofish *Gambusia holbrooki* (Pisces Poeciliidae). *Ethology Ecology & Evolution*, 7, 169-183.

Blanckenhorn, W. U. 2000. The evolution of body size: What keeps organisms small? *Quarterly Review of Biology*, 75, 385-407.

Blanckenhorn, W. U. 2005. Behavioral causes and consequences of sexual size dimorphism. *Ethology*, 111, 977-1016.

Blanckenhorn, W. 2007. Case studies of the differential-equilibrium hypothesis of sexual size dimorphism in two dung fly species. In: *Sex, size & gender roles. Evolutionary studies of sexual size dimorphism*, (Ed. by D. J. Fairbairn, W. U. Blanckenhorn, & T. Szkely), pp. 106-114. Oxford: Oxford University Press.

Boake, C. R. B. 1994. *Evaluation of applications of the theory and methods of quantitative genetics to behavioral evolution.*

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. 2003. The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist*, 161, 1-28.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C. & Vasseur, D. A. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26, 183-192.

Braum, E., Peters, N. & Stolz, M. 1996. The adhesive organ of larval pike *Esox lucius* L, (Pisces). *Internationale Revue Der Gesamten Hydrobiologie*, 81, 101-108.

Brown, C. & Laland, K. 2003. Social learning in fishes: a review. *Fish and Fisheries*, 4, 280-288.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. 2004. Toward a metabolic theory of ecology. *Ecology*, 85, 1771-1789.

Bry, C. 1996. Role of vegetation in the life cycle of pike. In: *Pike biology and exploitation*, (Ed. by J. F. Craig), pp. 45-67. London: Chapman & Hall.

Bry, C., Bonamy, F., Manelphe, J. & Duranthon, B. 1995. Early-life characteristics of pike, *Esox lucius*, in rearing ponds - temporal survival pattern and ontogenic diet shifts. *Journal of Fish Biology*, 46, 99-113.

Campeas, A., Brun-Bellut, J., Baras, E., Kestemont, P. & Gardeur, J. N. 2009. Growth heterogeneity in rearing sea bass (*Dicentrarchus labrax*): test of hypothesis with an iterative energetic model. *Animal*, 3, 1299-1307.

Casselman, E. J. 1996. Age, growth and environmental requirements of pike. In: *Pike biology and exploitation*, (Ed. by J. F. Craig), pp. 69-101. London: Chapman & Hall.

Casselman, J. M. & Lewis, C. A. 1996. Habitat requirements of northern pike (*Esox lucius*). *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 161-174.

Chapman, B. B., Hulthén, K., Blomqvist, D. R., Hansson, L., Nilsson, J., Brodersen, J., Anders Nilsson, P., Skov, C. & Brönmark, C. 2011. To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters*, 14, 871-876.

Claessen, D., de Roos, A. M. & Persson, L. 2000. Dwarfs and giants: Cannibalism and competition in size-structured populations. *American Naturalist*, 155, 219-237.

Clark, C. W. & Mangel, M. 2000. *Dynamic state variable models in ecology: Methods and applications.*

Clutton-Brock, T. & McAuliffe, K. 2009. Female mate choice in mammals. *Quarterly Review of Biology*, 84, 3-27.

Cluttonbrock, T., Albon, S. & Guinness, F. 1982. Competition between female relatives in a matrilocal mammal. *Nature*, 300, 178-180.

Cluttonbrock, T., Green, D., Hiraiwahasegawa, M. & Albon, S. 1988. Passing the buck - resource defense, lek breeding and mate choice in fallow deer. *Behavioral Ecology and Sociobiology*, 23, 281-296.

Cohen, J. E., Pimm, S. L., Yodzis, P. & Saldana, J. 1993. Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*, 62, 67-78.

Cohen, J., Jonsson, T. & Carpenter, S. 2003. Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 1781-1786.

Coleman, K. & Wilson, D. S. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour*, 56, 927-936.

Colgan, P. 1993. The motivational basis of fish behaviour. In: *Behaviour of teleost fishes*, (Ed. by T. . Pitcher), London: Chapman & Hall.

Craig, J. F. 1996. *Pike: biology and exploitation.* London: Chapman & Hall.

Craig, J. F. 2008. A short review of pike ecology. *Hydrobiologia*, 601, 5-16.

Crossman, E. J. 1996. Taxonomy and distribution. In: *Pike biology and exploitation*, (Ed. by J. F. Craig), pp. 1-11. London: Chapman & Hall.

Dall, S. R. X., Houston, A. I. & McNamara, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, 7, 734-739.

Darwin, C. 1859. *The origin of species by means of natural selection.* London: John Murray.

De Roos, A. M., Persson, L. & McCauley, E. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters*, 6, 473-487.

DeWitt, T. J., Sih, A. & Wilson, D. S. 1998. Costs and limits of phenotypic plasticity. *Trends in Ecology & Evolution*, 13, 77-81.

Dill, L. 1987. Animal decision-making and its ecological consequences - the future of aquatic ecology and behavior. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 65, 803-811.

Dingemanse, N. J. & Wolf, M. 2010. Recent models for adaptive personality differences: a review. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365, 3947-3958.

Dingemanse, N. J., Van der Plas, F., Wright, J., Reale, D., Schrama, M., Roff, D. A., Van der Zee, E. & Barber, I. 2009. Individual experience and evolutionary history of predation affect expression of heritable variation in fish personality and morphology. *Proceedings of the Royal Society B-Biological Sciences*, 276, 1285-1293.

Eklöv, P. & Diehl, S. 1994. Piscivore efficiency and refuging prey - the importance of predator search mode. *Oecologia*, 98, 344-353.

Fabricus, E. & Gustafson, K. 1958. Some new observations on the spawning behaviour of the pike, *Esox lucius* L. *Institute of Freshwater Research, Drottningholm*, 23-54.

Fago, D. 1977. *Northern pike production in managed spawning and rearing marshes.* Madison Wisconsin: Dept. of Natural Resources.

Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics*, 28, 659-687.

Fairbairn, F., Blanckenhorn, W. & Szkely, T. 2007. *Sex, size, and gender roles. Evolutionary studies of sexual size dimorphism.* Oxford University Press.

Frost, W. E. & Kipling, C. 1967. A study of reproduction early life weight-length relationship and growth of pike *Esox lucius* L. in Windermere. *Journal of Animal Ecology*, 36, 651-&.

Frost, W. 1954. The food of pike, *Esox lucius* L, in Windermere. *Journal of Animal Ecology*, 23, 339-360.

Galarowicz, T. L. & Wahl, D. H. 2005. Foraging by a young-of-the-year piscivore: the role of predator size, prey type, and density. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 2330-2342.

Ghiselin, M. 1974. *The economy of nature and the evolution of sex.* Berkeley: University of California Press.

Gosling, S. D. 2001. From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, 127, 45-86.

Grimm, M. P. & Klinge, M. 1996. Pike and some aspects of its dependence on vegetation. In: *Pike biology and exploitation*, (Ed. by Craig, J.F), pp. 125-156. London: Chapman & Hall.

Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. *Nature*, 313, 47-48.

Haugen, T. O., Winfield, I. J., Vøllestad, L. A., Fletcher, J. M., James, J. B. & Stenseth, N. C. 2006. The ideal free pike: 50 years of fitness-maximizing dispersal in Windermere. *Proceedings of the Royal Society B-Biological Sciences*, 273, 2917-2924.

Hazlett, B. 1995. Behavioral plasticity in crustacea: Why not more? *Journal of Experimental Marine Biology and Ecology*, 193, 57-66.

Heino, M. & Kaitala, V. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology*, 12, 423-429.

Houston, A. & McNamara, J. M. 1999. *Models of adaptive behaviour*. Cambridge University Press.

Huntingford, F. & Adams, C. 2005. Behavioural syndromes in farmed fish: implications for production and welfare. *Behaviour*, 142, 1207-1221.

Huntingford, F., Metcalfe, N., Thorpe, J., Graham, W. & Adams, C. 1990. Social-dominance and body size in Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology*, 36, 877-881.

Huston, M. & DeAngelis, D. 1987. Size bimodality in monospecific populations - a critical-review of potential mechanisms. *American Naturalist*, 129, 678-707.

Imre, I. 2002. Phenotypic plasticity in brook charr: changes in caudal fin induced by water flow. *Journal of Fish Biology*, 61, 1171-1181.

Ivanova, M. & Svirskay, A. 1995. Growth of juvenile pike, *Esox lucius*. *Journal of Ichtyology*, 35, 379-385.

Jaeger, A., Connan, M., Richard, P. & Cherel, Y. 2010. Use of stable isotopes to quantify seasonal changes of trophic niche and levels of population and individual specialisation in seabirds. *Marine Ecology-Progress Series*, 401, 269-277.

Jepsen, N., Beck, S., Skov, C. & Koed, A. 2001. Behavior of pike (*Esox lucius* L.) > 50 cm in a turbid reservoir and in a clearwater lake. *Ecology of Freshwater Fish*, 10, 26-34.

John-Alder, H. B. & Cox, R. M. 2007. Development of sexual size dimorphism in lizards: testosterone as a bipotential growth regulator. In: *Sex, size & gender roles. Evolutionary studies of sexual size dimorphism*, (Ed. by D. J. Fairbairn, W. Blanckenhorn, & T. Szkely), pp. 195-204. Oxford: Oxford University Press.

Kendall, B. & Fox, G. 2002. Variation among individuals and reduced demographic stochasticity. *Conservation Biology*, 16, 109-116.

Kestemont, P., Jourdan, S., Houbart, M., Melard, C., Paspatis, M., Fontaine, P., Cuvier, A., Kentouri, M. & Baras, E. 2003. Size heterogeneity, cannibalism and competition in cultured predatory fish larvae: biotic and abiotic influences. *Aquaculture*, 227, 333-356.

Kingsolver, J. G. & Pfennig, D. W. 2007. Patterns and power of phenotypic selection in nature. *BioScience*, 57, 561-572.

Kipling, C. & Frost, W. 1970. A study of mortality, population numbers, year class strengths, production and food consumption of pike, *Esox lucius* L, in Windermere from 1944 to 1962. *Journal of Animal Ecology*, 39, 115-&.

Knight, C. 2006. Utilisation of off-river habitats by lowland river fishes. PhD Thesis, University of Durham, UK.

Kobler, A., Klefoth, T. & Arlinghaus, R. 2008. Site fidelity and seasonal changes in activity centre size of female pike *Esox lucius* in a small lake. *Journal of Fish Biology*, 73, 584-596.

Kobler, A., Klefoth, T., Mehner, T. & Arlinghaus, R. 2009. Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? *Oecologia*, 161, 837-847.

Koli, L. 1990. *Suomen kalat.* Helsinki: WSOY [In Finnish].

Kolliker, M. 2005. Ontogeny in the family. *Behavior Genetics*, 35, 7-18.

Legrand, R. S. & Morse, D. H. 2000. Factors driving extreme sexual size dimorphism of a sit-and-wait predator under low density. *Biological Journal of the Linnean Society*, 71, 643-664.

LeLouarn, H. & Cloarec, A. 1997. Insect predation on pike fry. *Journal of Fish Biology*, 50, 366-370.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation - a review and prospectus. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 68, 619-640.

Lomnicki, A. 1988. *Population ecology of individuals.* Princeton, N.J.: Princeton University Press.

Lorenzoni, M., Corboli, M., Dorr, A. J. M., Mearelli, M. & Giovinazzo, G. 2002. The growth of pike (*Esox lucius* Linnaeus, 1798) in Lake Trasimeno (Umbria, Italy). *Fisheries Research*, 59, 239-246.

Magnhagen, C. 1990. Reproduction under predation risk in the sand goby, *Pomatoschistus minutus*, and the black goby, *Gobius niger*: The effect of age and longevity. *Behavioral Ecology and Sociobiology*, 26, 331-335.

Magurran, A. E. 1993. Individual differences and alternative behaviours. In: *Behaviour of teleost fishes*, (Ed. by T. Pitcher), London: Chapman & Hall.

Mann, R. H. K. 1980. The numbers and production of pike (*Esox lucius*) in 2 Dorset rivers. *Journal of Animal Ecology*, 49, 899-915.

Mann, R. & Beaumont, W. 1990. Fast- and slow-growing pike, *Esox lucius* L., and problems of age-determinations from scales. *Aquaculture and Fisheries Management*, 21, 471-478.

Martins, C. I. M., Schrama, J. W. & Verreth, J. A. J. 2005. The consistency of individual differences in growth, feed efficiency and feeding behaviour in

African catfish *Clarias gariepinus* (Burchell 1822) housed individually. *Aquaculture Research*, 36, 1509-1516.

Masters, J., Hodder, K., Beaumont, W., Gozlan, R., Pinder, R., Kenward, J. & Welton, S. 2005. Spatial behaviour of pike *Esox lucius* L. in the River Frome, UK. In: *Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe.*, (Ed. by M. Spedicato, G. Lembo, & G. Marmulla), pp. 179-190.

Matthews, B. & Mazumder, A. 2004. A critical evaluation of intrapopulation variation of delta C-13 and isotopic evidence of individual specialization *Oecologia*, 140, 361-371.

Maynard-Smith, J. 1982. *Evolution and the Theory of Games.* Cambridge: Cambridge University Press.

McElreath, R. & Strimling, P. 2006. How noisy information and individual asymmetries can make “personality” an adaptation: a simple model. *Animal Behaviour*, 72, 1135-1139.

McNamara, J. & Houston, A. 1986. The common currency for behavioral decisions. *American Naturalist*, 127, 358-378.

Miller, R.B. & Kennedy, W.A. 1948. Pike (*Esox lucius*) from four northern Canadian lakes. *Journal of the Fisheries Research Board of Canada*, 7, 190-199.

Morbey, Y. E. & Ydenberg, R. C. 2001. Protandrous arrival timing to breeding areas: a review. *Ecology Letters*, 4, 663-673.

Naef-Daenzer, B. 2000. Patch time allocation and patch sampling by foraging great and blue tits. *Animal Behaviour*, 59, 989-999.

Nilsson, P. A. & Brönmark, C. 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos*, 88, 539-546.

Nilsson, P. A., Skov, C. & Farrell, J. M. 2008. Current and future directions for pike ecology and management: a summary and synthesis. *Hydrobiologia*, 601, 137-141.

Paradis, A., Pepin, P. & Brown, J. 1996. Vulnerability of fish eggs and larvae to predation: Review of the influence of the relative size of prey and predator. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 1226-1235.

Parker, G. A. 1992. The evolution of sexual size dimorphism in fish. *Journal of Fish Biology*, 41, 1-20.

Peacor, S. D. & Pfister, C. A. 2006. Experimental and model analyses of the effects of competition on individual size variation in wood frog (*Rana sylvatica*) tadpoles. *Journal of Animal Ecology*, 75, 990-999.

Persson, L. & De Roos, A. M. 2007. Interplay between individual growth and population feedbacks shapes body-size distributions. In: *Body Size: The Structure and Function of Aquatic Ecosystems*, (Ed. by A. G. Hildrew, D. Raffaelli, & R. Edmonds-Brown), pp. 225-244. Cambridge: Cambridge University Press.

Persson, L., Bertolo, A. & De Roos, A. M. 2006. Temporal stability in size distributions and growth rates of three *Esox lucius* L. populations. A result of cannibalism? *Journal of Fish Biology*, 69, 461-472.

Pfister, C. 2003. Some consequences of size variability in juvenile prickly sculpin, *Cottus asper*. *Environmental Biology of Fishes*, 66, 383-390.

Pfister, C. & Stevens, F. 2003. Individual variation and environmental stochasticity: Implications for matrix model predictions. *Ecology*, 84, 496-510.

Polis, G. A. 1988. Exploitation competition and the evolution of interference, cannibalism and intraguild predation in age/size-structured populations. In: *Size-structured populations-ecology and evolution*, (Ed. by B. Ebenman & L. Persson), pp. 185-202. Heidelberg: Springer-Verlag.

Polis, G. 1984. Age structure component of niche width and intraspecific resource partitioning - can age-groups function as ecological species. *American Naturalist*, 123, 541-564.

Preziosi, R., Fairbairn, D., Roff, D. & Brennan, J. 1996. Body size and fecundity in the waterstrider *Aquarius remigis*: A test of Darwin’s fecundity advantage hypothesis. *Oecologia*, 108, 424-431.

Quevedo, M., Svanbäck, R. & Eklöv, P. 2009. Intrapopulation niche partitioning in a generalist predator limits food web connectivity. *Ecology*, 90, 2263-2274.

Raat, A. 1988. *Synopsis of biological data on the northern pike Esox lucius Linnaeus 1758.* FAO Fish. Synopsis.

Ragland, G. J. & Carter, P. A. 2004. Genetic covariance structure of growth in the salamander *Ambystoma macrodactylum*. *Heredity*, 92, 569-578.

Reale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82, 291-318.

Reale, D., Dingemanse, N. J., Kazem, A. J. N. & Wright, J. 2010. Evolutionary and ecological approaches to the study of personality.

Philosophical Transactions of the Royal Society B-Biological Sciences, 365, 3937-3946.

Rensch, B. 1959. Trends towards progress of brains and sense organs. *Cold Spring Harbor Symposia on Quantitative Biology*, 24, 291-303.

Ringler, N. 1983. Variation in foraging tactics of fishes. In: *Predators and prey in fishes*, (Ed. by D. L. G. Noakes, D. Lindquist, G. S. Helfman, & J. Ward), pp. 159-172. The Hague: Junk.

Robinson, B. W. & Wilson, D. S. 1994. Character release and displacement in fishes - a neglected literature. *American Naturalist*, 144, 596-627.

Roff, D. A. 1992. *The evolution of life histories: theory and analysis*. Springer.

Rose, K., Cowan, J., Clark, M., Houde, E. & Wang, S. 1999. An individual-based model of bay anchovy population dynamics in the mesohaline region of Chesapeake Bay. *Marine Ecology-Progress Series*, 185, 113-132.

Rosenzweig, M. & Bennett, E. 1996. Psychobiology of plasticity: effects of training and experience on brain and behavior. *Behavioural Brain Research*, 78, 57-65.

Salthe, S. & Mecham, J. 1974. Reproductive and courtship patterns. In: *Physiology of the Amphibia*, Vol 2 (Ed. by B. Lofts), pp. 309-521. New York: Academic Press Inc.

Schutz, D. & Taborsky, M. 2005. Mate choice and sexual conflict in the size dimorphic water spider *Argyroneta aquatica* (Araneae, Argyronetidae). *Journal of Arachnology*, 33, 767-775.

Sebens, K. P. 1987. The ecology of indeterminate growth in animals. *Annual Review of Ecology and Systematics*, 18, 371-407.

Shine, R. 1988. The evolution of large body size in females - a critique of Darwin's fecundity advantage model. *American Naturalist*, 131, 124-131.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism - a review of the evidence. *Quarterly Review of Biology*, 64, 419-461.

Shine, R. 1990. Proximate determinants of sexual differences in adult body size. *American Naturalist*, 135, 278-283.

Sih, A. & Bell, A. M. 2008. Insights for behavioral ecology from behavioral syndromes. In: *Advances in the Study of Behavior, Vol 38*, Vol 38 (Ed. by H. Brockmann, T. Roper, M. Naguib, K. WynneEdwards, C. Barnard, & J. Mitani), pp. 227-281. San Diego: Elsevier Academic Press Inc.

Sih, A., Bell, A. & Johnson, J. C. 2004a. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19, 372-378.

Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. 2004b. Behavioral syndromes: An integrative overview. *Quarterly Review of Biology*, 79, 241-277.

Simmons, L. W. 1986. Female choice in the field cricket *Gryllus bimaculatus* (Degeer). *Animal Behaviour,* 34, 1463-1470.

Skov, C. & Koed, A. 2004. Habitat use of 0+ year pike in experimental ponds in relation to cannibalism, zooplankton, water transparency and habitat complexity. *Journal of Fish Biology*, 64, 448-459.

Smith, B. R. & Blumstein, D. T. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, 19, 448-455.

Smith, T. B. & Skulason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics*, 27, 111-133.

Stamps, J. A. 2007. Growth-mortality tradeoffs and “personality traits” in animals. *Ecology Letters*, 10, 355-363.

Stearns, S. C. 1992. *The Evolution of Life Histories.* Oxford University Press, USA.

Stirling, D. G., Reale, D. & Roff, D. A. 2002. Selection, structure and the heritability of behaviour. *Journal of Evolutionary Biology*, 15, 277-289.

Svanbäck, R. & Bolnick, D. 2005. Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evolutionary Ecology Research*, 7, 993-1012.

Taborsky, M. 1999. Conflict or cooperation: what determines optimal solutions to competition in fish reproduction? In: *Behaviour and conservation of littoral fishes*, (Ed. by R. Oliveira, V. Almada, & E. Goncalves), pp. 301-349. Lisbon: ISPA.

Thornhill, R., Dodson, G. & Marshall, L. 1983. Sexual selection and insect mating behavior. *American Biology Teacher,* 45, 310-319.

Uchmanski, J. 1985. Differentiation and frequency distributions of body weights in plants and animals. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 310, 1-75.

van Oers, K., de Jong, G., van Noordwijk, A. J., Kempenaers, B. & Drent, P. J. 2005. Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour,* 142, 1185-1206.

Vehanen, T., Hyvärinen, P., Johansson, K. & Laaksonen, T. 2006. Patterns of movement of adult northern pike (*Esox lucius* L.) in a regulated river. *Ecology of Freshwater Fish*, 15, 154-160.

Werner, E. E. 1994. Ontogenetic scaling of competitive relations: size-dependent effects and responses in two anuran larvae. *Ecology*, 75, 197-213.

Werner, E. E. & Gilliam, J. F. 1984. The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology and Systematics*, 15, 393-425.

Werner, E. E. & Hall, D. J. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology,* 69, 1352-1366.

West-Eberhard, M. J. 1989. Phenotypic Plasticity and the Origins of Diversity. *Annual Review of Ecology and Systematics*, 20, 249-278.

Whishaw, I. Q., Gharbawie, O. A., Clark, B. J. & Lehmann, H. 2006. The exploratory behavior of rats in an open environment optimizes security. *Behavioural Brain Research*, 171, 230-239.

Wiegmann, D., Baylis, J. & Hoff, M. 1997. Male fitness, body size and timing of reproduction in smallmouth bass, *Micropterus dolomieui*. *Ecology*, 78, 111-128.

Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994. Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, 9, 442-446.

Wilson, D., Coleman, K., Clark, A. & Biederman, L. 1993. Shy bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*) - an ecological study of a psychological trait. *Journal of Comparative Psychology*, 107, 250-260.

Wolf, M. & Weissing, F. J. 2010. An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3959-3968.

Woodward, G. & Warren, P. 2007. Body size and predatory interactions in freshwaters: scaling from individuals to communities. In: *Ecological Reviews*, (Ed. by A. Hildrew, D. Raffaelli, & R. Edmonds-Brown), pp. 98-117.

Ziliukiene, V. & Ziliukas, V. 2006. Feeding of early larval pike *Esox lucius* L. reared in illuminated cages. *Aquaculture*, 258, 378-387.

Chapter 2

General methodology

To complete the objectives of the thesis, data were collected through a combination of field (Section 2.1) and experimental (Section 2.2) studies.

2.1 FIELD STUDIES

The field studies were carried out on a pike population of the River Frome, Dorset, England. Data were collected to identify the development of SSD by examining the growth trajectories of the pike from their first year of life to adulthood (Chapter 3), and subsequently, their spatial behaviour and trophic ecology related to the timing of size divergences (Chapters 4 and 5). The methodologies outlined here detail those that overlap between these chapters. The specific methodologies for each individual chapter are detailed within those chapters.

2.1.1 Study site

The study site of the River Frome was a 2 km section of the river and its connected side channels located close to the village of East Stoke in Dorset, UK (50°419 N; 2°119 W; Fig. 2.1). The river is a typical groundwater fed chalk stream with a meandering main channel (Crisp et al. 1982).

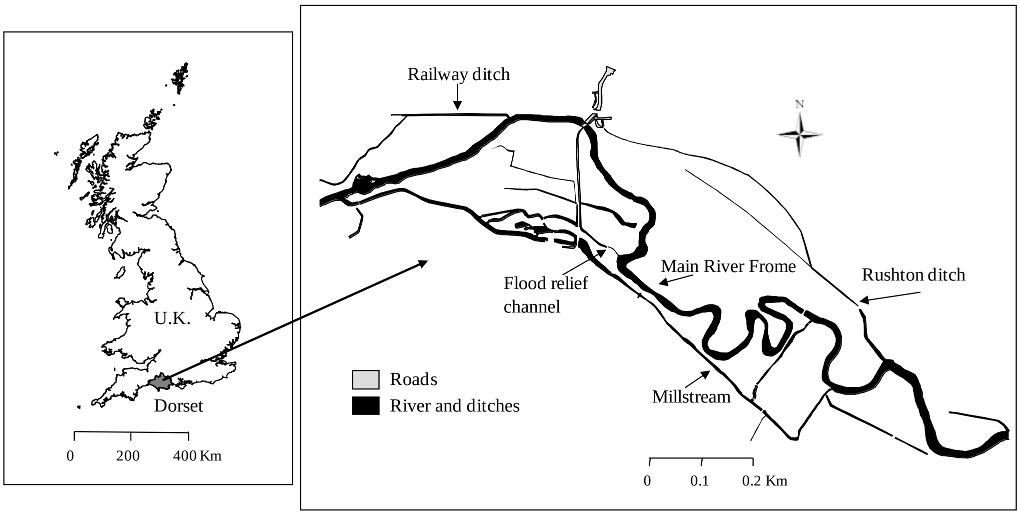

Figure 2.1. Map of the study section of the River Frome in Dorset, UK.

The side channels comprised three agricultural drainage ditches (Rushton, Railway, Flood relief) and a millstream (Fig. 2.1; Fig. 2.2). Furthest downstream was Rushton ditch; a 400 m long channel that flows across grazed fields prior to joining the river. It is mostly over 1 m deep in the centre of the channel, heavily silted with areas of gravel and large quantities of emergent and submerged vegetation. The Flood relief channel is a blind-ending channel of 160 m length. In its lower stretch it reaches 1.5 m deep and is covered with submerged vegetation. The Railway ditch is approximately 250 m long, mostly shallow (up to 50 cm) and runs alongside a rail track. All ditches are heavily vegetated (majority: *Glyceria fluitans*, *Phalariss arundinacea, Callitriche stagnalis, Potamogeton natans, Carex riparia, Juncus effusus*) and some tree cover, and the majority of the substrate is silt. All the ditches were very slow flowing and supported a rich invertebrate diversity (Armitage et al. 2003). Each ditch was divided into 10 m patches using marked posts to determine catch location of pike and detection location of individuals during tracking with a portable tag detection device (Section 2.1.4; Chapter 4). Adults were found to spawn in different drainage ditches during the same spawning period (pers. obs.). During the study the juvenile pike were never captured or detected in different drainage ditches, and therefore, no evidence for their movement between drainage ditches was found.

Figure 2.2. Views of (a) Flood relief channel, (b) Rushton ditch, (c) Railway ditch, and (d) Millstream.

A variety of fish species (e.g. eels *Anguilla anguilla* L., minnows) also inhabit and/or utilise the ditches as part of their lifecycle (Knight 2006), with pike using them as spawning and nursery habitats (Mann & Beaumont 1990; Knight 2006). In addition, pike from the main channel have been found to use ditches as feeding grounds during winter floods (Masters et al. 2002). Although normally unmanaged by the landowner and farmer, Rushton ditch was mechanically dredged in March 2009. The growth of the remaining vegetation sustained the invertebrate assemblages and the ditch community recovered quickly. Pike spawning was observed in that ditch later in April 2009, and out of the pike captured in the ditch before dredging, 40 % were subsequently recaptured, higher than the average proportion recaptured of 30 % over the whole study period. Thus, the dredging operation did not appear to detrimentally impact the study. The lower reach of the millstream used in the study was approximately 520 m in length and was comprised of shallow rifles (mean ± SE, 15 ± 2 cm) and deep pools (84 ± 4 cm, maximal depth = 104 cm). There were no barriers impeding fish moving in and out of the study area.

2.1.2 Fish sampling

The pike population of the study area was sampled by electric fishing using 50 MHz pulsed DC at approximately 2 Amps, with the electric fishing gear deployed being dependent on the habitat being fished and its water level. The main differences between fishing in the ditches, main river and the Millstream were: (i) the silt substrate of the ditches meant wading made the water too turbid to allow more than one sampling run per day; (ii) the main river was too deep to allow any quantitative sampling and so the electric fishing was primarily to collect samples of fish for processing and tagging (Sections 2.1.3 and 2.1.4); (iii) the section of the Millstream stream (520 m in length) was split into sections of approximately 50 m in length using stop nets (10 mm mesh), enabling 2 run electric fishing to be completed.

The ditches were always fished using back mounted electric fishing (Smith-Root LR-24, USA), with all operators wading. Each 50 m reach of the Millstream was fished twice in succession using portable electric fishing gear with a generator supply (Electracatch International, Wolverhampton, UK). During low water levels, the main river was sampled by using the hand-held electric fishing from a boat, where one operator was fishing at the front of the boat and placing captured netted fish into a holding bin in the boat’s centre. The other operator was responsible for rowing the boat. When water levels were sufficiently high, sampling was through electric fishing gear mounted on a boat (‘boom–boat’), which was powered by a small diesel engine (designed and constructed by staff at the Game- and Wildlife Trust, Dorset, UK). The boom boat had a series of cathodes trailing from the back, and two circular anodes with droppers hanging at the front. One person stood at the front of the boat ready to net the fish and put them in the holding bin in the centre of the boat and one person operated the engine and output for the electric fishing.

In all cases, the action of the electric field within the water temporarily immobilised the fish and enabled their capture with a hand net. The captured pike were then placed in water filled containers to allow recovery and holding prior to their data processing. Pike were also sampled from the main river channel using rod-and-line angling, especially at times when electric fishing was not feasible due to high water level or strong flow.

The fishing was conducted at intervals of 1 to 3 months from December 2008 to March 2011 (Table 1) in order to follow individual growth patterns and shifts in trophic positions. Individual data were able to be collected through tagging of the fish (Section 2.1.3). No electric fishing or angling was carried out during the spawning period of the pike. This reproductive period normally occurs in April in the River Frome (Mann & Beaumont 1990), but in this study, it was also observed in May (2009 and 2010). See Appendix I for details on the number of tagged pike in the ditches, Millstream and main river across the study.

2.1.3 Tagging of pike using passive integrated transponder (PIT) tags

To be able to obtain data to be collected at the individual level, the pike were tagged using passive integrated transponder (PIT) tags. The tagging procedure required each fish to be anaesthetised with MS-222 (tricaine methanesulphonate, 3.5 ml/litre of river water) before they were measured (fork length, FL, nearest mm) and weighed (nearest g). Any fish of ≥ 85 mm were tagged with 23.1 mm PIT tags (Texas Instruments, half-duplex, 3.85 mm diameter, 0.6 g) (following suggested minimum sizes of fish for tagging with 23.1 mm tags by Roussel et al. 2000; Zydlewski et al. 2001). Each tag was programmed with a unique signal code (tag id) which is then relayed after induction by an electro-magnetic field sent from a detector. As the tags have no internal battery and are thus long-lasting, they enable identification and long-term monitoring of individual fish when they are recaptured.

To insert a PIT tag into an anaesthetised fish, a small incision on the mid-ventral line through the peritoneum was made using a sterile sharp scalpel blade, and the PIT tag was gently pushed through the cut into the peritoneal cavity. At the same time, a small sample of the pelvic fin (≥ 0.5 mg dry weight) was also taken for stable isotope analysis (Section 2.1.5). A sample of scales was removed from above the lateral line by the dorsal fin from each fish for age determination (Section 2.1.6). An external sex determination was conducted through observing the appearance of the urogenital region as proposed by Billard (1996). There is a protuberance between the urogential pore and the anus in females which does not exist in males. Following processing, the pike were placed into aerated fresh river water and following recovery, were released back to their location of capture.

Following the first sampling date (19 December 2008), all pike captured were scanned with a handheld PIT tag detector (Allflex portable RFID reader) for identification of recaptured tagged fish. The PIT tag ID was noted and the fish were anaesthetised with MS-222, measured, weighed and fin-clipped before being released. A note of catch location and date was made for all captured pike. At each sampling date, two abundant prey species in the study site; the minnow, and the invertebrate water louse *Asellus aquaticus* (L.) (Isopoda, Crustacea), which are known to constitute an important part of the diet of pike in the River Frome (Mann 1976, 1982) were also collected for stable isotopes analyses (Section 2.1.5). These provided the baseline isotopic signatures as putative food resources. Samples for stable isotope analysis were transported on ice to Bournemouth University, where they were stored in a freezer (-20°C) and before being prepared later for analyses.

Date	Site	Purpose	Chapters
09/12/2008	Ditches	Telemetry, size, growth, SIA	4, 5
16/01/2009	Ditches	Telemetry, size, growth, SIA	4, 5
24/02/2009	Ditches	Telemetry, size, growth, SIA	4, 5
25/02/2009	River	Size, age, growth, SIA	3, 5
19/03/2009	Ditches	Telemetry, size, growth, SIA	4, 5
24/03/2009	River	Size, age, growth, SIA	3, 5
29/06/2009	Ditches	Telemetry, size, growth, SIA	4, 5
09/07/2009	River	Size, age, growth, SIA	3, 5
10/07/2009	Millstream	Size, age, growth, SIA	3, 5
13/08/2009	Ditches	Telemetry, size, growth, SIA	4, 5
25/08/2009	Ditches	Telemetry, size, growth, SIA	4, 5
15/10/2009	Ditches	Telemetry, size, growth, SIA	4, 5
29/10/2009	River	Size, age, growth, SIA	3, 5
24/02/2010	Ditches	Telemetry, size, growth, SIA	4, 5
27/02/2010	River	Size, age, growth, SIA	3, 5
10/06/2010	Millstream	Size, age, growth, SIA	3, 5
23/06/2010	River	Size, age, growth, SIA	3, 5
29/06/2010	Ditches	Telemetry, size, growth, SIA	4, 5
03/08/2010	Millstream	Size, age, growth, SIA	3, 5
18/08/2010	Ditches	Telemetry, size, growth, SIA	4, 5
20/08/2010	Ditches	Telemetry, size, growth, SIA	4, 5
03/09/2010	Millstream	Size, age, growth, SIA	3, 5
28/09/2010	River	Size, age, growth, SIA	3, 5
30/09/2010	Ditches	Telemetry, size, growth, SIA	4, 5
08/10/2010	River	Size, age, growth, SIA	3, 5
12/10/2010	River	Size, age, growth, SIA	3, 5
22/10/2010	Ditches	Telemetry, size, growth, SIA	4, 5
24/11/2010	River	Size, age, growth, SIA	3, 5
24/03/2011	Ditches	Telemetry, size, growth, SIA	4, 5
23/06/2011	Millstream	Size, age, growth, SIA	3, 5
04/07/2011	Ditches	Telemetry, size, growth, SIA	4, 5
03/08/2011	River	Size, age, growth, SIA	3, 5

Table 2.1. Date, site and purpose of sampling by electric fishing.

2.1.4 PIT telemetry

The PIT tagging also enabled tracking of individual fish using a portable antenna (see details in Chapter 4; Section 4.2.1). Portable PIT detectors have been developed for actively locating (PIT telemetry) tagged fishes in shallow waters enabling fine-scale studies in the wild of individual fish movements and habitat use (Roussel et al. 2004; Cunjak et al. 2005; Hill et al. 2006; Cucherousset et al. 2010) Use of PIT telemetry has greatly improved our understanding of fish ecology, behaviour and management (Roussel et al. 2004; Cunjak et al. 2005; Cucherousset et al. 2007).

2.1.5 Stable isotope analysis

Diet composition in fishes has traditionally been completed through stomach content analysis, but the method carries the disadvantages of usually being destructive and is not capable of being able to elucidate the extent to which a fish is assimilating their energy from their putative food resources either other fish or invertebrates (Paradis et al. 2008). More recently, substantial increases in the understanding of trophic relationships between organisms and their putative food sources have been gained by the use of stable isotope analyses (SIA) (Vander Zanden et al. 1999; Grey 2006). The ratios of the stable isotopes ($^{13}C/^{12}C$; $^{15}N/^{14}N$) reveal the trophic structure and pathways of energy flow in the studied food web as they vary predictably from resource to consumer (Fry 2006). Consumer $\delta^{13}C$ is an indicator of energy source because animals that feed on the same food source display an isotope composition similar to each other and to the food they assimilate for growth (DeNiro & Epstein 1978; Fry & Sherr 1984). The stable nitrogen isotope ($\delta^{15}N$) typically becomes enriched by 3 to 4% between prey and predator tissue and so is an indicator of consumer trophic position (Deniro & Epstein 1981; Minagawa & Wada 1984). This application of stable isotope techniques, using the predictable relationship between the isotopic composition of consumers and their diet, is a sensitive and powerful tool, which can detect among-individual feeding differences (Gu et al. 1997; Beaudoin et al. 1999; Fry 2006).

For pike, pelvic fin tissue was chosen (Section 2.1.3) for analysis of their stable isotope values. This was because SIA values from fin clips have been shown to correspond strongly with those of dorsal muscle tissue (Jardine et al. 2005; Kopp et al. 2009) but with the advantage of being non-destructive and not adversely affecting fish survival and growth (Gjerde & Refstie 1988; Pratt & Fox 2002). To provide the baseline isotopic signatures of the putative food resources of the pike, muscle samples of minnows, and specimens of water louse were obtained at the same time as the pike were sampled. A section of dorsal muscle was dissected from minnows, whereas whole specimens of water louse samples (n = 2-4) were pooled. All SIA samples were oven dried (60°C for 48 h), and then sent to Cornell Isotope Laboratory, USA, where they were weighed (all samples were 0.5-1 mg), ground into a homogenous powder, and analysed using a Thermo Delta V isotope ratio mass spectrometer with an elemental analyser (NC2500).

Stable isotope values of ^{13}C and ^{15}N of each individual sample are reported in the δ notation, where δ^{13}C or δ^{15}N = [Rsample/Rstandard-1] x 1000, and R is ^{13}C/^{12}C or ^{15}N/^{14}N. Standards references were Vienna Pee Dee Belemnite for δ^{13}C and atmospheric nitrogen for δ^{15}N. A standard of animal (mink) was run every 10 samples to calculate an overall standard deviation for both δ^{15}N and δ^{13}C to ascertain the reliability of the analyses. The overall standard deviation of the animal standard was not more than 0.23 ‰ for δ^{15}N and 0.14‰ for δ^{13}C. Single measurements were made for all samples in this study.

Trophic positions (TP) for each individual pike were calculated using the formula: TP = [(fish δ^{15}N - mean prey δ^{15}N)/3.4] + 2, where 3.4 represents a widely used single trophic level fractionation in δ^{15}N, and 2 corresponds to the trophic level of primary consumers (Vander Zanden et al. 2000; Post 2002; Paradis et al. 2008).

2.1.6 Scale ageing

The age of the pike was determined by counting the marks that are formed yearly on the scales during faster and slower growth periods (Bagenal 1978). These, so called annual marks or annuli, are most apparent in fish from the temperate regions where temperature differences between the seasons are the greatest. In winter, little or no growth takes place, but growth increases again with higher temperatures in early summer (Bagenal 1978). The age of each pike was determined through viewing all the sampled scales (n = 3-5) on a projecting microscope (x 24, x 48) and identifying and counting their annuli (Fig. 2.3). Ageing accuracy was determined through a proportion of fish in the samples being recaptured PIT- tagged fish, enabling comparison of estimated ages over time for fish of known age and between known time intervals. Ageing precision was maintained by blind reading (unknown length and sex when reading the scale) and by 25 % of the samples being aged by an independent and experienced operator.

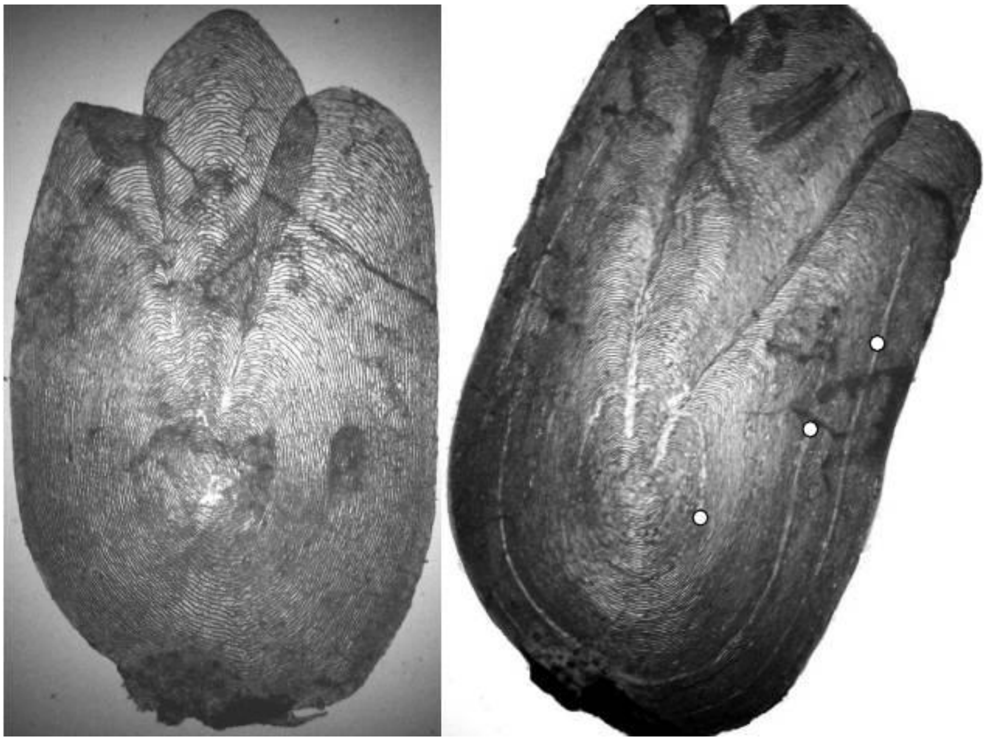

Figure 2.3. Left: Scale from a 280 mm pike aged 0+ (no visible annulus); Right: Scale from a 280 mm pike aged at 3+ years (3 visible annuli, denoted by white circles).

An individual's approximate growth history can then be estimated through back-calculation by measuring the annual growth patterns. The distances between the annuli from the centre of the scales (radii), the length of the full scale radius together with the length of the fish when captured enables back-calculation of the lengths at an earlier time. The fork lengths at each age were back-calculated using the body proportional equations, Dahl-Lea, as described in Francis (1990): $L_N = (S_N/S_T)*L_F$, where: L_N = length of fish when annulus was formed, L_F = Fork length of fish when scale sample was obtained, S_N = radius of annulus (at fish length L_N), and S_T = total scale radius. In this thesis, the age of the fish will be described on the assumption that hatching (earliest reported hatching time in the site) takes place in March with the end of a year of life in February. The ages will be denoted with + sign indicating the year of life (e.g. young-of-the-year: 0+).

2.2 EXPERIMENTAL STUDIES

Two experimental studies using young-of-the-year (YOY) pike collected from the wild were conducted in summer 2009 (Chapter 6) and 2010 (Chapter 7). The methodologies of the experiments are detailed in the specific chapters but their generic components are discussed next.

2.2.1 Collection and housing of fish

YOY pike (mean mass = 0.6 g) were captured in May 2009 and 2010 by hand netting in a drainage ditch (Holme Bridge ditch) of the River Frome, located 4 km downstream of the study site (50°419 N; 2°119 W). This ditch was used as it was close to the study area but the removal of the YOY pike would not impact their populations in the study ditches (Section 2.1.1). The fish were placed in 30 L buckets containing river water and air stones attached to a battery operated air pump to maintain oxygen levels before being immediately transported to aquarium facilities at Bournemouth University by car (maximum transit time: 40 min). After acclimatisation to the ambient laboratory temperature (16 °C) for a minimum of 12 hours, the pike were individually placed in identical 25 L glass aquaria containing conditioned tap water, an air stone attached to an air pump for oxygenation and plastic plants for habitat enrichment. Three sides of the aquaria were covered with black plastic to prevent visual contacts between individuals. Feeding regime varied between experiments conducted in 2009 and 2010 (see Chapter 6 and 7 for experimental protocols). A 14L: 10D photoperiod was maintained in the laboratory at all times.

Age-1 pike were captured from the same site by single-pass electric fishing (Smith-Root LR-24 backpack). These pike were kept individually in 60 L glass aquaria containing plenty of plant cover and were fed *ad libitum* with earthworms (*Dendrobaena veneta* Rosa) both years.

2.3 DATA ANALYSES

The specific growth rate (SGR) of each individual is determined using the formula: $[\ln(W_f)-\ln(W_i)] \times 100/t$, where W_i and W_f are the initial and final body sizes and t is the number of days between the size measurements. Whether body lengths or masses are used to calculate SGR is stated in each chapter.

To assess inter-individual variation in SGR, body size and behavioural measures, coefficient of variation (CV, %) was calculated as CV = [(SD/mean)*100]. Consistency of individual behaviour was calculated as their repeatability [± SE and 95% confidence intervals (CI)] using linear mixed-effects models for count data and generalised linear mixed-effects models for Gaussian data (Nakagawa & Schielzeth 2010). Both models had individual ID fitted as the random effect and the behavioural variable as the dependent factor.

All data were checked for normality by Kolmogorov-Smirnov's test and for homogeneity of variance by Levene's test prior to conducting parametric tests.

2.4 ETHICAL NOTE

The study was approved by an independent ethical review committee under the Bournemouth University's Home Office (HO) certificate (licence number: PLL 30/2626) in accordance with the UK Animals (Scientific Procedures) Act 1986. I obtained a personal HO licence (PIL 30/8546) for the induction and maintenance of general anaesthesia by immersion, implantation of PIT tags into the peritoneal cavity and biopsies of fin samples.

Permission to use electric fishing equipment was granted annually from the Environment Agency of England and Wales (EA) for the ditches and millstream at East Stoke (November-October), and for the main river (May-October). Permission to fish the main river in November to March was granted for specific fishing dates. Electric fishing was carried out at the minimum power settings needed to incapacitate the fish and thus no adverse impact on other wildlife should have been experienced.

Consents to collect the fish from the wild for the experimental work were also granted by the EA. In the laboratory, the fish were kept in isolation to prevent cannibalism and the pike were never in physical contact with other fish. All individuals resumed feeding within ten minutes after being returned to their holding tanks from the experimental tanks indicating low-stress levels. Individuals were observed daily for signs of disease or stress and were found to maintain a high level of feeding activity and health throughout the experimental period. At the end of the experimental periods, all the fish (2009, n = 55; 2010, n = 64) were euthanized as stipulated by the HO project licence; moreover, the fish were not released back into the wild due to legislative restrictions relating to fish stocking activities. The fish were euthanized according to the methods in the HO licence with an overdose of the anaesthetic MS-222 (10 minutes), followed by destruction of the brain.

2.5 REFERENCES

Armitage, P. D., Szoszkiewicz, K., Blackburn, J. H. & Nesbitt, I. 2003. Ditch communities: a major contributor to floodplain biodiversity. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 13, 165-185.

Bagenal, T. 1978. *Methods for assessment of fish production in fresh waters*. Oxford: Blackwell.

Beaudoin, C. P., Tonn, W. M., Prepas, E. E. & Wassenaar, L. I. 1999. Individual specialization and trophic adaptability of northern pike (Esox lucius): an isotope and dietary analysis. *Oecologia*, 120, 386-396.

Billard, R. 1996. Reproduction of pike: gametogenesis, gamete biology and early development. In: *Pike biology and exploitation*, (Ed. by J. Craig), pp. 298. London: Chapman & Hall.

Crisp, D., Matthews, A. & Westlake, D. 1982. The temperatures of 9 flowing waters in southern England. *Hydrobiologia*, 89, 193-204.

Cucherousset, J., Paillisson, J. M. & Roussel, J. M. 2007. Using PIT technology to study the fate of hatchery-reared YOY northern pike released into shallow vegetated areas. *Fisheries Research*, 85, 159-164.

Cucherousset, J., Britton, J. R., Beaumont, W. R. C., Nyqvist, M., Sievers, K. & Gozlan, R. E. 2010. Determining the effects of species, environmental conditions and tracking method on the detection efficiency of portable PIT telemetry. *Journal of Fish Biology*, 76, 1039-1045.

Cunjak, R. A., Roussel, J. M., Gray, M. A., Dietrich, J. P., Cartwright, D. F., Munkittrick, K. R. & Jardine, T. D. 2005. Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. *Oecologia*, 144, 636-646.

DeNiro, M. & Epstein, S. 1978. Influence of diet on distribution of carbon isotopes in animals. *Geochimica Et Cosmochimica Acta*, 42, 495-506.

DeNiro, M. & Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica Et Cosmochimica Acta*, 45, 341-351.

Fry, B. 2006. *Stable isotope ecology*. 1st edn. New York: Springer Science + Business Media.

Fry, B. & Sherr, E. B. 1984. δ13C measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions In Marine Science*, 27, 13-47.

Gjerde, B. & Refstie, T. 1988. The effect of fin-clipping on growth-rate, survival and sexual maturity of rainbow-trout. *Aquaculture*, 73, 383-389.

Grey, J. 2006. The use of stable isotope analyses in freshwater ecology: Current awareness. *Polish Journal of Ecology*, 54, 563-584.

Gu, B., Schelske, C. & Hoyer, M. 1997. Intrapopulation feeding diversity in blue tilapia: Evidence from stable-isotope analyses. *Ecology*, 78, 2263-2266.

Hill, M. S., Zydlewski, G. B. & Gale, W. L. 2006. Comparisons between hatchery and wild steelhead trout (*Oncorhynchus mykiss*) smolts: physiology and habitat use. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 1627-1638.

Jardine, T. D., Gray, M. A., McWilliam, S. M. & Cunjak, R. A. 2005. Stable isotope variability in tissues of temperate stream fishes. *Transactions of the American Fisheries Society*, 134, 1103-1110.

Knight, C. 2006. Utilisation of off-river habitats by lowland river fishes. PhD thesis, University of Durham, UK.

Kopp, D., Cucherousset, J., Syväranta, J., Martino, A., Cereghino, R. & Santoul, F. 2009. Trophic ecology of the pikeperch (*Sander lucioperca*) in its introduced areas: a stable isotope approach in southwestern France. *Comptes Rendus Biologies*, 332, 741-746.

Mann, R. H. K. 1976. Observations on age, growth, reproduction and food of pike *Esox lucius* (L.) in 2 rivers in southern England. *Journal of Fish Biology*, 8, 179-197.

Mann, R. H. K. 1982. The annual food-consumption and prey preferences of pike (*Esox lucius*) in the river Frome, Dorset. *Journal of Animal Ecology*, 51, 81-95.

Mann, R. & Beaumont, W. 1990. Fast- and slow-growing pike, *Esox lucius* L., and problems of age-determinations from scales. *Aquaculture and Fisheries Management*, 21, 471-478.

Masters, J. E. G., Welton, J. S., Beaumont, W. R. C., Hodder, K. H., Pinder, A. C., Gozlan, R. E. & Ladle, M. 2002. Habitat utilisation by pike *Esox lucius* L. during winter floods in a southern English chalk river. *Hydrobiologia*, 483, 185-191.

Minagawa, M. & Wada, E. 1984. Stepwise enrichment of N-15 along food-chains - further evidence and the relation between delta-N-15 and animal age. *Geochimica et Cosmochimica Acta*, 48, 1135-1140.

Nakagawa, S. & Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, 85, 935-956.

Paradis, Y., Bertolo, A. & Magnan, P. 2008. What do the empty stomachs of northern pike (*Esox lucius*) reveal? Insights from carbon (delta C-13) and nitrogen (delta N-15) stable isotopes. *Environmental Biology of Fishes*, 83, 441-448.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, 83, 703-718.

Pratt, T. C. & Fox, M. G. 2002. Effect of fin clipping on overwinter growth and survival of age-0 walleyes. *North American Journal of Fisheries Management*, 22, 1290-1294.

Roussel, J. M., Haro, A. & Cunjak, R. A. 2000. Field test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 1326-1329.

Roussel, J. M., Cunjak, R. A., Newbury, R., Caissie, D. & Haro, A. 2004. Movements and habitat use by PIT-tagged Atlantic salmon parr in early winter: the influence of anchor ice. *Freshwater Biology*, 49, 1026-1035.

Vander Zanden, M. J., Casselman, J. M. & Rasmussen, J. B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, 401, 464-467.

Vander Zanden, M., Shuter, B., Lester, N. & Rasmussen, J. 2000. Within- and among-population variation in the trophic position of a pelagic predator, lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 725-731.

Zydlewski, G. B., Haro, A., Whalen, K. G. & McCormick, S. D. 2001. Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. *Journal of Fish Biology*, 58, 1471-1475.

Chapter 3

The importance of early life growth for the development of sexual size dimorphism in pike *Esox lucius*

3.1 ABSTRACT

Intrapopulation growth and size variations, including sexual size dimorphism, are common in animals and may have important life history consequences for individuals. Identifying when growth history divergences arise in species where their growth continues after maturity is important in determining life-history consequences at both the individual and population level. Here, the consequences of considerable variability in the growth rates of 0+ pike for their subsequent growth rates and body lengths across their lifetime were tested through analysis of back-calculated lengths and growth increments of fish sampled between 2000 and 2011. Results showed that females were significantly larger and faster growing than male fish at most ages. Independent of sex, fish that were relatively small at age 1 then remained significantly smaller in body length at each subsequent age (up to at least the age of 8 years). However, from the age of 1 year, the annual growth increments of pike were similar, irrespective of their body lengths earlier in life, with this independent of sex and growth year. Thus, variation in the growth of pike in their first year of life had a significant effect on their subsequent lengths at age, with small fish at age 1 remaining relatively small throughout life, but not their growth increments. The potential implications of this for individual fitness and reproductive strategies are discussed.

3.2 INTRODUCTION

Body size has important implications on the outcome of many basic individual ecological processes that may then influence individual fitness, such as competition and predation (Arendt 1997; Kingsolver & Pfennig 2007). Although, an individual's optimal life history strategy may therefore be to grow fast to quickly achieve the benefits of a large body size, considerable intra-population variation in growth and body size at age is widespread in many species (Uchmanski 1985; Peacor 2006; Chown & Gaston 2010). Among such variation, a divergence in body size between or within the sexes, i.e. inter- or intra-sexual size dimorphism (SSD), is particularly common (Blanckenhorn 2005; Fairbairn et al. 2007). Identifying when growth history divergences arise in species where their growth continues after maturity, i.e. it is indeterminate (Sibly et al. 1985), is important in determining the demographics of a species, and the subsequent consequences for both the individual and the population (Osmundson 2006; Bulté et al. 2008).

Empirical evidence suggests that organisms in the wild rarely grow at their physiological maximum (Calow 1982), indicating that trade-offs between costs and benefits of fast growth are involved in determining growth at an individual level, with this having implications for body size (Abrams et al. 1996; Arendt & Wilson 1997). Individual growth histories, particularly of species with indeterminate growth, vary according to a set of abiotic factors, (e.g. temperature, day length etc.) and biological factors (e.g. population density, social status etc). These factors greatly influence system productivity, competition and hence food availability (Brett 1979; Metcalfe 1993), with implications on the mechanisms of compensatory growth (Björklund et al. 2003; Lohmus et al. 2010).

The individual growth history of fish can be determined through back-calculating their lengths at age from their calcified body structures, such as scales and otoliths (Francis 1990). Back-calculation also provides data on lengths for ages that are rarely observed due to, for example, inefficient sampling of juvenile fish (Francis 1990; Davis & West 1992). Moreover, as external sexual determination is rarely possible during the juvenile stages of fish, back-calculation of length at age of adult fish, for which external sex determination is possible, enables early growth rate comparisons within and between the sexes (D’Onghia et al. 2000).

In addition to inter- and intra-SSD, pike display significant differences in body lengths at the end of their first year of life (Raat 1988; Mann & Beaumont 1990), which makes it a useful model to study the long term implications of early growth histories on life-history traits and foraging behaviour. In pike, female fecundity increases with body size (Frost & Kipling 1967) and male spawning success tends to be determined through aggressive interactions, with larger males having reproductive advantages over small males (Fabricus & Gustafson 1958; Raat 1988). Intra-population, intra-SSD in pike therefore has potentially important implications for the individual reproductive fitness of both sexes.

The aim of this Chapter was therefore to determine, in situ, the extent of individual juvenile growth variation in the pike population of the River Frome study area and to identify the implications of such variation on future growth rates and adult body lengths. It was predicted that significantly slow-growing individuals during their first year of life will remain small as adults, revealed by relatively low sizes at age and slow growth rates, regardless of their gender.

3.3 MATERIALS AND METHODS

3.3.1 Fish sampling and growth analyses

Pike were sampled in the main river channel and the connected side channels of the River Frome (Chapter 2) during 2000 to 2005 and 2008 to 2011 using electric fishing (Section 2.1.2). Captured pike were measured for FL, sexed (immature, male, female) and between 3 and 5 scales were removed from above the lateral line just in front of the dorsal fin. An external sex determination was conducted (Section 2.1.3). For the purposes of a separate mark-recapture study, some of these fish were also tagged with passive integrated transponder (PIT) tags (Section 2.1.3). All fish were released back into their location of capture.

Following the derivation of the age estimate (Section 2.1.6), measurements of the distance from the scale focus to the scale edge, and the distance from the scale focus to each annulus, were taken to enable subsequent back calculation of length at each age to be made using the scale-proportional method (Section 2.1.6; Francis 1990). In subsequent analyses, data were only used from individuals aged between 1 and 8 years because of problems accurately measuring annuli in older fish as the increments that were produced then were very small, causing multiple annuli to form on the scale edge, affecting ageing accuracy.

3.3.2 Data analyses

Variation in length at age 1

To identify individual variation in length at age 1 from across all year classes in the samples, their back-calculated lengths at age 1 were used. As these were derived from fish aged between 1 and 8 years old, ANCOVA was used to test for potential differences in mean lengths at age 1 between year-classes, with mean annual summer temperature and age at capture as the covariates. The River Frome temperature data from 1994-2011 was provided by the Salmon & Trout Research Centre at East Stoke (Game & Wildlife Conservation Trust).

Body length, age and sex relationships

The effect of sex on body length and annual FL increments across ages was analysed using one-way ANOVAs. The effect of length at age 1 (the independent variable) on the FLs and FL increments ($L_{t+1} - L_t$, where L_t = length at age t) at subsequent ages (the dependent variables) was analysed using their standardised residuals in univariate linear regression for each sex. The residuals were first calculated as the difference between the individual back-calculated lengths and the mean back-calculated length per age. The standardised residuals were then calculated by dividing the overall mean residual values with the standard deviations of the residual back-calculated lengths for each individual at each age (Britton *et al*. 2010; Beardsley & Britton 2012). For each incremental age (i.e. age 1 to 2 years, age 2 to 3 years etc.), the mean and standard deviations were also calculated with the standardised residuals saved for each fish and increment. The regression analyses were performed separately for each age to avoid statistical complications of using multiple measurements from individual fish in the same test (Britton et al. 2010). Lengths between succeeding ages were correlated separately for the sexes using Pearson correlations. In addition, a one-way ANOVA was carried out to compare the mean annual FL increment and the annual difference in size between females and males. A larger difference between sexes than the mean annual FL increment would indicate that FL at age 1 predicts the sex of the individual.

The von Bertalanffy growth parameters of L_∞ (maximum theoretical length) and growth coefficient (K; annual rate at which L_∞ is reached) were then determined for females and males separately (von Bertalanffy 1938). The growth parameters were derived by plotting size at L_{t+1} against size at L_t in the Ford-Walford equation: $L_{t+1} = a + bL_t$ (Ford 1933, Walford 1946), where a = intercept, b = slope. The parameters L_∞ and K were then derived from $L_\infty = a / (1 - b)$ and $K = - \ln (b)$.

3.4 RESULTS

Between 2000 and 2011, 241 pike were sampled, of which 70 were female, 81 were male and the rest were immature (rather than unsexed adults). Thirty-four of these individuals were subsequently recaptured, and the between year ageing accuracy was 100 % (Table 3.1).

Variation in length at age 1

Observed lengths of pike at the end of their first year of life varied substantially, with, for example, the body lengths of pike of the 2008 year class at the end of their first year of life sampled in winter 2008/09 ranging between 120 and 250 mm. There was considerable variation in the lengths at age 1 within the year classes 1994 to 2006 (Fig. 3.1). The back-calculated lengths at age 1 revealed considerable length variation [n = 241, 15.1 ± 1.0 (mean ± SE), CV = 40.0 %]. Despite this, the means for the year classes did not differ significantly when adjusted for the effects of mean temperature during the first year of life and age at capture (ANCOVA, $F_{(11, 225)} = 1.79$, $P = 0.060$).

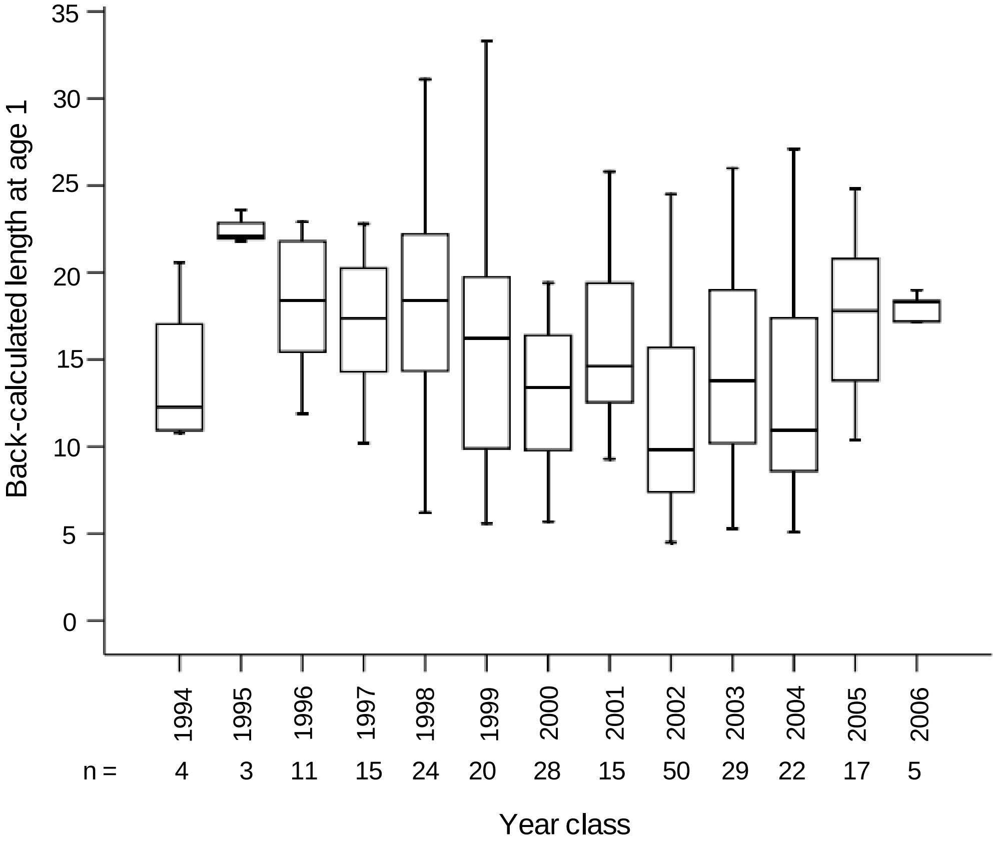

Figure 3.1. Box plot showing back-calculated lengths at age 1 by year class for pike sampled from the River Frome between 1994 and 2006. In each box plot, the top, mid-line and bottom of each box plot represent the 75^{th}, 50^{th} and 25^{th} percentiles, and the vertical bars represent the 10th and 90th percentiles.

Capture		Recapture 1		Recapture 2	
Date	Age	Date	Age	Date	Age
06/12/2004	0+	14/03/2005	1+		
17/03/2003	1+	12/03/2004	2+		
23/06/2003	1+	14/03/2005	3+	05/12/2005	3+
05/12/2003	1+	22/06/2004	2+		
09/12/2003	1+	14/03/2005	3+		
15/09/2004	1+	06/12/2005	2+		
14/03/2005	1+	05/12/2005	1+		
14/03/2005	1+	06/12/2005	1+		
14/03/2005	1+	05/12/2005	1+		
14/09/2005	1+	05/12/2005	1+		
24/03/2003	2+	07/01/2004	2++		
13/09/2004	2+	14/03/2005	3+		
13/09/2004	2+	05/12/2005	3+		
06/12/2004	2+	14/03/2005	3+	05/12/2005	3+
14/03/2005	2+	14/03/2005	2+		
14/03/2005	2+	18/04/2005	2+		
14/03/2005	2+	06/12/2005	2+		
15/03/2005	2+	06/12/2005	1+		
25/02/2009	2++	04/03/2010	4+		
10/09/2003	3+	12/03/2004	4+		
10/09/2003	3+	10/12/2004	4+	15/03/2005	5+
07/03/2009	3+	04/03/2010	4+		
24/03/2003	4+	12/03/2004	5+		
16/04/2003	4+	23/02/2004	4++		
25/03/2003	5+	24/02/2004	5++		
26/03/2003	5+	23/02/2004	5++		
05/08/2003	5+	23/02/2004	5++		
23/02/2004	5++	08/03/2005	7+		
24/02/2004	5++	21/07/2004	6+		
16/04/2003	6+	23/02/2004	6++		
16/03/2004	6+	08/03/2005	7+		
09/03/2009	6+	04/03/2010	7+		
25/03/2003	7+	24/02/2004	7++		
25/02/2009	7++	12/03/2009	8+		

Table 3.1. Dates of capture and recaptures and the corresponding ages of pike individuals. ++ indicates that the individual has almost reached the next year of age.

Body length, age and sex relationships

Compared to males, females had significantly larger lengths at all ages apart from ages 3 and 4 years. Female FL increments were also significantly higher at ages 1, 3, 5 and 6 (Table 3.2; Fig. 3.2). Females also had a higher L_∞ value and lower growth coefficient (n = 70, L_∞ = 1043 mm, K = 0.22) compared to males (n = 81, L_∞ = 719 mm, K = 0.37).

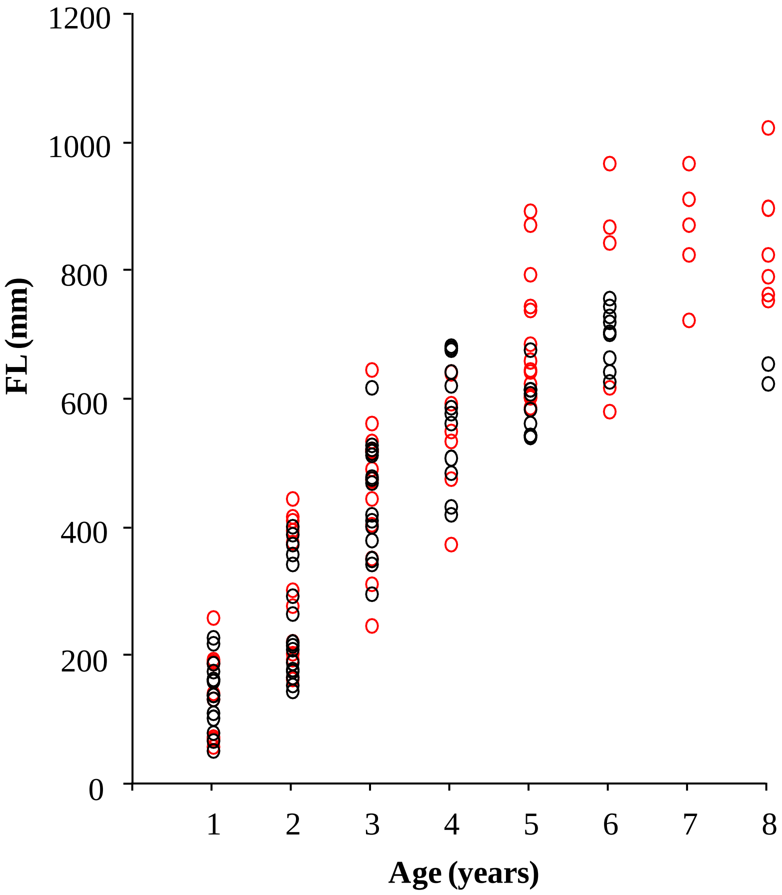

Figure 3.2. Observed fork lengths (FL) at ages 1 to 8 of males (black) and females (red) pike *Esox lucius* in the River Frome.

Source of variation	Age	df	Type-III sum of squares	F	P
FL (mm)	1+	1,149	17.85	4.666	**0.032**
	2+	1,125	165.95	4.421	**0.037**
	3+	1,97	247.50	2.453	0.120
	4+	1,68	344.93	3.323	0.071
	5+	1,49	399.25	4.035	**0.049**
	6+	1,25	1068.66	10.808	**0.002**
	7+	1,11	751.01	5.754	**0.024**
	8+	1,6	881.12	9.049	**0.012**
Increments (mm)	0-1	1,149	165.95	4.421	**0.037**
	1-2	1,125	9.70	0.211	0.646
	2-3	1,97	96.80	5.494	**0.021**
	3-4	1,68	14.27	1.206	0.276
	4-5	1,49	49.66	6.655	**0.013**
	5-6	1,25	34.41	8.422	**0.008**
	6-7	1,11	5.69	0.804	0.389
	7-8	1,6	0.04	0.013	0.914

Table 3.2 One-way ANOVAs testing for the effect of sex on FL (mm) and annual increments (mm) at ages 1 to 8. Significant ($P < 0.05$) p-values are shown in bold.

The relationship between body size at age 1 for individual fish and their subsequent lengths at age revealed positive and significant relationships, with small fish at age 1 remaining smaller from age 2 to 5 in both female (Fig. 3.3) and male fish (Fig. 3.4). In females, this relationship was significant also at ages 6 ($n = 16$, $R^2 = 0.47$, $P = 0.003$), 7 ($n = 11$, $R^2 = 0.63$, $P = 0.003$) and 8 ($n = 6$, $R^2 = 0.71$, $P = 0.036$).

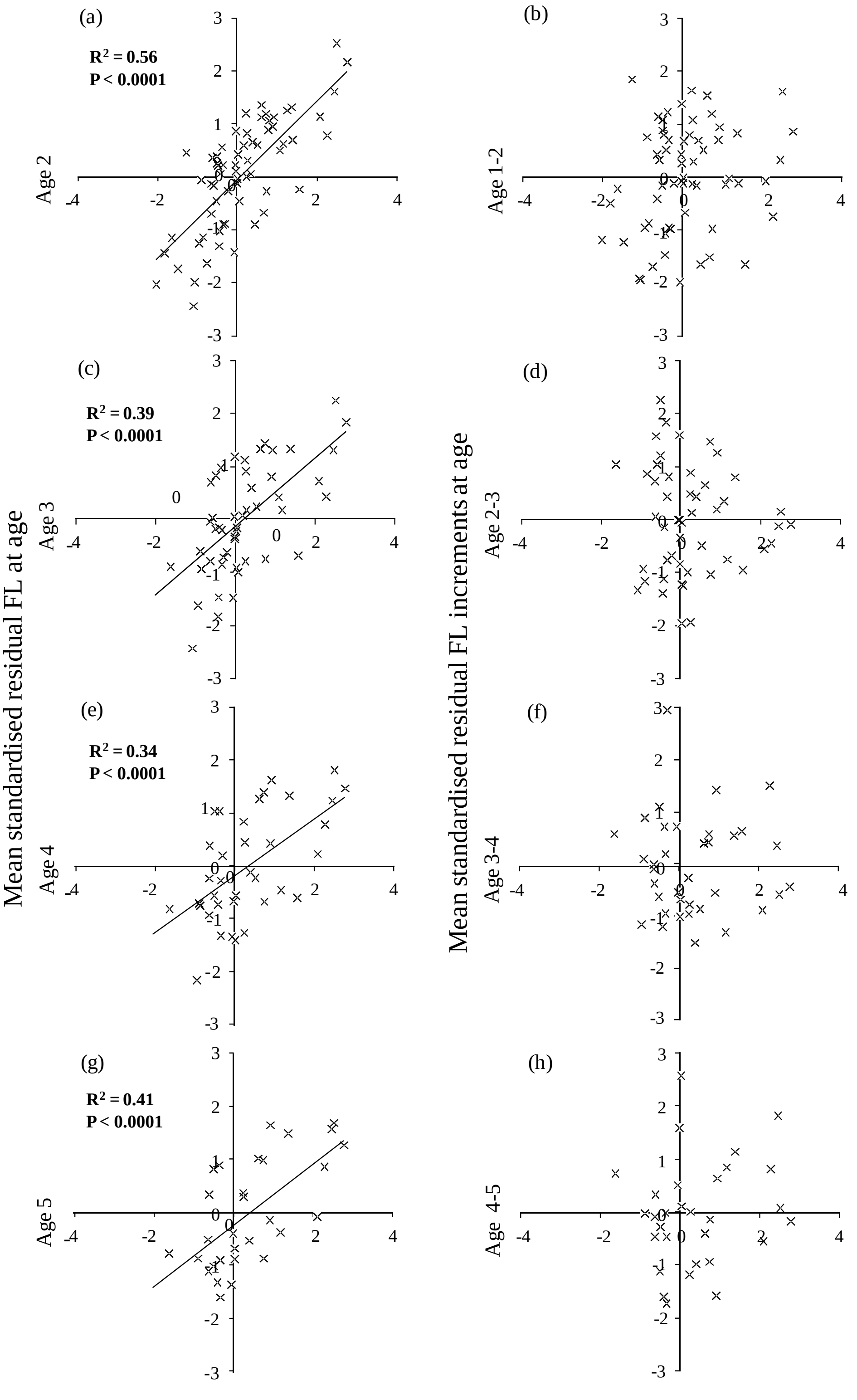

Figure 3.3. Mean standardised residual FL and increments at ages 2 (a-b), 3 (c-d), 4 (e-f) and 5 (g-h) in relation to the standardised residual FL at age 1 in female pike. Solid lines show significant relationships according to linear regression.

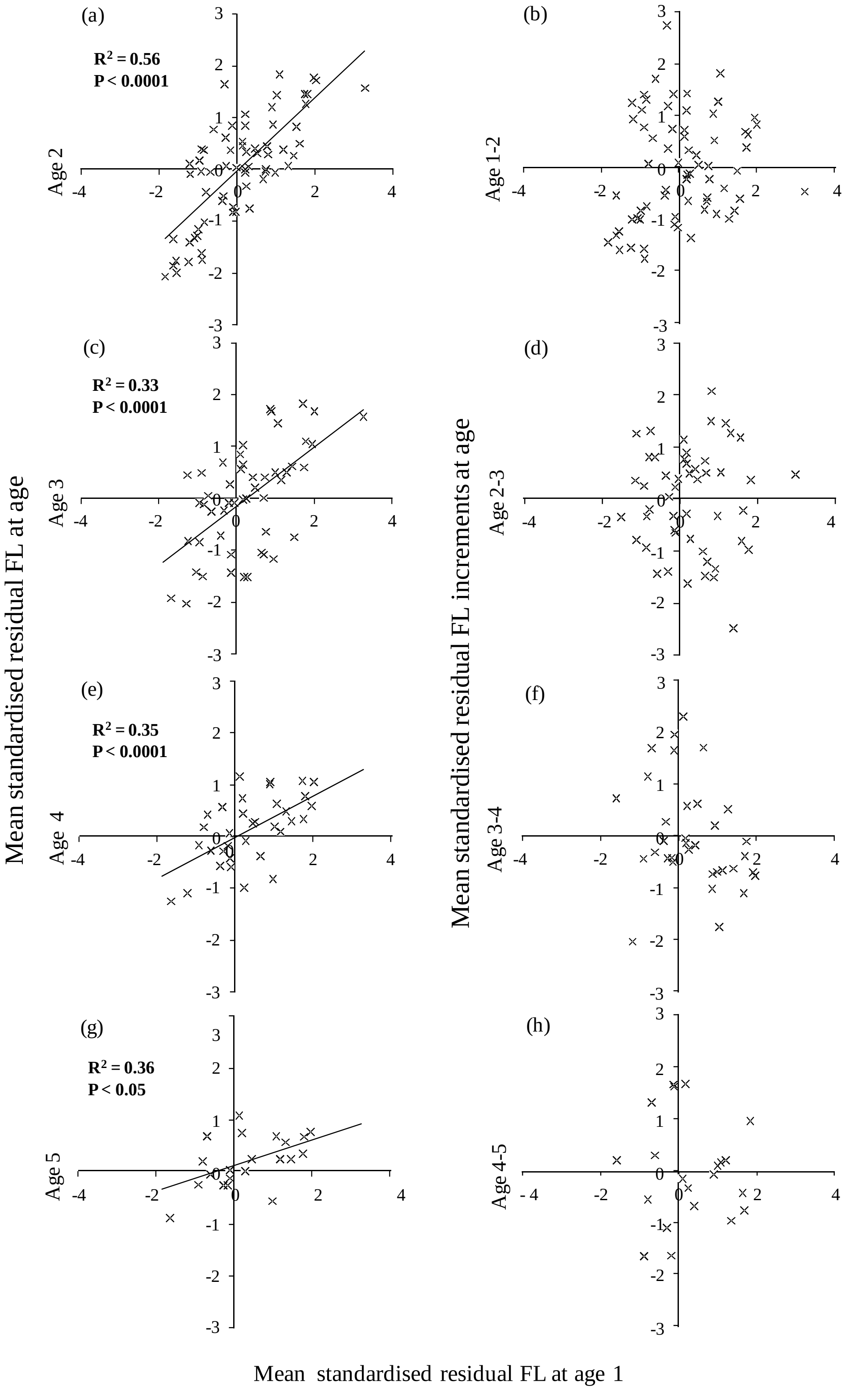

Figure 3.4. Mean standardised residual FL and increments at ages 2 (a-b), 3 (c-d), 4 (e-f) and 5 (g-h) in relation to the standardised residual FL at age 1 in male pike. Solid lines show significant relationships according to linear regression.

In males, no relationship between length at age 1 and length at age 6 was found (n = 11, R^2 = 0.21, P = 0.160), while there were not enough individuals of males at ages 7 (n = 2) and 8 (n = 2) to analyse. In contrast, length at age 1 had no significant effect on FL increments (Fig. 3.3; Fig. 3.4), except for females between age 6 and 7 (n = 11, R^2 = 0.41, P = 0.035). Significant correlations between individual lengths at all succeeding ages (FL_{t+1} vs. FL_t) were found in females and males (Table 3.3). The mean annual FL increment did not differ significantly from the mean annual difference in FL between the sexes (ANOVA, $F_{(1,12)}$ = 1.96, P = 0.186).

	Females			Males		
FL between ages	N	R	P	n	r	P
1 and 2	61	0.95	**0.003**	66	0.69	**0.044**
2 and 3	49	0.98	**0.001**	50	0.88	**0.001**
3 and 4	36	0.99	**<0.001**	34	0.93	**<0.001**
4 and 5	30	0.98	**<0.001**	21	0.98	**<0.001**
5 and 6	16	0.97	**0.001**	6	0.99	**<0.001**
6 and 7	11	1.00	**<0.001**	2	-	-
7 and 8	6	0.99	**<0.001**	2	-	-

Table 3.3. Pearson correlations between FL at succeeding ages in females and males (- is for missing data). Significant (P < 0.05) P-values are shown in bold.

3.5 DISCUSSION

There were significant variations in the body length at age 1 of pike in this population across year classes and this had significant implications on the individual adult body lengths. Pike that were relatively small at age 1 then generally remained smaller at least up to age 8 compared with larger pike at age 1 and this was independent of sex. This was a consequence only of the variability in the length at age 1 as there was no relationship between length at age 1 and the size of subsequent annual FL increments. Thus, the variability in the YOY growth rates produced considerable variation in lengths at age 1, with this appearing to be the key factor that underpinned the observed variations in body sizes within and between the sexes.

As for most invertebrates and lower vertebrates species (Andersson 1994; Abouheif & Fairbairn 1997), inter-sex size dimorphism was female-biased in the study population (Raat 1988), and could be explained by the fact that clutch sizes increase with body size. Larger females, at least in cold-blooded organisms, are thought to be favoured through fecundity selection (Darwin's fecundity advantage hypothesis: Darwin 1871; Stearns 1992; Andersson 1994). In comparison, gamete production has not been related to body size in males, where sexual selection is instead regarded as the main evolutionary force selecting for a larger size (Darwin 1871; Andersson 1994).

Existing empirical evidence indicates that inter-SSD is mainly driven by differences in development time in vertebrates, such as in birds (Teather & Weatherhead 1994) and reptiles (Shine 1994; Lagarde et al. 2001). This has also been reported in fish, for example, in the percid species walleye (*Sander vitreus* Mitchill) and yellow perch (*Perca flavescens* Mitchill) the emergence of inter-sex size dimorphism was related to an earlier maturation and subsequent slower growth in males (Rennie et al. 2008). Also, in the Colorado pikeminnow (*Ptychocheilus lucius* Girard), growth divergence between the sexes is thought to coincide with the onset of maturation (Osmundson 2006). Despite studies of pike showing that males reach maturity earlier than females (Raat 1988; Knight 2006), here there was a strong association between the divergences in size between the sexes and early growth differences. The mean individual annual FL increment did not differ significantly from the mean annual difference between males and females, suggesting that the larger individuals at age 1 are females and the smaller are males. Although mean female and male body lengths did not differ at ages 3 and 4, females still had significantly higher body lengths at all other ages, as well as higher FL increments at most ages. This, together with a higher female L_∞, indicates that males were unable to 'catch up' in their overall lengths. In a cannibalistic species, such as pike, where cannibalism has been found to occur already at larval stages (Bry et al. 1995), a factor why SSD emerges at an early age may be a dynamic interaction between size-dependent competition and cannibalism, with large cannibals and dwarf-sized non-cannibals coexisting in a single population (Claessen et al. 2000, 2002). Moreover, medium-sized individuals may be more vulnerable to intra-specific predation as they still have high energy requirement and hence may take more risks during foraging compared to small-sized individuals (Polis 1981; Byström et al. 2004). Whether females have higher cannibalistic propensities than males, however, requires further investigation.

Individual variation in length was maintained across ages both in males and females, transcending the onset of sexual maturity of pike, for which ages ranging from 1 to 4 have been reported (Frost & Kipling 1967; Raat 1988; Knight 2006). Individual variation in size within sexes is frequently observed in species with indeterminate growth (Taborsky 1999). In many fishes, the expression of intra-SSD is common and given the implications for the fitness of individuals, is often associated with alternative reproductive tactics (ART), especially within males (Blanckenhorn 2005; Taborsky & Brockmann 2010). The most commonly reported body size-related ARTs in fish are the so-called ‘bourgeois’ and ‘parasitic’ tactics (Taborsky 1997, 2001). The bourgeois males typically invest in resources to attract mates (e.g. large body size) or/and to fight other males, while the parasitic males (‘sneakers’) attempt to steal fertilisations from a spawning pair (Oliveira et al. 2005; Reichard et al. 2007). A species where this has been well studied is the coho salmon (*Oncorhynchus kisutch* Walbaum), where large and small males gain access to females by fighting and sneaking respectively (Gross 1985). While intermediate-sized males are at a competitive disadvantage, evidence that the small and large male coho salmon achieve similar lifetime fitness has been reported (Gross 1985). The occurrence of two modes of reproductive strategies has also been indicated in male pike (Fabricus & Gustafson 1958; Knight 2006). Consequently, early growth may have important consequences on individual reproductive success and drive the emergence of ART in pike populations. This, however, remains to be tested explicitly and is not covered in this thesis.

In summary, the outputs here revealed that individual growth variation during the first year of life of pike in the River Frome study population had lifetime consequences for individual body sizes, but not growth rates. This suggests that early growth is the main driver of sexual size dimorphism in this species, which differs from general patterns shown in other vertebrates. Individual growth rates during the juvenile stages may therefore have important effects on overall fitness, and drive the formation of alternative reproductive strategies in this pike population. The focus of the following chapters is to identify potential drivers of growth variation during the first year of life. This includes investigating the role of diet, movement, habitat shifts and underlying personality traits in relation to growth differences.

3.6 REFERENCES

Abouheif, E. & Fairbairn, D. J. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch’s rule. *The American Naturalist*, 149, 540-562.

Abrams, P. A., Olof Leimar, Nylin, S. & Wiklund, C. 1996. The effect of flexible growth rates on optimal sizes and development times in a Seasonal environment. *The American Naturalist*, 147, 381-395.

Andersson, M. 1994. *Sexual selection.* Princeton, N.J.: Princeton University Press.

Arendt, J. D. 1997. Adaptive intrinsic growth rates: An integration across taxa. *Quarterly Review of Biology*, 72, 149-177.

Arendt, J. D. & Wilson, D. S. 1997. Optimistic growth: competition and an ontogenetic niche-shift select for rapid growth in pumpkinseed sunfish (*Lepomis gibbosus*). *Evolution*, 51, 1946-1954.

Beardsley, H. & Britton, J.R. 2012. Contribution of temperature and nutrient loading to growth rate variation of three cyprinid fishes in a lowland river. *Aquatic Ecology*, 46, 143-152.

Björklund, M., Hirvonen, H., Seppä, T., Peuhkuri, N. & Piironen, J. 2003. Phenotypic variation in growth trajectories in the Arctic charr *Salvelinus alpinus*. *Journal of Evolutionary Biology*, 16, 543-550.

Blanckenhorn, W. U. 2005. Behavioral causes and consequences of sexual size dimorphism. *Ethology*, 111, 977-1016.

Brett, J. R. 1979. Environmental factors and growth of fish. In: *Fish Physiology*, Vol VIII (Ed. by W. S. Hoar, D. J. Randall, & J. R. Brett), pp. 599-675. London: Academic Press.

Britton, J. R., Davies, G. D. & Harrod, C. 2010. Trophic interactions and consequent impacts of the invasive fish *Pseudorasbora parva* in a native aquatic foodweb: a field investigation in the UK. *Biological Invasions*, 12, 1533-1542.

Bry, C., Bonamy, F., Manelphe, J. & Duranthon, B. 1995. Early-life characteristics of pike, *Esox lucius*, in rearing ponds - temporal survival pattern and ontogenic diet shifts. *Journal of Fish Biology*, 46, 99-113.

Bulté, G., Gravel, M.-A. & Blouin-Demers, G. 2008. Intersexual niche divergence in northern map turtles (*Graptemys geographica*): the roles of diet and habitat. *Canadian Journal of Zoology*, 86, 1235-1243.

Byström, P., Andersson, J., Persson, L. & De Roos, A. M. 2004. Size-dependent resource limitation and foraging-predation risk trade-offs: growth and habitat use in young arctic char. *Oikos*, 104, 109-121.

Calow, P. 1982. Homeostasis and Fitness. *The American Naturalist*, 120, 416-419.

Chown, S. L. & Gaston, K. J. 2010. Body size variation in insects: a macroecological perspective. *Biological Reviews*, 85, 139-169.

Claessen, D., De Roos, A. M. & Persson, L. 2000. Dwarfs and giants: Cannibalism and competition in size-structured populations. *American Naturalist*, 155, 219-237.

Claessen, D., Van Oss, C., De Roos, A. M. & Persson, L. 2002. The impact of size-dependent predation on population dynamics and individual life history. *Ecology*, 83, 1660-1675.

D’Onghia, G., Basanisi, M. & Tursi, A. 2000. Population structure, age and growth of macrourid fish from the upper slope of the Eastern-Central Mediterranean. *Journal of Fish Biology*, 56, 1217-1238.

Darwin, C. 1871. *The descent of man, and selection in relation to sex.* London: John Murray.

Davis, T. L. O. & West, G. J. 1992. Growth and mortality of *Lutjanus vittus* (Quoy and Gaimard) from the north-west shelf of Australia. *Fishery Bulletin*, 90, 395-404.

Fabricus, E. & Gustafson, K. 1958. Some new observations on the spawning behaviour of the pike, *Esox lucius* L. *Institute of Freshwater Research, Drottningholm*, 23-54.

Fairbairn, F., Blanckenhorn, W. & Szkely, T. 2007. *Sex, size, and gender roles. Evolutionary studies of sexual size dimorphism.* Oxford University Press.

Francis, R. I. C. C. 1990. Back-calculation of fish length: a critical review. *Journal of Fish Biology*, 36, 883-902.

Frost, W. E. & Kipling, C. 1967. A study of reproduction early life weight-length relationship and growth of pike *Esox lucius* L. in Windermere. *Journal of Animal Ecology*, 36, 651-&.

Kingsolver, J. G. & Pfennig, D. W. 2007. Patterns and power of phenotypic selection in nature. *BioScience*, 57, 561-572.

Knight, C. 2006. Utilisation of off-river habitats by lowland river fishes. PhD Thesis, University of Durham, UK.

Lagarde, F., Bonnet, X., Henen, B. T., Corbin, J., Nagy, K. A. & Naulleau, G. 2001. Sexual size dimorphism in steppe tortoises (*Testudo horsfieldi*): growth, maturity, and individual variation. *Canadian Journal of Zoology*, 79, 1433.

Lohmus, M., Björklund, M., Sundström, L. F. & Devlin, R. H. 2010. Effects of temperature and growth hormone on individual growth trajectories of wild-type and transgenic coho salmon *Oncorhynchus kisutch*. *Journal of Fish Biology*, 76, 641-654.

Mann, R. & Beaumont, W. 1990. Fast- and slow-growing pike, *Esox lucius* L., and problems of age-determinations from scales. *Aquaculture and Fisheries Management*, 21, 471-478.

Metcalfe, N. B. 1993. Behavioural causes and consequences of life history variation in fish. *Marine Behaviour and Physiology*, 23, 205-217.

Oliveira, R. F., Ros, A. F. H. & Goncalves, D. M. 2005. Intra-sexual variation in male reproduction in teleost fish: a comparative approach. *Hormones and Behavior*, 48, 430-439.

Osmundson, D. B. 2006. Proximate causes of sexual size dimorphism in Colorado pikeminnow, a long-lived cyprinid. *Journal of Fish Biology*, 68, 1563-1588.

Peacor, S. D. 2006. Behavioural response of bullfrog tadpoles to chemical cues of predation risk are affected by cue age and water source. *Hydrobiologia*, 573, 39-44.

Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics*, 12, 225-251.

Raat, A. 1988. *Synopsis of biological data on the northern pike Esox lucius Linnaeus 1758.* FAO Fish. Synopsis.

Reichard, M., Le Comber, S. C. & Smith, C. 2007. Sneaking from a female perspective. *Animal Behaviour*, 74, 679-688.

Rennie, M. D., Purchase, C. F., Lester, N., Collins, N. C., Shuter, B. J. & Abrams, P. A. 2008. Lazy males? Bioenergetic differences in energy acquisition and metabolism help to explain sexual size dimorphism in percids. *Journal of Animal Ecology*, 77, 916-926.

Shine, R. 1994. Allometric Patterns in the ecology of Australian snakes. *Copeia*, 1994, 851-867.

Stearns, S. C. 1992. *The Evolution of Life Histories.* Oxford University Press, USA.

Taborsky, M. 1997. Bourgeois and parasitic tactics: do we need Collective, functional terms for alternative reproductive behaviours? *Behavioral Ecology and Sociobiology,* 41, 361-362.

Taborsky, M. 1999. Conflict or cooperation: what determines optimal solutions to competition in fish reproduction? In: *Behaviour and conservation of littoral fishes*, (Ed. by R. Oliveira, V. Almada, & E. Goncalves), pp. 301-349. Lisbon: ISPA.

Taborsky, M. 2001. The evolution of bourgeois, parasitic, and cooperative reproductive behaviors in fishes. *Journal of Heredity*, 92, 100-110.

Taborsky, M. & Brockmann, H. J. 2010. Alternative reproductive tactics and life history phenotypes. In: *Animal Behaviour: Evolution and Mechanisms*, (Ed. by P. Kappeler), pp. 537-586. Berlin, Heidelberg: Springer Berlin Heidelberg.

Teather, K. L. & Weatherhead, P. J. 1994. Allometry, adaptation, and the growth and development of sexually dimorphic birds. *Oikos*, 71, 515-525.

Uchmanski, J. 1985. Differentiation and frequency distributions of body weights in plants and animals. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 310, 1-75.

von Bertalanffy, L. 1938. A quantitative theory of organic growth. *Human Biology*, 10, 181-213.

Chapter 4

Is individual variation in movement related to trophic niche, body size and growth rate in juvenile pike (*Esox lucius* L)?

4.1 ABSTRACT

Although individual variation in movement may have important ecological effects for population- and ecosystem-level processes, factors affecting movement remain poorly understood. Here, inter-individual variability in movement in juvenile pike of ages 0+ and 1+ years inhabiting side-channels of the River Frome was assessed in relation to body size, age, growth rate and trophic niche using a combination of telemetry and stable isotope analysis. The results revealed significant size-dependent and repeatable in individual movement within age-classes, which was unrelated to trophic niche or growth rate. The study therefore provides rare insight into the relationship between consistent individual behaviour and size variation during the development of size dimorphism and indicates that individual variation within a wild population is more than just noise around an adaptive mean. The association between a higher level of movement and a higher susceptibility to intraspecific interference or/and predation, and hence boldness is discussed.

4.2 INTRODUCTION

Most animals rely on a certain level of displacements to forage, avoid predators or to compete for resources, making movement an important attribute of survival (Turchin 1998; Bergman et al. 2000). Natural selection is therefore predicted to favour foraging tactics that maximise the assimilation of energy and hence growth as a fitness proxy, such as movement associated with food location and capture (Stearns 1992). However, intraspecific variability in movement still exists, as observed in mammals (e.g. Pinter-Wollman 2009), birds (e.g. Catry et al. 2011) and fish (e.g. Kobler et al. 2009), and is suggested to reflect underlying behavioural strategies of individual (Austin et al. 2004; Salomon 2009). Indeed, activity involving risk-taking is often considered to be indicative of boldness (Bell 2005; Harcourt et al. 2009), and as bolder individuals tend to be superior competitors, it is often positively associated with somatic growth and, ultimately, fitness (Höjesjö et al. 2002; Sundström et al. 2004; Ward et al. 2004).

Consistent individual variation in growth rates is common in many animals, especially in animals with indeterminate growth (Stamps 2007; Section 1.4). Two contrasting theories explain the maintenance of individual variation in growth rates by life-history trade-offs related to foraging. According to the growth-mortality trade-off, individuals with higher activity acquire resources that enable faster growth but tend to take more risks and so are exposed to a higher risk of predation (Werner & Anholt 1993; Mangel & Stamps 2001; Stamps 2007). Alternatively, trade-offs between activity and growth occur where individuals with increased levels of activity have decreased growth rates due to increased energy expenditure in foraging that is not balanced by the acquisition of additional resources (Koch & Wieser 1983; Rennie et al. 2005; Killen et al. 2007; Reinbold et al. 2009). Indeed, experimental studies on several fish species have revealed growth differences to be related to foraging behaviour (Jobling & Baardvik 1994; Wang et al. 1998; Qian et al. 2001; Martins et al. 2005; Imsland et al. 2009). For example, in juvenile Atlantic salmon, faster growing fish swam more (Martin-Smith & Armstrong 2002) supporting the former theory, while the opposite was found in Crucian carp (*Carassius carassius* L.) (Johansson & Andersson 2009). Studies on wild populations are, however, comparatively rare due to difficulty in repeated sampling of the same individuals in their natural habitat (Bell et al. 2009; Archard & Braithwaite 2010) Finally, although ontogeny might affect variability, with individuals becoming more variable and/or specialised with age (Polis 1984), age is not always being accounted for in these studies.

As an apex predator fish, pike is a strong model species for studying these potential behaviours related to growth and foraging, as considerable variation in early-life growth rates have been found in both wild populations (Chapter 3; Raat 1988; Mann & Beaumont 1990; Cucherousset et al. 2007) and under controlled conditions (Bry et al. 1995; Ziliukiene & Ziliukas 2006). Moreover, several studies on pike have revealed high inter-individual variation in their spatial behaviour (Masters et al. 2005; Vehanen et al. 2006; Andersen et al. 2008, Cucherousset et al. 2009) and trophic ecology (Chapman et al. 1989; Beaudoin et al. 1999; Skov et al. 2003). Studies also suggest that individuals show a high degree of movement between their ambush sites (Diana 1980; Masters 2003). While ontogenetic diet shifts of juveniles typically follows a sequence of microcrustacea, insects, macrocrustacea and then fish (Raat 1988; Skov et al. 2003; Ziliukiene & Ziliukas 2006), the timing of this shift to piscivory differs between populations, between individuals within populations and even between individuals within the same cohort (Giles et al. 1986; Mann & Beaumont 1990; Wolska-Neja & Neja 2006).

Consequently, through using pike in their initial years of life, the aim of this chapter was to test the relationship between individual movement and trophic position with their body size, age and somatic growth. The following hypotheses were tested: (i) inter-individual variation in movement is consistent within age-classes; (ii) movement varies between age-classes, with age 1+ individuals exhibiting a higher level movement than those of 0+; and (iii) individuals that consistently move more will be more active foragers (i.e. risk-takers), and consequently, experience faster growth rates, attain larger body sizes and higher trophic positions compared to individuals that move less (risk-averse). Individual movement was determined using PIT telemetry (Section 2.14) and their trophic ecology of was determined through stable isotope analyses of $\delta^{13}C$ and $\delta^{15}N$ (Section 2.1.5).

4.3 MATERIALS AND METHODS

4.3.1 Fish sampling and tracking

PIT telemetry was carried out in three side channels (Railway, Flood relief and Rushton) (Section 2.1) during three periods (spring 2009, spring 2010 and winter 2010/11). Prior to the start of each tracking period, pike were captured by electric fishing, PIT tagged, measured, weighed, sampled for scales (for ageing) and fin tissue (SIA) (Section 2.1). Following their recovery from the tagging procedure, the pike were released close to their individual capture point. During the telemetry surveys, the locations of PIT-tagged pike were established using a portable PIT antenna system (Texas Instruments; TIRIS S-2000). The system consisted of a half-duplex reader module (RIRFM- 008B-30) operating at 134.2 kHz, connected to a control module (RI-CTL-MB2B-30). The modules were powered by a rechargeable 12 V battery. The system was connected to an electric buzzer to indicate tag detection. All components were enclosed in a water proof case inside a small rigid-frame backpack. The reader module was connected to an open loop inductor antenna (LF-HHLOOP) that generated an electromagnetic field and received transmitted signals from the tag. A waterproof personal digital assistant (PDA, Meazura, Aceeca, NZ) was connected to the control module via an RS-232 serial cable. A software program (www.oregonrfid.com) was continuously displayed and logged tag ids were sent from the control module along with the date and the time. The PDA was carried outside of the backpack so that the operator could see the displayed tag ids (Fig. 4.1).

Figure 4.1. Tracking in the ditch ‘Flood relief’ using the portable antenna.

The detection range, measured as the distance between the plane of the antenna loop and the tag, varied with tag orientation, ranging from 55 cm when the tag was horizontal to 85 cm when the tag was vertical. The antenna was swept just above the water surface to detect the pike and when water depth was higher than the minimum detection distance of 55 cm, the antenna was submerged vertically to increase the detection efficiency. The pike were tracked in a downstream direction from each side of the bank, except for Railway ditch, where it was only possible from one bank due a railway track on the left-hand bank. While the effect of the tracking direction has been shown not to affect the detection efficiency of pike (Cucherousset et al. 2010); a downstream direction was chosen for consistency across ditches and tracking periods. The tracking survey for all side channels took on average 4.5 hours (Railway ditch 1.5 h, Flood relief 1h and Rushton ditch 2 h). To test for the effect of time of day on tracking, it was conducted at different times of day and started at dawn (0600 to 0800 hours, n = 5), day (1000 to 1400 hours, n = 6) or dusk (1600 to 1700 hours, n = 6) during spring 2009. As this revealed no significant effect of time of day on the number of fish detected (ANOVA, $F_{(2,19)} = 0.13$, $P > 0.05$) or the average movement (ANOVA, $F_{(2,19)} = 0.94$, $P > 0.05$), all subsequent surveys were conducted during daylight hours (0900 and 1700 hours). During a tracking survey, the patch number and distances along the length of the patch and to the closest bank (nearest 0.1 m) were recorded at tag detection (Section 2.1.1). A total of 17 surveys per ditch were carried out from 24 March to 31 May 2009, 13 surveys from 11 March to 27 May 2010, and 12 surveys from 5 January to 22 February (see Appendix II for specific dates of tracking and number of fish detected in each ditch). Railway ditch was not sampled in winter 2010/11 due to few individual pike (n=2) being captured prior to the tracking period. As winter and spring trackings were separated in time with a minimum of one month, a comparison between ages and tracking season was simplified by giving pike of the same year-class the same age in winter and spring. For example, pike in their first year of life (i.e. 0+) were also categorised as 0+ during spring trackings, albeit they would just have started their second year of life. As growth rates of pike remain very low at temperatures below 12^{o}C (e.g. at 10^{o}C $SGR_{FL} = 0.05$ % day^{-1}) (Casselman 1996), pike in the spring would be physiologically similar to fish sampled 2 months earlier. Electric fishing was conducted after each tracking period to recapture detected fish for size measurements and fin-clipping in order to determine growth rates and change in trophic position respectively (Section 2.1). To avoid taking into account localisations of lost tags (due to tag expulsion or fish mortality), detected individuals that were not recaptured at a subsequent date were excluded from the subsequent analyses.

The detection efficiency (%) was using the formula: $100(N_d/N_p)$, where N_d is the number of tagged individuals detected with the antenna during a tracking session and N_p is the number of tagged individuals present in the study area during tracking. Individuals were classed as present in the study area at a particular tracking session if they were subsequently recaptured during one of the following electric fishing events (Cucherousset et al. 2010). The tracking efficiency was determined using the last tracking session of each tracking survey (spring 2009, 2010 and winter 2010/11) for the side channels surveyed, giving a total number of 8 calculations of tracking efficiency.

4.3.2 Trophic niche

Fin samples of individuals that were detected and then recaptured at the end of the tracking surveys were analysed for their stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to determine their trophic niche and trophic position (TP) (Section 2.1.5)

4.3.3 Data analyses

Movements of individual pike were quantified by plotting each fish location into two-dimensional coordinates values y (metre transects along the ditch length) and x (equidistant strata across the ditch width (Roussel et al. 2004; Cucherousset et al. 2009). The mean position for each individual was calculated by averaging the x coordinate values for all points (x_1, x_2, x_3,...) to obtain $\bar{x}$, and the y coordinate values (y_1, y_2, y_3,...) to obtain $\bar{y}$. This mean position ($\bar{x}$, $\bar{y}$) is the point from where the distance to all other points is the smallest (Lair 1987). Radial distances (d_1, d_2, d_3,...), the measured distances from the mean position ($\bar{x}$, $\bar{y}$) and every location were calculated to provide an estimation of fish dispersal around its arithmetic mean position. The arithmetic mean radial distance ($\bar{d}$) was then calculated by averaging the radial distances. Distances between two successive positions were calculated and divided by time (in days) to provide a measurement of the average distance travelled per day ($\bar{v}$).

The specific growth rate (SGR) of each individual was determined for 0+ and 1+ pike using the initial and final fork lengths (mm) measured prior to and after the specific tracking period respectively and then the calculation was as per Section 2.4. To account for the influence of water temperature on the SGR, temperatures (°C) in each ditch were recorded hourly (middle of the stretch) using TinyTag data loggers (Gemini Data Loggers, Chichester, UK). The mean water temperature for each tracking period was then used in the analyses.

4.3.4 Statistical analyses

To test whether pike detected in the different three ditches (Rushton, Flood relief and Railway) differed in the measured variables (movement, TP, SGR, and FL) for each tracking period (spring 2009, spring 2010, winter 2010/11) and age, one-way ANOVAs were performed with ditch as a categorical factor. In tracking periods where pike of different ages were detected in all ditches two-way ANOVAs were performed with age as categorical factors in periods to enable the interaction term (ditch × age). As there were no differences in the measured variables between ditches with non-significant interaction terms (all $P > 0.05$), individuals sampled from the different ditches were combined in subsequent analyses.

To identify whether individual movement was consistent within age-classes (Hypothesis 1), repeatability analyses (± SE and 95% CI) of individual radial distances moved (d_1, d_2, d_3,...) and distances between each successive location was calculated using restricted maximum likelihood model (GLMMs). Individual ID was fitted as the random effect and the radial distance as the dependent factor (rptR package in R, Nakagawa & Schielzeth 2010). To compare repeatability estimates, the effect sizes and the 95 % CI were compared, along with determining whether the confidence intervals overlapped with zero (Nakagawa 2004; Garamszegi 2006; Nakagawa & Cuthill 2007).

As only 0+ pike were detected in spring 2009, GLMs that included data from only 2010 and 2011 were built to test for the possible effects of age (0+, 1+) and season (spring 2010, winter 2010/11) (Hypothesis 2) and their interaction, on movement ($\overline{d}$ or $\overline{v}$) as the response variable. Since the number of detections could have been related to movement, this was included as a covariate in these two models. Similar models were built with TP, $\delta^{15}N$, or $\delta^{13}C$ as the response variable; however, as body size generally relates to trophic niche, FL was used as the single covariate here. The effects of age and period on SGR with FL and mean temperature as covariates (growth is generally temperature and size dependent in fish) were also analysed, as well as on initial FL, but without the use a covariate.

To test whether there was a relationship between movement, SGR, FL or trophic niche (Hypothesis 3), a GLMM was performed rather than a GLM as the number of detections varied between individuals. In the model, $\bar{d}$ was fitted as the response variable and individual identity as the random variable. Each model was initially fitted with all other measured variables (FL, SGR, TP or $\delta^{15}N$, $\delta^{13}C$ and number of detections) as fixed predictors, and subsequently, only with the factors that were significant. If a significant effect of the number of detections was found, the individuals with the lowest number of detections were removed from the analyses until no significant effect was detected. This is because an association between the number of detections and movement may be a consequence of the number of individual data points in the model.

To obtain normal and homogenous variances prior to parametric analyses, mean radial distance moved ($\bar{d}$), average distance travelled per day ($\bar{v}$), SGR, and TP were ln (x+1) transformed. The repeatability analyses were conducted using R 2.12.2 (R Development Core Team 2009), and all other analyses were conducted in STATISTICA, version 7.

4.4 RESULTS

4.4.1 Sample sizes and detection efficiency

The total number of tagged pike at age was 100 at 0+, 53 at 1+, 4 at 2+ and 2 at 3+. Of these, 35 individuals of 0+ and 15 of 1+ were recaptured after the tracking periods, but none of the 2+ and 3+ pike were recaptured. Thus, only 0+ and 1+ fish were included in the statistical analyses. An external sex determination had not been possible as the fish were too young.

During the three tracking surveys, a mean (± SD) of 70.7 (± 11.7) % of the pike present in the side channels were detected. Detection efficiency may depend on the species studied (Cucherousset et al. 2010), but also on the water depth in the study site. In similar tracking studies using portable antennae, detections efficiencies of 19.6 to 81.7 % have been reported (Roussel et al. 2000; Cucherousset et al. 2005, 2007; Enders et al. 2007). In these studies the water depths were between 9 and 32 cm. As the mean depths (± SD) of the side channels in the present study were higher (34 ± 18 cm in Railway, 45 ± 20 cm in Rushton and 53 ± 10 cm in Flood relief), the portable detector used was considered to have relatively high detection efficiency.

The overall average number of detections (including all three tracking periods) per fish was 8.6 (± 4.0 SD, range: 2 to 17; Table 4.1), but did not differ significantly between ages (ANOVA, $F_{1,48} = 0.51$, $P > 0.05$), or between tracking period for either 0+ (ANOVA, $F_{1,27} = 1.10$, $P > 0.05$) or for 1+ (ANOVA, $F_{1,13} = 0.45$, $P > 0.05$) individuals. The mean time between two successive detections (including all three tracking sessions) of the same individual was 4.7 days (± 3.8 SD).

	Spring 2009 0+ (n=22)	Spring 2010 0+ (n=7)	Spring 2010 1+ (n=5)	Winter 2010/11 0+ (n=4)	Winter 2010/11 1+ (n=11)
N detections / individual	9.1 ± 4.7	7.4 ± 3.7	7.6 ± 4.5	10.0 ± 2.3	8.4 ± 2.8
Mean radial distance moved (m)	13.4 ± 10.1	12.0 ± 7.6	16.7 ± 7.5	2.03 ± 0.7	17.0 ± 18.5
Mean movement/day (m)	2.7 ± 4.4	3.4 ± 2.9	1.5 ± 1.7	0.3 ± 0.1	2.3 ± 1.9
Mean δ^{15}N	15.4 ± 0.9	15.3 ± 0.3	16.6 ± 1.5	14.8 ± 1.4	15.8 ± 0.5
Mean δ^{13}C	-29.1 ± 0.4	-29.9 ± 0.7	-31.7 ± 1.4	-31.9 ± 1.5	-32.6 ± 1.4
Mean TP	3.3 ± 0.6	3.2 ± 0.6	3.1 ± 0.4	3.0 ± 0.3	3.1 ± 0.3
Mean SGR^{FL} (% day^{-1})	0.11 ± 0.05	0.15 ± 0.05	0.08 ± 0.02	0.07 ± 0.04	0.02 ± 0.06
Initial mean FL (mm ± SD)	188.0 ± 26.8	184 ± 27.8	250.6 ± 46.2	138.8 ± 40.5	246.3 ± 17.4
Final mean FL (mm ± SD)	245.2 ± 50.8	265.3 ± 54.0	295.7 ± 40.3	158.4 ± 41.6	258.8 ± 34.8
Initial mean BM (g ± SD)	49.8 ± 19.9	47.1 ± 19.0	126. ± 75.6	24.0 ± 22.4	117.1 ± 23.6
Final mean BM (g ± SD)	139.2 ± 109.9	158.2 ± 98.0	227.0 ± 106.3	34.9 ± 27.7	157.4 ± 32.9

Table 4.1. Mean (± SD) number of detections, distances moved (mean radial distance), stable isotope values (carbon and nitrogen), trophic positions, specific growth rate (SGR) initial and final fork lengths (FL) and body masses (BM) per season and age.

4.4.2 Age- and seasonal related differences in movement, trophic ecology, body size and growth

Age did not have significant effects on $\overline{d}$ or $\overline{v}$, while the interaction of age and season on $\overline{d}$ was significant, indicating that 1+ pike moved more in the winter than spring, whilst 0+ pike moved more in the spring than in winter (Table 4.2; Fig. 4.2). A significant effect of tracking period on $\overline{d}$ was found with a higher movement in spring 2010 compared to winter 2010/11 (Fig. 4.2).

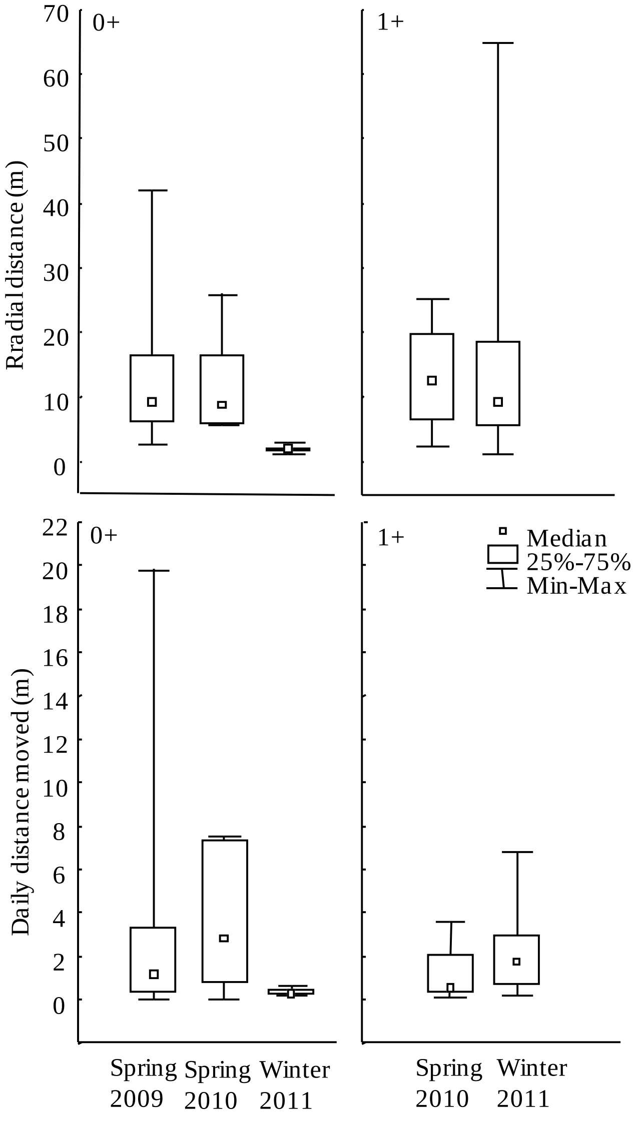

Figure 4.2. Mean radial distance ($\overline{d}$) moved (upper panels) and daily distance ($\overline{v}$) moved (lower panels) of 0+ (left) and 1+ (right) individuals during the springs 2009, 2010 and winter 2011. See table 4.2 for statistics.

Parameter	Source of variation	SS	df	F	p
$\overline{d}$ *	Number of detections	0.02	1	0.13	0.724
	Age	0.65	1	4.12	0.055
	Year	0.82	1	5.24	**0.032**
	Age x Year	0.73	1	4.67	**0.042**
	Error	3.45	22		
$\overline{v}$*	Number of detections	0.01	1	0.05	0.830
	Age	0.01	1	0.03	0.853
	Year	0.24	1	1.12	0.302
	Age x Year	2.67	1	12.46	**0.002**
	Error	4.71	22		
TP	Initial FL	0.10	1	1.20	0.286
	Age	1.01	1	12.58	**0.002**
	Year	0.29	1	3.66	0.069
	Age x Year	0.23	1	2.85	0.105
	Error	1.77	22		
δ^{15}N	Initial FL	0.00	1	0.00	0.955
	Age	2.88	1	3.50	0.075
	Year	1.26	1	1.53	0.229
	Age x Year	0.07	1	0.09	0.772
	Error	18.12	22		
δ^{13}C	Initial FL	0.36	1	0.23	0.640
	Age	5.49	1	3.45	0.077
	Year	9.17	1	5.76	**0.025**
	Age x Year	1.43	1	0.90	0.353
	Error	35.05	22		
SGR*	Mean temperature	0.01	1	0.52	0.480
	Initial FL	0.18	1	10.55	**0.004**
	Age	0.07	1	4.06	0.057
	Year	0.03	1	1.87	0.186
	Age x Year	0.01	1	0.49	0.490
	Error	0.36	21		
FL	Age	38293.28	1	43.83	**<0.001**
	Year	2011.50	1	2.30	0.143
	Age x Year	4156.89	1	4.76	**0.040**
	Error	20094.10	23		

Table 4.2. Results of GLMs on the effects of age (0+ and 1+) and season (spring 2010, winter 2010/11) on mean individual radial distance moved, trophic position, stable isotope values, specific growth rate and fork length in juvenile pike *E. lucius* (n=27). Significant p-values are indicated in bold. *Variables ln (x+1) transformed.

No effects of age on δ^{13}C or δ^{15}N were found, whereas trophic position was higher for 1+ than 0+ pike (Table 4.2). Values of δ^{13}C values were significantly higher in spring than in winter, while no seasonal differences in δ^{15}N or TP were found (Table 4.2). A significant effect on SGR by initial FL was found when mean temperature was the covariate, with smaller sized pike growing at a faster rate. Despite 1+ pike having a higher initial FL compared to 0+, no effect of age on SGR was found (Table 4.2). There was also a significant interaction between age and year on initial FL, whereby 0+ pike were larger in spring 2010 than winter, whereas the 1+ (in their second year of life) pike were of larger size in winter 2010/11 than spring 2010 (Table 4.2).

4.4.3 Individual variation in movement

Whilst there was no significant effect of age on movement (Table 4.2), there was considerable variation between individuals within age-class (Fig. 4.3) and tracking periods. The mean $\overline{d}$ of 0+ fish in spring 2009 ranged from 2.6 to 42.1 m, in spring 2010 from 5.8 to 25.0 m, and in winter 2010/11 from 1.2 and 3.1 m. In 1+ pike, it ranged from 10.4 to 25.0 m in spring 2010 and 1.3 to 64.9 m in winter 2010/11. Significant repeatability estimates were found for $\overline{d}$ and $\overline{v}$ for each tracking period (except winter 2010/11) and age-class (Table 4.3). However, only repeatability outputs from $\overline{d}$ for 0+ pike of spring 2009 and 1+ of winter10/11 had 95 % CI that did not overlap with zero, together with higher effect sizes and sample sizes compared to the other analyses (Table 4.3).

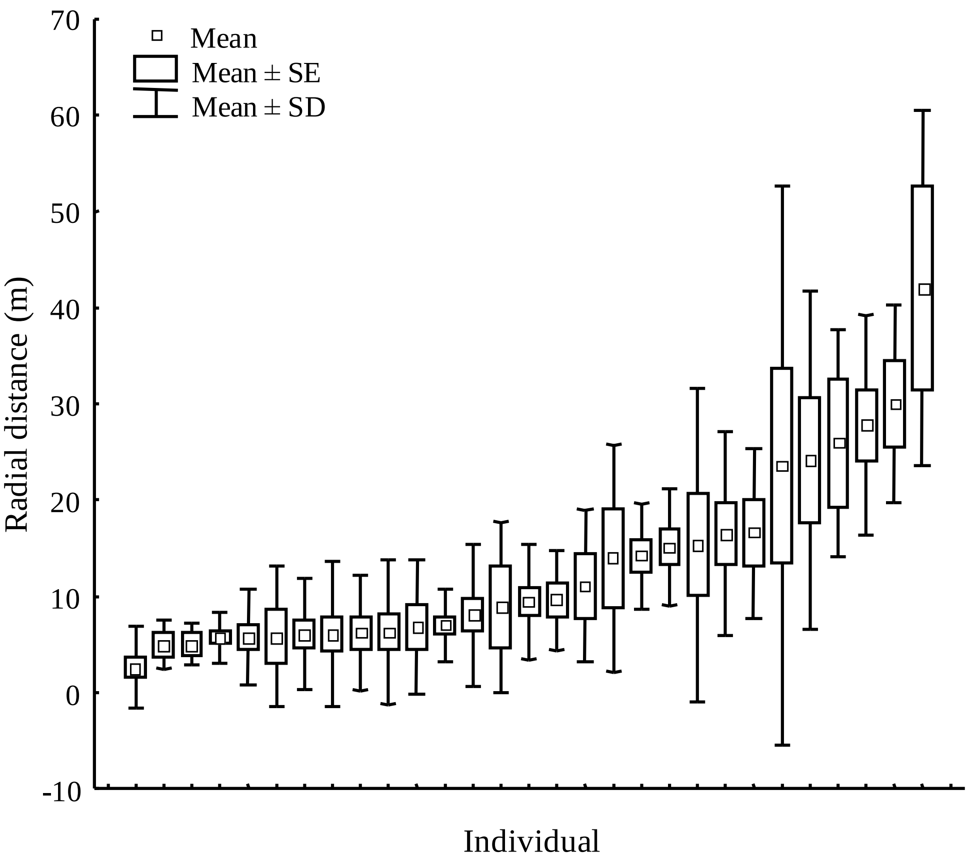

Figure 4.3. Mean (± SE and SD) radial distances (m) per individual of age 0+ detected (> 6 times) during springs 2009 and 2010 (n=29).

	Season & year	**Age**	**N**	**R**	**SE**	**95 % CI**	**p**
(a)	Spring 2009	0+	22	0.46	0.09	0.26 to 0.61	**0.001**
	Spring 2010	0+	7	0.36	0.17	0.00 to 0.63	**0.004**
	Spring 2010	1+	5	0.19	0.16	0.00 to 0.53	**0.047**
	Winter 2010/11	0+	5	0.23	0.15	0.00 to 0.54	**0.011**
	Winter 2010/11	1+	11	0.61	0.13	0.30 to 0.78	**0.001**
(b)	Spring 2009	0+	22	0.12	0.07	0.00 to 0.25	**0.014**
	Spring 2010	0+	7	0.26	0.16	0.00 to 0.55	**0.027**
	Spring 2010	1+	5	0.40	0.22	0.00 to 0.74	**0.035**
	Winter 2010/11	0+	5	0.10	0.11	0.00 to 0.35	0.114
	Winter 2010/11	1+	11	0.02	0.05	0.00 to 0.19	0.248

Table 4.3. The repeatability (R) of (a) radial distance moved (m) and (b) daily distance moved (m) in juvenile pike *E. lucius*.

4.4.4 Does SGR, FL or trophic niche explain individual movement?

As no differences in movement were found between 0+ individuals tracked in spring 2009 and 2010 (ANOVA, $F_{(1,\ 28)} = 0.001$, $n = 29$, $p = 0.997$), the data from both spring periods were combined for the GLMM. This revealed that the number of detections had a significant effect on movement, with higher movement associated with individuals with a low number of detections. This effect disappeared when individuals with less than 7 detections were removed from the model and revealed non-significant effects of the stable isotope values ($\delta^{13}C$ or $\delta^{15}N$), TP and SGR on the radial distance moved, thus these variables were removed from the model. A significant positive effect on $\overline{d}$ was found of initial FL (GLMM, $F_{(1,\ 196)} = 5.24$, $n = 19$, $P = 0.036$) and the random variable of individual identity (GLMM, $F_{(1,\ 196)} = 6.74$, $n = 19$, $P < 0.0001$) (Fig. 4.3). The ANOVA component of the model indicated that identity accounted for 33.9 % and fork length accounted for 23.7 % of the variance in movement. There were too few individuals of 1+ in spring 2010 ($n = 5$) or either age group in winter 2010/11 (0+, $n = 4$; 1+, $n = 11$) to build similar GLMMs after removing individuals detected on a low number of occasions.

4.5 DISCUSSION

The study revealed that within age-classes, individuals were repeatable in their level of movement in this wild population of pike. Whilst this variation was related to differences in body length, within each age-class it was independent of growth rate and trophic position. With larger fish showing higher movement, and as growth rates generally decrease with body size in fishes, the non-significant relationship between growth and movement may not be surprising. Nevertheless, a larger body size within an age-class indicates a higher previous growth rate. Although these results therefore do not support the growth-activity trade-off theory (where a higher activity to acquire resources is associated with decreased growth rates due to higher energy expenditure), they present evidence (albeit indirectly due to larger body size rather than growth) for the growth-mortality trade-off theory, where a higher activity increases predation risk, but if successful, increases growth rate. Thus, the study does indicate that individual variation within a wild population is ecologically important and should be considered as more than just noise around an adaptive mean (Archard & Braithwaite 2010; Bolnick et al. 2011).

The high intrapopulation variation in movement within ages is similar to findings from several fish taxa (Bourke et al. 1997; Morbey et al. 2006; Hammerschlag-Peyer & Layman 2010), including in pike for both 0+ (Cucherousset et al. 2009) and adults (Jepsen et al. 2001; Masters et al. 2005; Vehanen et al. 2006; Kobler et al. 2009). However, none of these studies explicitly tested for consistent individual variation. The high repeatabilities found here correspond to a meta-analysis on repeatability studies showing higher repeatabilities in field compared to laboratory studies (Bell et al. 2009). Although it included fewer field studies than experimental ones, high behavioural consistency in wild populations has been suggested to have an adaptive advantage over flexibility (Dall et al. 2004). This is because flexible behaviour may be costly in a changing environment as in order to behave appropriately when conditions change an individual will need to have (recent) experience of alternative environments (Dall et al. 2004). Moreover, selective pressures may be stronger in the wild compared to captivity, where selection may be more relaxed (Archard & Braithwaite 2010). Spatial and temporal variation in the environment may therefore be the driving force behind the maintenance of behavioural variability in wild populations (Wilson 1998; Dingemanse et al. 2004; Archard & Braithwaite 2010). Furthermore, Dingemanse et al. (2010) noted that the type of habitat where individuals are assayed, for example, habitat with high or low predation or/and competition pressure, may influence the consistency in the behaviour measured (e.g. risk-taking). In the habitats (ditches) surveyed in the present study, pike experienced low interspecific competition and predation pressure, but high intraspecific competition including risk of cannibalism. Therefore, activity was risky for these pike, particularly for slightly smaller individuals.

In juvenile fishes, the vulnerability of predation decreases with increasing body size due to, for example, gape-size limitation among piscivorous predators (Nilsson & Brönmark 2000), thus body size is an important determinant of individual survival probability, and indeed, is often used as a fitness proxy (Brown et al. 2007). The positive relationship between movement and body length found in 0+ pike may indicate that an active (and bold) strategy either influenced previous growth or was influenced by a larger body size. Alternatively, Careau et al. (2008) suggested that as higher activity increases energy metabolism, a positive feedback between activity and energy intake takes place, which then explains the consistency in foraging activity. However, this reasoning does not take into account the bioenergetic consideration that the relative energetic demands for movement in fishes decreases with size (Peters 1986; Arendt 1997). This may, indeed, result in higher movement of larger individuals, which may in turn intimidate slightly smaller individuals and hence their movement is kept at a lower level. For example, the mere presence of conspecifics has been found to have a negative effect on foraging activity in pike (Engström-Öst & Lehtiniemi 2004; Nilsson et al. 2006). The use of laboratory experiments on YOY pike also revealed individual consistency in foraging activity across risky situations consisting of the presence/absence of a competitor or predator (Chapter 6). As some individuals maintained a high activity across situations, these were bold following the definition of boldness as the propensity to take risks (Wilson 1998; Bell 2005). This suggests that a higher activity in the present field study could also be associated with a higher susceptibility to intraspecific interference or/and predation, and hence with boldness.

An overall reduced movement in the winter compared to spring found in the present study corresponds to reports on the movement of adult pike (Vehanen et al. 2006; Kobler et al. 2008). The decrease in movement may be explained by the decreased water temperature in winter reducing the metabolic and physiological rates of the fish and their associated activities (Charnov & Gillooly 2004). Movement was not only influenced by season but also the age of the pike, with 1+ fish having increased movement in both seasons compared to 0+ individuals. As 1+ fish were larger than 0+, it may be that they are, therefore, less vulnerable to predation and so more risk-taking, as indicated by their higher movement. Interestingly, 1+ pike had a higher movement in winter compared to spring, but this maybe an artefact resulting from lower samples sizes of 1+ pike in spring (n = 5) than in winter (n = 11) in conjunction with high variation in individual movement in winter (mean ± SD: 17.0 ± 18.5 m). Male pike may reach sexual maturity as early as age-1 (Raat 1988), thus the male 1+ fish in winter, which were at the end of their 2nd year of life, may have been exhibiting activity related to reproduction (Knight 2006).

In most fishes, growth rate decreases with age and size (Bry et al. 1991; Margenau et al. 2008) and 1+ pike were slower growing than 0+ pike, although their body sizes were significantly larger and they had elevated $\delta^{13}C$ values. These results highlight the need to control for the effect of age when studying individual variation. In adult riverine pike, a negative association between movement and SGR has been reported (Koed et al. 2000) while no association has been reported in lacustrine pike (Kobler et al. 2009). Animals with indeterminate growth need to allocate energy to both reproduction (including maturation in juveniles) and somatic growth throughout their lives (Stearns 1992; Thorpe 2007). Resource availability plays an essential part in this allocation, which is influenced by ecological interactions such as intra- and interspecific competition, predation and parasitism, which in turn is age and size dependent (Heino & Kaitala 1999). Similarly to our findings, results on adult pike have also showed positive associations between movement and body size; however, this may reflect an effect of age, as this was not controlled in these studies (Masters et al. 2005; Vehanen et al. 2006).

Although diet composition is hypothesised to affect life history traits, such as life stage durations and growth rate in immature animals (Caswell

2001), there was no significant relationship between trophic positions and growth or body size in the juvenile pike. Indeed, individual variability in trophic niche was relatively low, indicating that pike (even from different ditches) fed on similar food sources and/or that prey assemblages are maintained along the length of the ditches. If food resources are not limiting or competition is very low, there would be no need for resource partitioning and specialisation on different prey among individuals. Individual specialisation in resource use within a population often develops where there is low interspecific competition (but high intraspecific competition) and availability of open niches (Skulason & Smith 1995; Bolnick et al. 2003; Bolnick 2004; Svanbäck & Bolnick 2004; Araujo et al. 2011). While few other predatory species are found in the ditches, high pike density may not provide the availability of open niches, which is required for specialisation. Without individual specialisation in habitat or resource use, the development of related morphological traits (resource polymorphism) is uncharacteristic (Smith & Skulason 1996; Bolnick et al. 2003; Cucherousset et al. 2011).

In conclusion, this chapter revealed that consistency in individual variation in movement was positively size-dependent, likely to be due to risks associated with moving in this cannibalistic species. The association between movement and size also indicated that individual variation in movement during early life may have influenced or been influenced by the development of size dimorphism. While this chapter focused on the pike inhabiting the ditches only, pike in the side channels and river are compared and their dispersal from the ditches into the river is investigated in the following chapter.

4.6 REFERENCES

Andersen, M., Jacobsen, L., Gronkjaer, P. & Skov, C. 2008. Turbidity increases behavioural diversity in northern pike, *Esox lucius* L., during early summer. *Fisheries Management and Ecology*, 15, 377-383.

Araújo, M. S., Bolnick, D. I. & Layman, C. A. 2011. The ecological causes of individual specialisation. *Ecology Letters*, 14, 948-958.

Archard, G. A. & Braithwaite, V. A. 2010. The importance of wild populations in studies of animal temperament. *Journal of Zoology*, 281, 149-160.

Arendt, J. D. 1997. Adaptive intrinsic growth rates: An integration across taxa. *Quarterly Review of Biology*, 72, 149-177.

Austin, D., Bowen, W. D. & McMillan, J. I. 2004. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos,* 105, 15-30.

Beaudoin, C. P., Tonn, W. M., Prepas, E. E. & Wassenaar, L. I. 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. *Oecologia*, 120, 386-396.

Bell, A. M. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology*, 18, 464-473.

Bell, A. M., Hankison, S. J. & Laskowski, K. L. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77, 771-783.

Bergman, C., Schaefer, J. & Luttich, S. 2000. Caribou movement as a correlated random walk. *Oecologia*, 123, 364-374.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. 2003. The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist*, 161, 1-28.

Bolnick, D. I. 2004. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution*, 58, 608-618.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C. & Vasseur, D.A. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution*, 26, 183-192.

Bourke, P., Magnan, P. & Rodríguez, M. A. 1997. Individual variations in habitat use and morphology in brook charr. *Journal of Fish Biology*, 51, 783-794.

Brown, C., Jones, F. & Braithwaite, V. A. 2007. Correlation between boldness and body mass in natural populations of the poeciliid Brachyrhaphis episcopi. *Journal of Fish Biology*, 71, 1590-1601.

Bry, C., Hollebecq, M. G., Ginot, V., Israel, G. & Manelphe, J. 1991. Growth-patterns of pike (*Esox lucius* L) larvae and juveniles in small ponds under various natural temperature regimes. *Aquaculture*, 97, 155-168.

Bry, C., Bonamy, F., Manelphe, J. & Duranthon, B. 1995. Early-life characteristics of pike, *Esox lucius*, in rearing ponds - temporal survival pattern and ontogenic diet shifts. *Journal of Fish Biology*, 46, 99-113.

Careau, V., Thomas, D., Humphries, M. M. & Reale, D. 2008. Energy metabolism and animal personality. *Oikos*, 117, 641-653.

Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation.* Sunderland (USA): Sinauer Associates.

Casselman, E. J. 1996. Age, growth and environmental requirements of pike. In: *Pike biology and exploitation*, (Ed. by J. F. Craig), pp. 69-101. London: Chapman & Hall.

Catry, I., Dias, M., Catry, T., Afanasyev, V., Fox, J., Franco, A. & Sutherland, W. 2011. Individual variation in migratory movements and winter behaviour of Iberian lesser kestrels *Falco naumanni* revealed by geolocators. *IBIS*, 153, 154-164.

Chapman, L. J., Mackay, W. C. & Wilkinson, C. W. 1989. Feeding flexibility in northern pike (*Esox lucius*) - fish versus invertebrate prey. *Canadian Journal of Fisheries and Aquatic Sciences*, 46, 666-669.

Charnov, E. & Gillooly, J. 2004. Size and temperature in the evolution of fish life histories. *Integrative and Comparative Biology*, 44, 494-497.

Cucherousset, J., Roussel, J. M., Keeler, R., Cunjak, R. A. & Stump, R. 2005. The use of two new portable 12-mm PIT tag detectors to track small fish in shallow streams. *North American Journal of Fisheries Management*, 25, 270-274.

Cucherousset, J., Paillisson, J. M. & Roussel, J. M. 2007. Using PIT technology to study the fate of hatchery-reared YOY northern pike released into shallow vegetated areas. *Fisheries Research*, 85, 159-164.

Cucherousset, J., Paillisson, J. M., Cuzol, A. & Roussel, J. M. 2009. Spatial behaviour of young-of-the-year northern pike (Esox lucius L.) in a temporarily flooded nursery area. *Ecology of Freshwater Fish*, 18, 314-322.

Cucherousset, J., Britton, J. R., Beaumont, W. R. C., Nyqvist, M., Sievers, K. & Gozlan, R. E. 2010. Determining the effects of species, environmental conditions and tracking method on the detection efficiency of portable PIT telemetry. *Journal of Fish Biology*, 76, 1039-1045.

Cucherousset, J., Acou, A., Blanchet, S., Britton, J. R., Beaumont, W. R. C. & Gozlan, R. E. 2011. Fitness consequences of individual specialisation in resource use and trophic morphology in European eels. *Oecologia*, 167, 75-84.

Dall, S. R. X., Houston, A. I. & McNamara, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, 7, 734-739.

Diana, J. 1980. Diel activity pattern and swimming speeds of northern pike (*Esox lucius*). *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 1454-1458.

Dingemanse, N. J., Both, C., Drent, P. J. & Tinbergen, J. M. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271, 847-852.

Dingemanse, N. J., Kazem, A. J. N., Reale, D. & Wright, J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25, 81-89.

Enders, E. C., Clarke, K. D., Pennell, C. J., Ollerhead, L. M. N. & Scruton, D. A. 2007. Comparison between PIT and radio telemetry to evaluate winter habitat use and activity patterns of juvenile Atlantic salmon and brown trout. *Hydrobiologia*, 582, 231-242.

Engström-Öst, J. & Lehtiniemi, M. 2004. Threat-sensitive predator avoidance by pike larvae. *Journal of Fish Biology*, 65, 251-261.

Garamszegi, L. 2006. Comparing effect sizes across variables: generalization without the need for Bonferroni correction. *Behavioral Ecology*, 17, 682-687.

Giles, N., Wright, R. M. & Nord, M. E. 1986. Cannibalism in pike fry, *Esox lucius* L. - some experiments with fry densities. *Journal of Fish Biology*, 29, 107-113.

Hammerschlag-Peyer, C. & Layman, C. 2010. Intrapopulation variation in habitat use by two abundant coastal fish species. *Marine Ecology-Progress Series*, 415, 211-220.

Harcourt, J. L., Sweetman, G., Johnstone, R. A. & Manica, A. 2009. Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks. *Animal Behaviour*, 77, 1501-1505.

Heino, M. & Kaitala, V. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology*, 12, 423-429.

Höjesjö, J., Johnsson, J. I. & Bohlin, T. 2002. Can laboratory studies on dominance predict fitness of young brown trout in the wild? *Behavioral Ecology and Sociobiology,* 52, 102-108.

Imsland, A. K., Jenssen, M. D., Jonassen, T. M. & Stefansson, S. O. 2009. Best among unequals? Effect of size grading and different social environments on the growth performance of juvenile Atlantic halibut. *Aquaculture International*, 17, 217-227.

Jepsen, N., Beck, S., Skov, C. & Koed, A. 2001. Behavior of pike (*Esox lucius* L.) > 50 cm in a turbid reservoir and in a clearwater lake. *Ecology of Freshwater Fish*, 10, 26-34.

Jobling, M. & Baardvik, B. M. 1994. The influence of environmental manipulations on interindividual and intraindividual variation in food acquisition and growth-performance of arctic charr, *Salvelinus-alpinus*. *Journal of Fish Biology*, 44, 1069-1087.

Johansson, F. & Andersson, J. 2009. Scared fish get lazy, and lazy fish get fat. *Journal of Animal Ecology*, 78, 772-777.

Killen, S. S., Brown, J. A. & Gamperl, A. K. 2007. The effect of prey density on foraging mode selection in juvenile lumpfish: balancing food intake with the metabolic cost of foraging. *Journal of Animal Ecology*, 76, 814-825.

Kobler, A., Klefoth, T., Wolter, C., Fredrich, F. & Arlinghaus, R. 2008. Contrasting pike (*Esox lucius* L.) movement and habitat choice between summer and winter in a small lake. *Hydrobiologia*, 601, 17-27.

Kobler, A., Klefoth, T., Mehner, T. & Arlinghaus, R. 2009. Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? *Oecologia*, 161, 837-847.

Koch, F. & Wieser, W. 1983. Partitioning of energy in fish: can reduction of swimming activity compensate for the cost of production? *Journal of Experimental Biology*, 107, 141 -146.

Koed, A., Mejlhede, P., Balleby, K. & Aarestrup, K. 2000. Annual movement and migration of adult pikeperch in a lowland river. *Journal of Fish Biology*, 57, 1266-1279.

Mangel, M. & Stamps, J. 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evolutionary Ecology Research*, 3, 583-593.

Mann, R. & Beaumont, W. 1990. Fast- and slow-growing pike, *Esox lucius* L., and problems of age-determinations from scales. *Aquaculture and Fisheries Management*, 21, 471-478.

Margenau, T. L., AveLallemant, S. P., Giehtbrock, D. & Schram, S. T. 2008. Ecology and management of northern pike in Wisconsin. *Hydrobiologia*, 601, 111-123.

Martins, C. I. M., Schrama, J. W. & Verreth, J. A. J. 2005. The consistency of individual differences in growth, feed efficiency and feeding behaviour in African catfish *Clarias gariepinus* (Burchell 1822) housed individually. *Aquaculture Research*, 36, 1509-1516.

Martin-Smith, K. M. & Armstrong, J. D. 2002. Growth rates of wild stream-dwelling Atlantic salmon correlate with activity and sex but not dominance. *Journal of Animal Ecology*, 71, 413-423.

Masters, J. 2003. Temporal variation in the behaviour of pike *Esox lucius* L. PhD thesis, University of St Andrews, UK.

Masters, J., Hodder, K., Beaumont, W., Gozlan, R., Pinder, R., Kenward, J. & Welton, S. 2005. Spatial behaviour of pike *Esox lucius* L. in the River Frome, UK. In: *Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe.*, (Ed. by M. Spedicato, G. Lembo, & G. Marmulla), pp. 179-190.

Morbey, Y. E., Addison, P., Shuter, B. J. & Vascotto, K. 2006. Within-population heterogeneity of habitat use by lake trout *Salvelinus namaycush*. *Journal of Fish Biology*, 69, 1675-1696.

Nakagawa, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology*, 15, 1044-1045.

Nakagawa, S. & Cuthill, I. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, 82, 591-605.

Nakagawa, S. & Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, 85, 935-956.

Nilsson, P. A. & Brönmark, C. 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos*, 88, 539–546.

Nilsson, P. A., Turesson, H. & Bronmark, C. 2006. Friends and foes in foraging: intraspecific interactions act on foraging-cycle stages. *Behaviour*, 143, 733-745.

Peters, R. H. 1986. *The ecological implications of body size*. Cambridge University Press.

Pinter-Wollman, N. 2009. Spatial behaviour of translocated African elephants (*Loxodonta africana*) in a novel environment: using behaviour to inform conservation actions. *Behaviour*, 146, 1171-1192.

Polis, G. 1984. Age structure component of niche width and intraspecific resource partitioning - can age-groups function as ecological species. *American Naturalist*, 123, 541-564.

Qian, X., Cui, Y., Xie, S., Lei, W., Zhu, X., Xiong, B. & Yang, Y. 2001. Individual variations in growth, food intake and activity in juvenile Chinese sturgeon *Acipenser sinensis* Gray. In: *4th International Symposium on Strugeon*, pp. 695-698. Oshkosh, Wisconsin.

R development core team. 2009. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.

Raat, A. 1988. *Synopsis of biological data on the northern pike Esox lucius Linnaeus 1758.* FAO Fish. Synopsis.

Reinbold, D., Thorgaard, G. H. & Carter, P. A. 2009. Reduced swimming performance and increased growth in domesticated rainbow trout, *Oncorhynchus mykiss*. *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 1025-1032.

Rennie, M. D., Collins, N. C., Shuter, B. J., Rajotte, J. W. & Couture, P. 2005. A comparison of methods for estimating activity costs of wild fish populations: more active fish observed to grow slower. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 767-780.

Roussel, J. M., Haro, A. & Cunjak, R. A. 2000. Field test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 1326-1329.

Roussel, J. M., Cunjak, R. A., Newbury, R., Caissie, D. & Haro, A. 2004. Movements and habitat use by PIT-tagged Atlantic salmon parr in early winter: the influence of anchor ice. *Freshwater Biology*, 49, 1026-1035.

Salomon, M. 2009. Social environment and feeding state influence movement decisions in a web-building spider. *Ethology*, 115, 916-927.

Skov, C., Lousdal, O., Johansen, P. H. & Berg, S. 2003. Piscivory of 0+ pike (*Esox lucius* L.) in a small eutrophic lake and its implication for biomanipulation. *Hydrobiologia*, 506, 481-487.

Skulason, S. & Smith, T. B. 1995. Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution*, 10, 366-370.

Smith, T. B. & Skulason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics*, 27, 111-133.

Stamps, J. A. 2007. Growth-mortality tradeoffs and “personality traits” in animals. *Ecology Letters*, 10, 355-363.

Stearns, S. C. 1992. *The Evolution of Life Histories.* Oxford University Press, USA.

Sundström, L., Petersson, E., Höjesjö, J., Johnsson, J. & Järvi, T. 2004. Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): implications for dominance. *Behavioral Ecology*, 15, 192-198.

Thorpe, J. E. 2007. Maturation responses of salmonids to changing developmental opportunities. *Marine Ecology-Progress Series*, 335, 285-288.

Turchin, P. 1998. *Quantitative analysis of movement: Measuring and modeling population redistribution in animals and plants.* Sunderland (USA): Sinauer Associates.

Vehanen, T., Hyvärinen, P., Johansson, K. & Laaksonen, T. 2006. Patterns of movement of adult northern pike (*Esox lucius* L.) in a regulated river. *Ecology of Freshwater Fish*, 15, 154-160.

Wang, N., Hayward, R. S. & Noltie, D. B. 1998. Effect of feeding frequency on food consumption, growth, size variation, and feeding pattern of age-0 hybrid sunfish. *Aquaculture*, 165, 261-267.

Ward, A., Thomas, P., Hart, P. & Krause, J. 2004. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology And Sociobiology*, 55, 561-568.

Werner, E. E. & Anholt, B. R. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *The American Naturalist*, 142, 242-272.

Wilson, D. S. 1998. Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 353, 199-205.

Wolska-Neja, B. & Neja, Z. 2006. Grow-out of northern pike (*Esox lucius* L.) larvae under uncontrolled conditions. *Acta ichthyologica et piscatoria*, 36, 105-112.

Ziliukiene, V. & Ziliukas, V. 2006. Feeding of early larval pike *Esox lucius* L. reared in illuminated cages. *Aquaculture*, 258, 378-387.

Chapter 5

Body size and trophic niche as drivers of individual variation in dispersal

5.1 ABSTRACT

Variation in dispersal between individuals in a population, where some disperse while others remain residents, is a common phenomenon among many species. Despite that such differences in dispersal may have important ecological consequences, the drivers behind individual dispersal tendencies and the individual long-term effects of these are poorly understood. In this chapter, body size and trophic niche were tested as drivers for dispersal variation in juvenile pike of the River Frome moving from side-channels into the main river. A mark-recapture study was conducted to identify growth consequences of differences in dispersal. The results revealed that dispersers had lower trophic positions and body sizes than residents, a counter-intuitive outcome. Nevertheless, dispersers that were recaptured in the river experienced greater subsequent growth than residents recaptured in the ditches. This study suggests that habitat exclusion of less competitive individuals plays an important part in driving variation in dispersal. However, surviving dispersers subsequently reap the benefits by successfully settling in a more profitable habitat in terms of prey availability.

5.2 INTRODUCTION

Intraspecific variation in behaviour, physiology and/or morphology within natural populations is now widely recognised as a crucial mechanism with potentially important ecological and evolutionary consequences (Magurran

1993; Bolnick et al. 2003, 2011; Dall et al. 2004). Since Bolnick et al. (2003) reviewed and highlighted the importance of individual variation in niche use (exploitation of habitat and/or trophic resources) together with the occurrence of individual specialisation, where an individual's niche is narrower than its population's niche, independent of sex, age or morphology, the number of studies showing individual specialisation in a variety of species and taxa has increased by more than two-fold (Araújo et al. 2011). Individual variation in niche use resulting in resource partitioning can reduce intraspecific competition (Smith & Skulason 1996) and promotes the co-existence of species (Barbault & Stearns 1991). It may also lead to the development of discrete morphs that differ in their foraging ecology and habitat use within a population, known as resource or trophic polymorphism (Skulason & Smith 1995; Smith & Skulason 1996; Bolnick et al. 2003; Cucherousset et al. 2011).

Among resource partitioning, inter-individual variation in dispersal is particularly common and has been demonstrated in many species of fish, birds, amphibians, insects and mammals (Jonsson & Jonsson 2001; Skov et al. 2008; Nilsson et al. 2008; Grayson & Wilbur 2009; Hebblewhite & Merrill 2009). However, little is known of the underlying mechanisms causing some individuals to disperse to a new habitat and others to stay (Bolnick et al. 2003; Chapman et al. 2011), and its function in the development of trophic polymorphism. Specifically, evidence into whether individual variation in trophic resources and/or resource polymorphism precedes or follows differences in dispersal behaviour remains rare (Biro & Ridgway 2008).

In many fish species, specifically lacustrine populations, habitat segregation is most common between individuals inhabiting the littoral and pelagic zones (Robinson & Wilson 1994). For example, in European perch (*Perca fluviatilis* L.), individuals occupying the pelagic zone are more streamlined and slower growing than the deeper bodied and faster growing individuals in the littoral zone (Hjelm et al. 2001; Svanbäck & Eklöv 2002, 2003). Furthermore, foraging efficiency of the perch has also been found to be related to individual morphology, with the more streamlined perch using a higher attack velocity than deeper-bodied perch (Svanbäck & Eklöv 2004). Apart from decreasing both intra- and interspecific competition for resources, habitat partitioning may also be a mechanism for individuals to directly decrease their predation vulnerability (Lima & Dill 1990; Eklöv & Svanbäck 2006; Svanbäck et al. 2008; Skov et al. 2011). For example, in a partially migratory elk population (*Cervus elaphus* L.) in the Canadian Rockies, migrants reduced exposure to wolf predation risk by 70% compared to resident individuals (Hebblewhite & Merrill 2009). To explain why only some individuals decide to shift habitat requires characterising behaviour and attributes at an individual level (Chapman et al. 2011).

Recently, an increasing number of studies have shown that variation in observed behavioural patterns between individuals, i.e. their personality traits such as boldness or aggression, underlies other observed behavioural patterns that vary among individuals. Inter-individual behavioural differences, particularly in boldness, have been directly linked to differences in exploration of novel environments (Budaev 1997), dispersal (Fraser et al. 2001; Cote & Clobert 2007; Cote et al. 2010) and settlement in new habitats (Armstrong et al. 1997). In the Trinidad killifish (*Rivulus hartii* Boulenger), bolder individuals dispersed longer distances in the wild (Fraser et al. 2001). Growth of surviving dispersers was higher than of the individuals that stayed, suggesting a fitness advantage among survivors that undertook risky dispersal (Fraser et al. 2001). Similarly, in roach (*Rutilus rutilus* L.), boldness and body size (although unrelated) were found to influence migration tendencies in the wild, with bolder or smaller individuals more likely to migrate during winter from areas of higher predation risk to areas of lower predation risk (Chapman et al. 2011). Bolder individuals increase their attention to predators through higher activity, whereas smaller individuals may be at higher risk to predation due to the gape-limitation of their predators. Therefore, by migrating to an area of lower predator presence, bolder or smaller individuals may reduce the risk of predation (Skov et al. 2011; Chapman et al. 2011). As relative metabolic needs and energy demands for movement decrease with size, larger individuals would have a greater chance, at least on an energetic level, to survive migration than small bodied (Arendt 1997). Furthermore, endurance and cruising speed for fishes increases with body size, hence their ability to escape predation is greater (Arendt 1997).

Empirical studies of mechanisms driving individual differences in dispersal tendencies and habitat shifts are lacking, despite being important for the understanding of fundamental population processes (Hansson & Hylander 2009; Hebblewhite & Merrill 2009; Skov et al. 2011). Here, in the pike population of the River Frome study site (Section 2.1), individual variation in dispersal from nursery habitats is already known to occur (Mann & Beaumont 1990). Adult pike tend to reproduce in April in side channels connected to the main river (Mann 1980; Mann & Beaumont 1990; Masters 2003; Knight 2006; pers. obs.). Some individuals of the 0+ cohort subsequently move into the main river during the first summer, while others remain in the nursery habitat (ditches) until the following summer (Mann & Beaumont 1990), or even longer (Knight 2006; personal observation). Indeed, previous data have suggested that this spatial segregation and the associated differences in prey availability - and so pike diet - results in growth dimorphism (Mann & Beaumont 1990). The pike dispersing into the main channel are thought to become faster growing and piscivorous, while pike remaining in the ditches continue to feed mainly on invertebrates (Mann 1982; Mann & Beaumont 1990). Whilst there is a clear energetic advantage of shifting habitat in order to access a higher availability of fish prey species, this is most likely to coincide with increased predation risk through presence of larger piscivores (i.e. adult pike) and less refuges in the main channel when compared to the highly vegetated ditches (Masters 2003; Knight 2006). As with many species of fish, variation in movement from the nursery habitat may reflect an ontogenetic habitat niche shift due to size-dependent changes in their requirements for food and shelter (Hawkins et al. 2003; Gozlan & Copp 2005). Indeed, in a cannibalistic species such as pike, body size would strongly influence their habitat use (Raat 1988; Bry

1996). In comparison, size-independent movement and size-dependent dispersal were found in hatchery-reared YOY pike released into a temporarily flooded nursery area (Cucherousset et al. 2007, 2009).

Thus, the aim of this chapter was to investigate whether intraspecific variation in trophic positions and/or body size is correlated to habitat use and dispersal characteristics in riverine juvenile pike. This was completed by firstly comparing body size and trophic niche between pike of the same age captured in the two habitat types (river/ditches) to assess the temporal stability of the differences that have reported previously for this pike population (Mann 1982; Mann & Beaumont 1990). The role of individual diet variation in driving dispersal from the nursery habitats and the effect of individual variation in dispersal on individuals' subsequent growth and trophic niche is then determined through a mark-recapture study. Considering reports of positive relationships between boldness and movement in several fish species, irrespective of the direction of movement e.g. towards riskier habitats (Fraser et al. 2001) or safer habitats (Chapman et al. 2011), it was hypothesised that (i) individual variation in trophic niche drives dispersal, with dispersers having higher trophic positions, and consequently, larger body sizes than pike remaining in the ditches, and (ii), dispersers experience a subsequent faster increase in trophic position and growth than stayers.

5.3 MATERIALS AND METHODS

5.3.1 Fish sampling

The pike population of the River Frome and its connected side channels were sampled by electric fishing from 9 December 2008 to 3 August 2011 (Section 2.1.2; Table 2.1). To compare differences in body size, growth and diet between individual pike in the river and ditches, captured pike were measured for fork length (FL, nearest mm), body mass (BM, nearest g), fin clipped for stable isotope analysis (SIA), and scales were removed for age determination (Section 2.1). Individuals were PIT tagged and processed as described in Chapter 2. When a tagged pike was recaptured, measurements of FL and BM were taken to determine their growth increment and rate since tagging, and fin clips were taken to identify changes in trophic niche (Section 2.1.5). To identify differences in body size and trophic niche between individuals remaining in the ditches (i.e. stayers) and individuals moving into the river (i.e. dispersers), fyke netting to capture individuals moving out from the ditches into the river in combination with regular electric fishing of individuals in the ditches, was carried out from 18 June to 12 October 2010 and 10 June to 14 August 2011 in Rushton Ditch and Flood Relief Channel (Section 2.1.1). The fyke nets (8 mm mesh) were placed in the ditches near the connection to the river to capture pike moving from the ditches into the river (Fig. 5.1). The fyke nets were continuously in use (i.e. 24 hour sampling) and fish catches were checked and processed daily. Fish were processed as described previously, and released downstream of the fyke nets (towards the river) as the fish were moving in this direction when captured. Any other species captured in the nets were immediately released downstream.

Fin samples from pike and two of their putative prey items were collected for analyses of the stable isotopes $\delta^{13}C$ and $\delta^{15}N$ in order to determine the trophic niche and calculate their trophic positions (TP) (Section 2.1.5).

5.3.2 Data analyses

All data were checked for normality using Kolmogorov-Smirnov’s test and for homogeneity of variance using Levene’s test. To obtain normal and homogenous variances prior to parametric analyses, log transformations of continuous variables were performed as outlined below. All analyses were conducted in STATISTICA, version 7.

A total number of 196 fish of ages 0+ to 2+ were captured in the river and ditches during the study period (2009-2011). Since TP, FL or SGR did not differ between ditches in any of the years between 2009 and 2011 (ANOVA, all $P > 0.05$), ditches were combined for further analyses.

However, as pike across all relevant ages (i.e. 0+ to 2+) were not captured in each year in ditches and river; separate GLMs had to be performed for each age. Whilst this meant that a relatively high number of age-specific models were built, this avoided the issue of removing whole age-classes from analyses. Consequently, the GLMs were built with either trophic position or body length as the dependent variable, habitat (river/ditch) and year as categorical independent variables, and capture date, calculated as the number of days from the first sampling date (9 December), as a continuous independent variable. Capture date required ln (x+1) transformation to attain normality.

Figure 5.1. View of the Flood Relief Channel near the connection point to the main river channel, with the opening of the fyke net directed towards the ditch in order to capture fish moving from the ditch into the main channel.

Trophic or size-dependent dispersal?

Fyke netting was conducted over a longer period in 2010 (18/6-12/10) than 2011 (10/6-14/8) as the number of dispersers were very low, with no pike captured from 5 August 2011. The former period was therefore divided into summer and autumn to enable a comparison between years for summer (June-August). To avoid pseudoreplication, any pike initially captured in the ditches and then recaptured in the fyke nets were subsequently excluded from stayers and were regarded as dispersers. As no 0+ pike were captured in the ditches during summer 2011 (2 individuals were captured in the fyke nets), the years were analysed separately, which then enabled an inclusion of age 0+ for summer 2010. To investigate trophic and size-dependent migration, GLMs were then performed with TP or FL as the dependent variable, dispersal status (stayer/disperser), age (0+ to 2+), and migration date (calculated as the number of days after the first capture date) as independent variables. The influence of trophic position and body length on the timing of dispersal (i.e. only including dispersers) was analysed for each year using a GLM with timing (date of capture) as the dependent variable, and TP, FL, and age as explanatory variables.

Growth consequences of individual dispersal

SGR was calculated from initial and final FLs as detailed in Section 2.1.4. A GLM was conducted to analyse differences in SGR between pike that had undergone habitat shift (from ditches to river) and remained in the ditches, with SGR as the dependent variable, initial FL, change in TP and the number of days between captures as continuous independent variables, and habitat shift (yes/no) and age (0+ to 1+) as categorical independent variables. As only two individuals of age 2+ (recaptured in the ditches) and one age 3+ (recaptured in the river) were captured, these were excluded to allow a GML model with an interaction term of age x dispersal status.

5.4 RESULTS

When controlling for capture date and year of sampling, fish of 0+ and 1+ in the river were significantly larger and had higher trophic positions than those of captured in the ditches (Fig. 5.2; Table 5.1). At age 2+, significant differences remained for FL but not TP (Fig 5.2; Table 5.1).

Parameter	Age	Source of variation	SS	df	F	P
FL	0+	Capture date	2378.45	1	2.50	0.118
		Year	3531.67	1	3.72	0.058
		Habitat	27243.23	1	28.68	**<0.0001**
		Year x Habitat	11873.83	1	12.50	**0.001**
	1+	Capture date	17971.22	1	6.20	**0.015**
		Year	40950.04	2	7.07	**0.001**
		Habitat	66174.32	1	22.84	**<0.0001**
	2+	Capture date	5086.42	1	1.76	0.209
		Habitat	91944.03	1	31.82	**0.0001**
TP	0+	Capture date	0.36	1	2.17	0.146
		Year	0.34	1	2.06	0.156
		Habitat	5.41	1	33.12	**<0.0001**
		Year x Habitat	0.79	1	4.76	**0.033**
	1+	Capture date	0.01	1	0.05	0.819
		Year	0.25	2	0.90	0.410
		Habitat	2.48	1	18.05	**<0.0001**
		Year x Habitat	1.63	2	5.92	**0.004**
	2+	Capture date	0.02	1	0.10	0.763
		Habitat	1.12	1	4.30	0.060

Table 5.1. Results of GLMs on the effects of capture date, year (2009, 2010, 2011) and habitat (river/ditch) on the FL and TP of pike of ages 0+ to 2+. Interaction effects are only shown where they were significant at $P < 0.05$. See Appendix III for full model output. Number of individuals sampled (ditch/river) of age 0+: 2009 (n=28/15) and 2010 (n=24/8), 1+: 2009 (n=23/14), 2010 (n=32/15), 2011 (n=6/2), and 2+: 2010 (n=8/7).

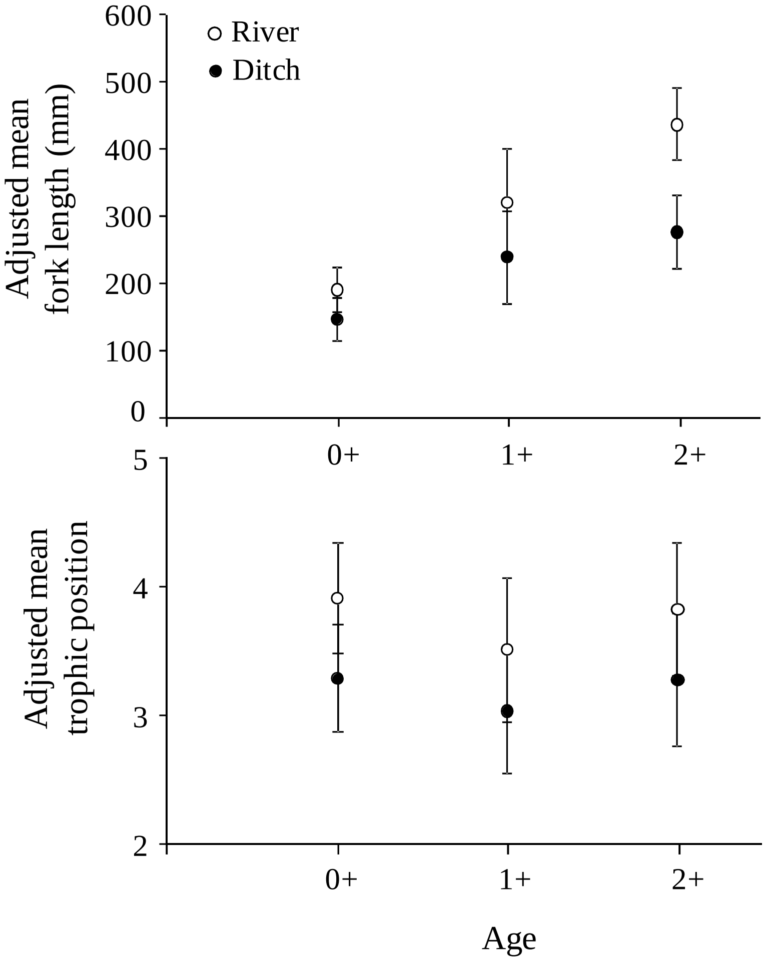

Figure 5.2. Adjusted mean (± SD; from GLM) (a) fork length and (b) trophic positions (TP) for pike *Esox lucius* sampled of ages 0+ to 2+ in the river and ditches in 2009, 2010 and 2011. Number of individuals sampled (ditch/river) of 0+: 2009 (n=28/15) and 2010 (n=24/8), 1+: 2009 (n=23/14), 2010 (n=32/15), 2011 (n=6/2), and 2+: 2010 (n=8/7). Dispersers are omitted from the figure.

5.4.1 Trophic or size-dependent dispersal?

Dispersal of pike from the ditches to the main river was apparent in both sampling years; in 2010 a total of 28 individuals moved out of the ditches, and 37 remained in the ditches, and in the shorter study period in 2011 there were 13 dispersers (excluding 2 individuals of 0+) and 11 stayers. The proportion of stayers and dispersers varied between years and ages (0+ to 2+) (Table 5.2).

Pike of ages 1+ and 2+ were had higher TPs and FLs than age 0+ in summer 2010 (Table 5.2). In the same period, stayers had significantly higher TP than dispersers (Table 5.2; Fig. 5.2). Thus, dispersing individuals had significantly lower trophic positions at all ages compared to stayers in summer 2010. In 2011, no significant effects of dispersal status or age (1+ and 2+) were found on either TP or FL (Table 5.2; Fig. 5.2). In autumn 2010, pike of age-1 and 2 had significantly higher TP values and FLs than 0+, while no differences between dispersal statuses were identified (Table 5.2; Fig. 5.3). A significant effect of body length on the timing of dispersal was found in 2010, with larger fish of all ages moving later in the study period, whereas no effects were detected in summer 2011 (Table 5.3).

Parameter	Period	Source of variation	SS	df	F	P
FL	Summer 2010	Capture date	3202.70	1	1.93	0.17
		Age	297821.33	2	89.51	**<0.0001**
		Dispersal status	2272.62	1	1.37	0.25
	Autumn 2010	Capture date	2661.67	1	0.42	0.52
		Age	53600.47	2	4.26	**0.026**
		Dispersal status	3036.83	1	0.48	0.49
	Summer 2011	Capture date	1277.46	1	0.67	0.42
		Age	7099.29	1	3.73	0.07
		Dispersal status	15.48	1	0.01	0.93
TP	Summer 2010	Capture date	0.32	1	3.92	**0.06**
		Age	1.33	2	8.15	**0.0013**
		Dispersal status	1.23	1	15.12	**0.0004**
	Autumn 2010	Capture date	0.01	1	0.13	0.72
		Age	0.74	2	5.19	**0.013**
		Dispersal status	0.11	1	1.57	0.22
	Summer 2011	Capture date	0.02	1	0.11	0.74
		Age	0.04	1	0.21	0.65
		Dispersal status	0.01	1	0.08	0.78

Table 5.2. Results of GLMs on the effects of capture date, age and dispersal status (stayer/disperser) on the FL and TP of pike sampled in summer 2010, autumn 2010 and summer 2011. The interaction effect between age x dispersal status were not significant in any models. See Appendix III for full model output. Number of individuals of each age and dispersal status (stayers/dispersers) in summer 2010: 0+ (n=11/8), 1+ (n=9/6) and 2+ (n=3/4), autumn 2010: 0+ (n=6/6), 1+ (n=7/3) and 2+ (n=1/1), summer 2011: 1+ (n=6/9) and 2+ (n=7/2).

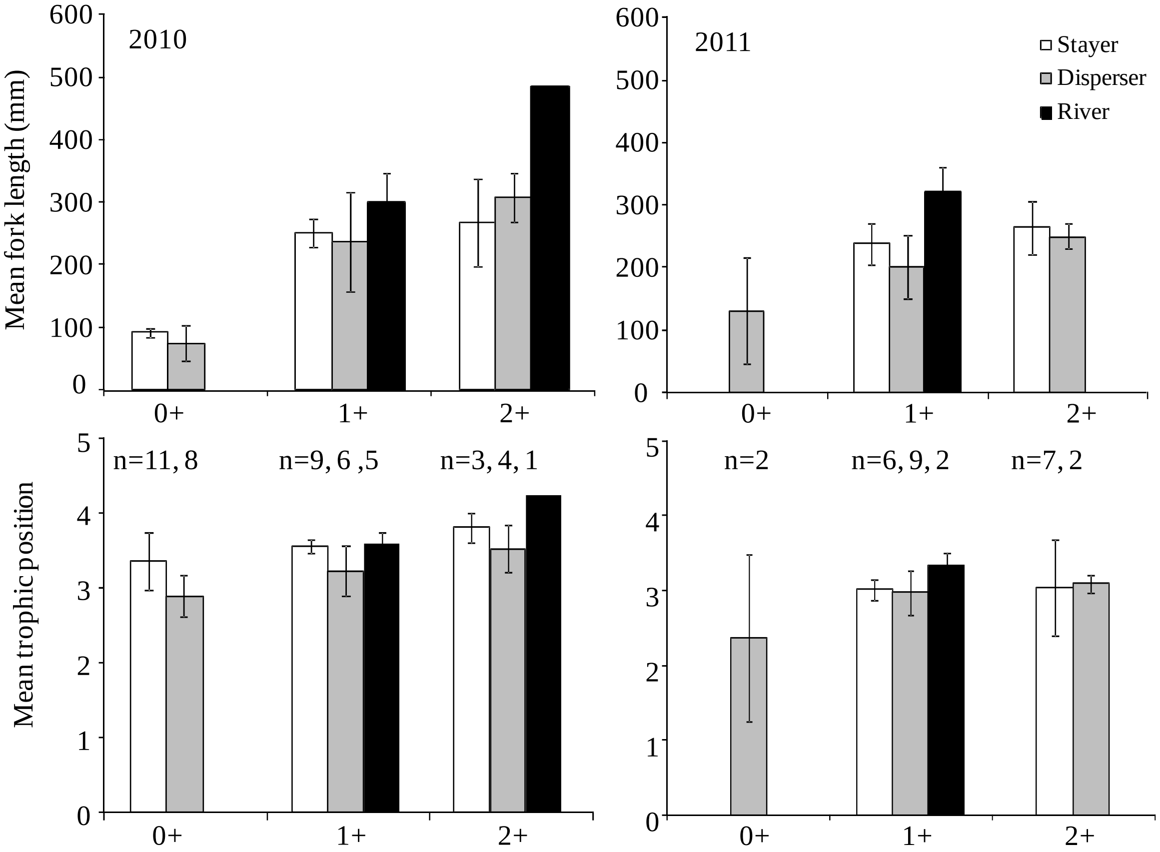

Figure 5.3. Mean fork lengths (upper panel) and trophic positions (lower panel) (±SD) of stayers, dispersers and river pike *Esox lucius* of ages 0+ to 2+ sampled in summer 2010 (left panel) and 2011 (right panel).

Period	Source of variation	SS	df	F	p
2010	Age	49.03	2	0.02	0.983
	TP	1445.41	1	1.04	0.319
	FL	11406.24	1	8.18	**0.009**
2011	Age	18.63	2	0.06	0.939
	TP	0.91	1	0.01	0.940
	FL	1.29	1	0.01	0.929

Table 5.3. Results of GLMs on the effects of age, TP and FL on the timing of dispersal of pike captured in the fyke nets in 2010 (n=32) and summer 2011 (n=13). The interaction effect between age x FL or age x TP was not significant in any models. See Appendix III for full model output. Significant ($P < 0.05$) p-value is shown in bold.

5.4.2 Growth consequences of individual movement

Of 143 tagged pike sampled in the ditches, 46 were recaptured in the ditches and only 7 were recaptured in the river. None of the 23 pike captured in the fyke nets in 2010 were subsequently recaptured in the river. The number of days between captures and recaptures ranged from 51 to 579 days. The results revealed a significant effect of movement on SGR, with dispersers (from ditches to river) having higher SGRs than pike recaptured in the ditches (Table 5.4). In addition, there was a significant negative effect of the number of days between capture and recapture and initial FL on SGR (Table 5.4).

Parameter	Source of variation	SS	df	F	P
SGR	FL	0.05	1	11.41	**0.002**
	Day of capture*	0.04	1	7.36	**0.010**
	Change in TP	0.00	1	0.88	0.354
	Age	0.00	1	0.51	0.478
	Dispersal status	0.02	1	4.56	**0.040**
	Age x Dispersal status	0.00	1	0.28	0.603

Table 5.4. Results of a GLM on the effects of FL, day of capture, change in TP, age, dispersal status (recaptured in ditch or river), and the interactions age x dispersal status on the specific growth rate of pike initially captured in the ditch. See Appendix III for full model output. *Day of capture was log-transformed. Number of individuals of 0+: stayers (n=28), leavers (n=5), and 1+: stayers (n=16), leavers (n=1).

5.5 DISCUSSION

The results indicated that there was trophic and body-size driven dispersal in juvenile pike from the ditches into the main river channel. Although the mean body lengths and trophic positions were lower in dispersers compared to stayers in both sampling years, the only statistically significant difference was found for trophic position in 2010. However, the findings contradicted the first hypothesis that stated that dispersers would be of larger size and of higher trophic position. The results did, however, provide rare evidence for long-term effects of individual variation in dispersal. This was because the pike that migrated into the river, i.e. the dispersers, which were smaller and of significantly lower trophic positions than the stayers, subsequently attained faster growth rates. This is consistent with the second hypothesis (‘dispersers experience a subsequent faster growth than stayers’).

The ability to compete for scarce resources is a primary aspect of population dynamics, ultimately influencing individual survival (Vøllestad & Quinn 2003). Territoriality may exclude conspecifics and force some individuals to occupy poorer quality habitat and increase mortality (Sutherland 2006). For example, in the highly colonial seabird, the common guillemot (*Uria aalge* Pontoppidan), a population increase leads to a greater use of poorer sites by individuals of lower competitive ability (Kokko et al. 2004). Individual variation in resource use can also affect the competitive ability (Duffy 2010), which provides an explanation for the relationship between trophic positions and dispersal status as found here in pike. Reports on whether pike occupy territories vary, with Nilsson (2006) showing that adult pike spatially avoid larger conspecifics creating a size-dependent distribution pattern, while Hawkins et al. (2003) found no evidence for its occurrence in juveniles.

Several studies report on high interference intensity in juvenile pike, with cannibalism taking place on individuals that are up to 75 % of their body length (Craig & Kipling 1983; Bry et al. 1995). Body size therefore becomes a very important determinant of competitive ability and avoidance of cannibalism by siblings, with great consequences on survival of juvenile pike. By combining behavioural experiments with physiology and population modelling, Edeline et al. (2010) showed that an increase in pike density, while controlling prey availability, had no effect on the degree of interference or exploitative competition. However, increased pike density induced a neuroendocrine stress response with a significant decrease in the thyroid production of thyroxine and triiodothyronine in the pike, and depressed their energetic status and lowered body growth rate. This physiological stress increased with a smaller body size, indicating a size-dependent dominance hierarchy. Although an increased pike density did not change the food intake, individual somatic growth in both length and mass was decreased, suggesting a depressed energetic status (Edeline et al. 2010). Similarly, the smaller pike with lower trophic positions leaving the ditches may be an effect of social stress if it is not through direct interference intimidation or competitive exclusion by slightly larger pike. The significant effect of body length on the timing of dispersal detected in 2010 may be influenced by the growth of individuals, with individuals leaving later in autumn having had more time to grow or they may represent the larger previous stayers.

The results also showed that pike inhabiting the river of all ages had higher trophic positions than pike captured in the ditches, verifying the dietary differences between ditch and river pike previously detected using stomach content analyses by Mann (1982). The larger size at age and thus faster growth rate of pike in the river compared to pike in the ditches found here also corresponds to the findings of Mann & Beaumont (1990). Despite pike moving out from the ditches being smaller and of lower trophic positions, providing that they survive the dispersal event and successfully settle in the river, then they are more likely to become piscivorous earlier in life than fish in the side channels, due to the higher fish prey availability (i.e. increased predation risk but also higher potential for body growth). This then facilitates faster growth despite the potential for greater energy expenditure in the river. Indeed, individuals recaptured in the river, which had been initially captured and tagged in the ditches, achieved a faster growth compared to conspecifics remaining in the ditches. The low number of individuals recaptured in the river compared to the ditches is likely to be due to high mortality risk in the main channel compared to the ditches. Alternatively, it could be an artefact of decreased sampling efficiency (albeit different sampling equipment) due to the larger volume in the river compared to the ditches. An alternative explanation for the size and trophic differences between the river and ditch pike is the possibility of pike spawning in the main river, although it remains a rare occurrence (Masters 2003; Knight 2006). Pike hatching in the main river would be expected to shift to a piscivorous diet during their first summer as reported in juvenile pike in areas sustaining diverse fish communities (Mittelbach & Persson 1998; Skov et al. 2003; Ziliukiene & Ziliukas 2006).

Despite receiving a great deal of research attention in recent years, few studies have explored whether trophic positions, in combination with body size, is related to individual variation in dispersal in natural populations. Indeed, variation in trophic positions among individuals is a useful indication of competitive ability for resources (Bolnick et al. 2003). Here, the results showed that although dispersing individuals had lower trophic values and body sizes (suggesting they were poorer foragers), perhaps as a consequence of social stress or intimidation by slightly larger pike, individuals that successfully settled in the river (i.e. recaptured at a later stage) clearly benefited from dispersing by increased subsequent growth and trophic position (i.e. becoming more successful foragers). Therefore, this study highlights the importance of habitat exclusion of less competitive individuals in driving variation in dispersal or partial migration (i.e. where only part of the population migrates to new habitats).

5.6 REFERENCES

Araújo, M. S., Bolnick, D. I. & Layman, C. A. 2011. The ecological causes of individual specialisation. *Ecology Letters*, 14, 948-958.

Arendt, J. D. 1997. Adaptive intrinsic growth rates: An integration across taxa. *Quarterly Review of Biology*, 72, 149-177.

Armstrong, J. D., Braithwaite, V. A. & Huntingford, F. A. 1997. Spatial strategies of wild Atlantic salmon parr: exploration and settlement in unfamiliar areas. *Journal of Animal Ecology*, 66, 203-211.

Barbault, R. & Stearns, S. 1991. Towards an evolutionary ecology linking species interactions, life-history strategies and community dynamics - an introduction. *Acta Oecologica-International Journal of Ecology*, 12, 3-10.

Biro, P. A. & Ridgway, M. S. 2008. Repeatability of foraging tactics in young brook trout, *Salvelinus fontinalis*. *The Canadian Field-Naturalist*, 122, 40-44.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. 2003. The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist*, 161, 1-28.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C. & Vasseur, D. A. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26, 183-192.

Bry, C. 1996. Role of vegetation in the life cycle of pike. In: *Pike biology and exploitation*, (Ed. by J. Craig), London: Chapman & Hall.

Bry, C., Bonamy, F., Manelphe, J. & Duranthon, B. 1995. Early-life characteristics of pike, *Esox lucius*, in rearing ponds - temporal survival pattern and ontogenetic diet shifts. *Journal of Fish Biology*, 46, 99-113.

Budaev, S. 1997. Alternative styles in the European wrasse, *Symphodus ocellatus*: Boldness-related schooling tendency. *Environmental Biology of Fishes*, 49, 71-78.

Chapman, B. B., Hulthén, K., Blomqvist, D. R., Hansson, L.-A., Nilsson, J.-Å., Brodersen, J., Anders Nilsson, P., Skov, C. & Brönmark, C. 2011. To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters*, 14, 871-876.

Cote, J. & Clobert, J. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B-Biological Sciences*, 274, 383-390.

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T. & Sih, A. 2010. Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). 277, 1571-1579.

Craig, J. F. & Kipling, C. 1983. Reproduction effort versus the environment - case-histories of Windermere perch, *Perca fluviatilis* L, and pike, *Esox lucius* L. *Journal of Fish Biology*, 22, 713-727.

Cucherousset J., Paillisson J.-M. & Roussel J.-M. 2007. Using PIT Telemetry to study the fate of hatchery-reared YOY northern pike released into shallow vegetated areas. *Fisheries Research*, 85, 159-164.

Cucherousset, J., Paillisson, J. M., Cuzol, A. & Roussel, J. M. 2009. Spatial behaviour of young-of-the-year northern pike (*Esox lucius* L.) in a temporarily flooded nursery area. *Ecology of Freshwater Fish*, 18, 314-322.

Dall, S. R. X., Houston, A. I. & McNamara, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, 7, 734-739.

Duffy, M. A. 2010. Ecological consequences of intraspecific variation in lake Daphnia. *Freshwater Biology*, 55, 995-1004.

Edeline, E., Haugen, T. O., Weltzien, F. A., Claessen, D., Winfield, I. J., Stenseth, N. C. & Vollestad, L. A. 2010. Body downsizing caused by non-consumptive social stress severely depresses population growth rate. *Proceedings of the Royal Society B-Biological Sciences*, 277, 843-851.

Eklöv, P. & Svanbäck, R. 2006. Predation risk influences adaptive morphological variation in fish populations. *American Naturalist*, 167, 440-452.

Fraser, D., Gilliam, J., Daley, M., Le, A. & Skalski, G. 2001. Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *American Naturalist*, 158, 124-135.

Gozlan, R. E. & Copp, G. H. 2005. Early ontogenetic ecology of sofie Chondrostoma toxostoma: an integrated approach to organism-environment relationships. *Journal of Fish Biology*, 67, 86-99.

Grayson, K. L. & Wilbur, H. M. 2009. Sex- and context-dependent migration in a pond-breeding amphibian. *Ecology*, 90, 306-312.

Hansson, L.-A. & Hylander, S. 2009. Size-structured risk assessments govern Daphnia migration. *Proceedings of the Royal Society B-Biological Sciences*, 276, 331-336.

Hawkins, L. A., Armstrong, J. D. & Magurran, A. E. 2003. Settlement and habitat use by juvenile pike in early winter. *Journal of Fish Biology*, 63, 174-186.

Hebblewhite, M. & Merrill, E. H. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, 90, 3445-3454.

Hjelm, J., Svanbäck, R., Byström, P., Persson, L. & Wahlström, E. 2001. Diet-dependent body morphology and ontogenetic reaction norms in Eurasian perch. *Oikos*, 95, 311-323.

Jonsson, B. & Jonsson, N. 2001. Polymorphism and speciation in Arctic charr. *Journal of Fish Biology*, 58, 605-638.

Knight, C. 2006. Utilisation of off-river habitats by lowland river fishes. PhD thesis, University of Durham, UK.

Kokko, H., Harris, M. & Wanless, S. 2004. Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. *Journal of Animal Ecology*, 73, 367-376.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation - a review and prospectus. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 68, 619-640.

Magurran, A. E. 1993. Individual differences and alternative behaviours. In: *Behaviour of teleost fishes*, (Ed. by T. . Pitcher), London: Chapman & Hall.

Mann, R. H. K. 1980. The numbers and production of pike (*Esox lucius*) in 2 Dorset rivers. *Journal of Animal Ecology*, 49, 899-915.

Mann, R. H. K. 1982. The annual food-consumption and prey preferences of pike (*Esox lucius*) in the river Frome, Dorset. *Journal of Animal Ecology*, 51, 81-95.

Mann, R. & Beaumont, W. 1990. Fast- and slow-growing pike, *Esox lucius* L., and problems of age-determinations from scales. *Aquaculture and Fisheries Management*, 21, 471-478.

Masters, J. 2003. Temporal variation in the behaviour of pike *Esox lucius* L. PhD thesis, University of St Andrews, UK.

Mittelbach, G. & Persson, L. 1998. The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 1454-1465.

Nilsson, P. A. 2006. Avoid your neighbours: size-determined spatial distribution patterns among northern pike individuals. *Oikos,* 113, 251-258.

Nilsson, A. L. K., Alerstam, T. & Nilsson, J. A. 2008. Diffuse, short and slow migration among blue tits. *Journal of Ornithology,* 149, 365-373.

Raat, A. 1988. *Synopsis of biological data on the northern pike Esox lucius Linnaeus 1758.* FAO Fish. Synopsis.

Robinson, B. W. & Wilson, D. S. 1994. Character release and displacement in fishes - a neglected literature. *American Naturalist*, 144, 596-627.

Skov, C., Lousdal, O., Johansen, P. H. & Berg, S. 2003. Piscivory of 0+pike (*Esox lucius* L.) in a small eutrophic lake and its implication for biomanipulation. *Hydrobiologia*, 506, 481-487.

Skov, Brodersen, J., Nilsson, P. A., Hansson, L. A. & Brönmark, C. 2008. Inter- and size-specific patterns of fish seasonal migration between a shallow lake and its streams. *Ecology of Freshwater Fish*, 17, 406-415.

Skov, C., Baktoft, H., Brodersen, J., Brönmark, C., Chapman, B. B., Hansson, L.-A. & Nilsson, P. A. 2011. Sizing up your enemy: individual predation vulnerability predicts migratory probability. *Proceedings of the Royal Society B: Biological Sciences*, 278, 1414 -1418.

Skulason, S. & Smith, T. B. 1995. Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution*, 10, 366-370.

Smith, T. B. & Skulason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics*, 27, 111-133.

Sutherland, W. J. 2006. Predicting the ecological consequences of environmental change: a review of the methods. *Journal of Applied Ecology*, 43, 599-616.

Svanbäck, R. & Eklöv, P. 2002. Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. *Oecologia*, 131, 61-70.

Svanbäck, R. & Eklöv, P. 2003. Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? *Oikos*, 102, 273-284.

Svanbäck, R. & Eklöv, P. 2004. Morphology in perch affects habitat specific feeding efficiency. *Functional Ecology*, 18, 503-510.

Svanbäck, R., Eklöv, P., Fransson, R. & Holmgren, K. 2008. Intraspecific competition drives multiple species resource polymorphism in fish communities. *Oikos*, 117, 114-124.

Vøllestad, L. A. & Quinn, T. P. 2003. Trade-off between growth rate and aggression in juvenile coho salmon, *Oncorhynchus kisutch*. *Animal Behaviour*, 66, 561-568.

Ziliukiene, V. & Ziliukas, V. 2006. Feeding of early larval pike *Esox lucius* L. reared in illuminated cages. *Aquaculture*, 258, 378-387.

Chapter 6

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Behavioural syndrome in a solitary predator is independent of body size and growth rate

6.1 ABSTRACT

Models explaining behavioural syndromes often focus on state-dependency, linking behavioural variation to individual differences in other phenotypic features. Empirical studies are, however, rare. Here, the presence of a size and growth-dependent stable behavioural syndrome in the juvenile-stages of a pike, shown as repeatable foraging behaviour across risk, was investigated. Pike swimming activity, latency to prey attack, number of successful and unsuccessful prey attacks was measured during the presence/absence of visual contact with a competitor or predator. Foraging behaviour across risks was considered an appropriate indicator of boldness in this solitary predator where a trade-off between foraging behaviour and threat avoidance has been reported. Support was found for a behavioural syndrome, where the rank order differences in the foraging behaviour between individuals were maintained across time and risk situation. However, individual behaviour was independent of body size and growth in conditions of high food availability, showing no evidence to support the state-dependent personality hypothesis. The importance of a combination of spatial and temporal environmental variation for generating growth differences is highlighted.

6.2 INTRODUCTION

Empirical studies across a range of animal taxa are increasingly demonstrating the existence of personalities, where individuals within populations vary consistently in their behaviour over time (Gosling 2001; Sih et al. 2004a; Smith & Blumstein 2008). When individual behaviours are consistent or co-vary across situations or contexts, where a context is a functional behavioural category (e.g. feeding, mating, predator avoidance or dispersal), and a situation is the set of conditions at a particular time which can involve different levels along an environmental gradient (e.g. foraging behaviours in different habitats), it is referred to as a behavioural syndrome (Sih et al. 2004a, b; Bell & Sih 2007). Although individual consistency of single behaviours is considered to contribute meaningfully to the stability of the behavioural syndrome they comprise (Lee & Bereijikian 2008; Logue et al. 2009; Gabriel & Black 2010), repeated observations of individuals over time within situations or contexts are lacking in many studies (Bell & Sih 2007; Wilson & McLaughlin 2007; Schurch & Heg 2010). Despite this, and in conjunction with inconsistent methodologies employed to assess behavioural traits (Reale et al. 2007; Toms et al. 2010), behavioural syndromes are considered to be widespread (Sih et al. 2004a). Furthermore, a focus on characterising behavioural syndromes in social or territorial species that show parental care or build nests and exhibit dominance hierarchies or other social structures, such as shoaling (Reale et al. 2007; Conrad et al. 2011), has resulted in a paucity of studies in other species, such as in solitary apex predators. Yet characterizing behavioural syndromes in ecologically-different species with contrasting behavioural life-histories should improve our understanding of the extent of behavioural syndromes and their ecological importance. For example, identifying behavioural syndromes in an apex predator may be particularly important for understanding their effect on trophic interactions and influence on prey fish communities (Moya-Larano 2011; Bolnick et al. 2011).

Behavioural syndromes are temporally stable when the same association between different behaviours occurs at different stages in time (Bell & Stamps 2004; Sih et al. 2004b). Temporal stability in behavioural syndromes suggests that individual behaviours may not be able to evolve independently and are therefore considered to be of particular evolutionary significance (Stamps 1991; Sih et al. 2004b). Exploring the mechanisms involved in maintaining behavioural syndromes in animals has therefore recently received considerable theoretical attention, with a focus on state-dependency. Individuals differ consistently in a range of features or 'states', for example in morphology, physiology and even in aspects of their environment (Houston & McNamara 1999). State-dependent behavioural models are therefore based on the fact that an individual's state influences the fitness costs and benefits of its behavioural decisions (Houston & McNamara 1999; Wolf & Weissing 2010). As stable individual variation in growth rate has been reported in a variety of species with indeterminate growth (Stamps 2007), growth has also been suggested as a key factor in maintaining personality differences due to growth-mortality tradeoffs (Stamps 2007; Biro & Stamps 2008). Indeed, traits such as boldness, aggression and activity may correlate with higher growth rates, but these behaviours may also increase mortality through greater risk-taking (Mangel & Stamps 2001; Biro et al. 2006; Stamps 2007). As few empirical studies have tested predictions derived from state-dependent models, this is now needed to further our insight of behavioural syndromes (Dingemanse & Wolf 2010).

Individual variation in risk-taking was originally used to define boldness in animals (Wilson et al. 1994; Wilson 1998), which subsequently lead to a variety of interpretations on its measurement (Budaev & Brown 2011). Boldness has been measured, for example, by response to threatening stimuli, novel objects or food sources, predator inspection, latency to emerge from cover and foraging under predation threat (*cf.* Budaev & Brown 2011). Although a consensus on the measurement of boldness is valuable for comparative purposes, a consideration of behaviours and related situations that would represent boldness in the species of interest is important (Bell 2007; Toms et al. 2010; Conrad et al. 2011). While the biological significance of individual behavioural variation is increasingly recognised, the fundamental differences between functionally different species should not be overlooked. To interpret results from studies using different tests for measuring the same personality trait, the specific context and methods should be considered (Conrad et al. 2011).

Pike exhibit considerable growth differences in their wild populations, with size dimorphism already apparent in YOY (Raat 1988; Mann & Beaumont 1990), thus making it a strong model to test size- and growth dependent personality. Pike is a solitary and cannibalistic predator species that does not live in groups during any stage of its life (Casselman & Lewis 1996). Cannibalism usually occurs between fish of different ages (Mann 1982), but as considerable size variations occur within the same cohort (Chapter 3) individuals have been found to cannibalise on conspecifics that are 50–91% of their body size (Grimm 1981a; Giles et al. 1986; Ziliukiene & Ziliukas 2006). In addition, pike are vulnerable to attack from conspecifics of similar size while handling prey (Nilsson & Bronmark 1999). Due to the strong pressures from both intra- and interspecific predators on juvenile pike in their nursery habitats (Grimm 1981b; Raat 1988; Bry et al. 1995), an important trade-off has been suggested to occur between foraging activity in order to out-grow piscivores (due to piscivorous gape limitation) and anti-predator avoidance (Lehtiniemi 2005). A measure of foraging behaviour across a gradient of risks is therefore considered as an appropriate indicator of boldness in this solitary apex predator. Foraging under risk of predation has been used as a measure of boldness in several fish species (e.g. Ward et al. 2004; Wilson & Stevens 2005; Magnhagen & Staffan 2005; Bell 2005), but has recently been criticised as the behaviour measured might be motivated by hunger instead of boldness (Toms et al. 2010). To overcome this, equal starvation periods prior to measurements of foraging behaviour are commonly used to ensure similar hunger levels among the test animals (Wang et al. 2003; Galarowicz & Wahl 2005).

Consequently, in the present study, the presence of a behavioural syndrome in juvenile pike was determined by estimating the repeatabilities of individual foraging behaviours through time and across risk situations, including at different stages over time, and its relationship to individual state (i.e. body mass) and growth rate. The following hypotheses were tested: (i) individuals exhibit stable behavioural syndromes, shown by repeatable foraging behaviour within and across risk situations; and (ii) in high-risk situations, larger-bodied individuals consistently forage at higher rates compared to smaller individuals, and so have higher growth rates in conditions of abundant food.

6.3 MATERIALS AND METHODS

6.3.1 Collection and housing of fish

The YOY pike were captured in a tributary of the River Frome, Dorset (50°419 N; 2°119 W), between 15th and 20th May 2009. Details on collection and housing of the fish are provided in Section 2.2.1. Fish were kept in isolation and fed *ad libitum* using *Gammarus* spp. for 10 days prior to the first experiment, which then continued between the experiments.

As predation by larger conspecifics (i.e. cannibalism) is a common threat to YOY pike (Grimm 1981b; Mann 1982), to provide differential levels of predation risk in the experiments, age-1 pike (220-250 mm fork length) were captured from the same site on 22nd May 2009. Details on the collection and housing of these fish are also provided in Section 2.2.1.

6.3.2 Experimental protocol

Thirty-four YOY pike (initial mass W_i = 0.53 ± 0.03 g, mean ± SE) were used as the focal fish in the experiments. This number of fish was chosen as previous work on repeated individual response experiments suggests a sample size of 30 will provide a moderate effect size and statistical power > 0.8 (e.g. Bell 2005; Pronk et al. 2010). Individual consistency in foraging behaviour, as an indication of boldness, was measured repeatedly within and across three risk situations (treatments): i) no visual contact to other fish (control: no risk); ii) visual contact to a similar-sized age-0 stimulus pike (competitor: low risk); and iii) visual contact to larger-bodied age-1 stimulus pike (predator: high risk). Prior to each experiment, focal fish were starved for 24 h to ensure similar hunger levels among the individuals. Juvenile pike have high evacuation rate of ingesta, with 100 % evacuation in 18-22 h and 24 h for juveniles of 0.15 g and 3 g respectively at 18°C (Kaushik et al. 1985). The initial body masses of individuals studied here ranged from 0.23 to 1.21 g. Although the lower temperature in our experiments (16°C) may decrease the evacuation rates slightly, a starvation period of 24 hours is likely to be sufficient to standardise hunger levels. In addition, for the welfare of the fish, a starvation period of over 24 hours was not allowed within the HO project licence.

Each focal fish was removed from their keeping tank by scooping using a 0.5 L beaker (to eliminate handling) and transferred to an experimental tank (30 x 20 x 20 cm) with a water depth of 10 cm. The water temperature and oxygen levels in the experimental tanks were the same as in the holding tanks. The fish were then acclimatised for 30 minutes with visual contact to the neighbouring tank, which, depending on the experimental treatment, was either empty (control), or contained a stimulus fish of age-0 (competitor) or age-1 (predator). Feeding behaviour was measured by filming their response to the subsequent introduction of ten live gammarids for 15 minutes. The fish were subsequently transferred back (by scooping) into their individual tanks. The control treatment was repeated six times, and the competitor and predator treatments were each repeated four times (repeats are from now referred to as trials), with this replication level satisfactory according to Bell *et al.* (2009). Each trial was completed in two days (between 9.00 and 18.00 h). Four to five days elapsed between trials and they were conducted in the following treatment-sequence: control, competitor and predator. Two additional control trials were carried out after this sequence had been repeated four times to increase the number of repeated measurements. All 14 trials were conducted between 1 June and 31 August 2009 (91 days). Large variation in growth rates during a similar time period has been reported in juvenile pike in the wild (Mann & Beaumont 1990;

Cucherousset et al. 2007) and in experimental conditions (Bry et al. 1995; Ivanova & Svirskay 1995).

The focal and competitor stimulus fish were matched for size (± 5 mm). A minimum of ten different fish were used as competitor stimulus fish in one day, and a stimulus fish was not used twice in a row. Three predator stimulus pike were used, and they were kept in their experimental tanks throughout the experimental day. Focal fish were assigned randomly to the predator stimulus fish. No effect of time of day of the experiment or stimulus fish individual used (competitors or predators) was found to influence the behaviour of the focal fish (ANOVA, $P > 0.05$). At the end of the experimental period (91 days), final mass (W_f) was measured for each individual. The specific growth rate (SGR) of each individual over the experimental period was calculated using the initial and final body masses (Section 2.4).

6.3.3 Video analysis

Video analysis enabled quantification of the following foraging behaviours: (i) latency of first prey attack (s); (ii) number of captured prey; (iii) number of unsuccessful attacks; and (iv) swimming activity (i.e. time spent moving). An unsuccessful attack was interpreted as when the captured prey escaped or was expelled. Individuals that did not attack prey were given latency times of 15 minutes so as not to remove the animals that were least likely to attack prey, but they were excluded from the variable ‘number of unsuccessful attacks’. All films were analysed by the same operator in randomised order.

6.3.4 Statistical analysis

To evaluate whether the pike perceived the different risks Kruskal–Wallis tests were used to examine differences in the behavioural measures between treatments.

To test the first hypothesis, consistency of an individual’s behaviour over time within situations and across situations (behavioural syndrome) was calculated as their repeatability (± SE and 95% CI) according to

Nakagawa and Schielzeth (2010) (Section 2.4). Temporal stability of behavioural syndromes was tested by conducting four separate repeatability analyses using one trial of each treatment (control, competitor and predator) conducted closest in time. As one trial was conducted weekly (with 4-5 days apart) and in the same sequence (control, competitor and predator). Thus, the closest time between the control and competitor, and competitor and predator trials was 4 to 5 days, and between control and predator trials 8 to 10 days. The number of captured prey and unsuccessful attacks constituted 'count' data and were analysed using the Poisson multiplicative overdispersion model fitted by PQL (penalised quasi-likelihood) estimation on the original scale. Latency to first attack and swimming activity were log-transformed and analysed for repeatability using the restricted maximum likelihood model. Both models use a randomisation procedure for significance tests. Only behavioural measures that were repeatable across time or situations were used in the subsequent analyses. In addition, between-situation correlations of the same behavioural measures and between different behavioural measures within-situations were investigated using Spearman's ranking test (r_s). To test the second hypothesis, correlation analyses (r_s) between repeatable behavioural measures and body mass (initial and final) and SGR were performed. All statistical analyses were conducted using R 2.12.1 (R development core team 2009). To compare repeatability estimates, the effect sizes and the 95 % CIs were compared in addition to determining whether the confidence intervals overlapped with zero rather than basing inferences purely on probability values (Nakagawa 2004; Garamszegi 2006; Nakagawa & Cuthill 2007).

6.4 RESULTS

The number of captured prey and swimming activity differed significantly between the three experimental situations (captured prey: K-W, Chi = 25.69, df = 2, $P < 0.0001$; swimming: K-W, Chi = 34.84, df = 2, $P < 0.0001$, Table 6.1). Higher numbers of captured prey and increased swimming activity were detected in the control and competition treatments compared to the predation treatments, suggesting adjusted responses according to risk levels.

	Trial	Latency to attack (s)	No. of captured prey	No. of un-successful attacks	Swimming activity (s)
(a)	1	52.8 ± 16.2	5.9 ± 0.6	1.6 ± 0.3	36.3 ± 5.8
	2	152.2 ± 26.0	6.7 ± 0.5	1.1 ± 0.2	36.0 ± 3.3
	3	200.2 ± 47.7	5.4 ± 0.7	0.4 ± 0.1	23.1 ± 2.8
	4	222.5 ± 46.9	3.9 ± 0.6	0.4 ± 0.1	36.5 ± 4.4
	5	175.8 ± 48.4	5.4 ± 0.7	0.9 ± 0.3	30.4 ± 3.8
	6	207.3 ± 46.1	3.9 ± 0.7	0.7 ± 0.2	39.0 ± 7.3
(b)	1	111.3 ± 22.4	3.3 ± 0.4	0.6 ± 0.1	18.8 ± 1.9
	2	161.3 ± 37.6	4.3 ± 0.7	0.4 ± 0.1	17.1 ± 2.0
	3	214.4 ± 46.0	4.2 ± 0.7	0.7 ± 0.2	29.4 ± 4.5
	4	150.4 ± 32.8	4.9 ± 0.7	0.7 ± 0.2	40.2 ± 5.5
(c)	1	80.2 ± 36.1	1.9 ± 0.3	1.0 ± 0.3	9.3 ± 1.9
	2	215.9 ± 63.0	1.7 ± 0.4	0.1 ± 0.1	14.4 ± 2.9
	3	332.6 ± 64.2	1.3 ± 0.4	0.3 ± 0.2	16.0 ± 2.8
	4	218.9 ± 54.3	3.3 ± 0.7	0.6 ± 0.2	27.0 ± 4.4

Table 6.1. Mean behavioural measurements (± SE) of juvenile pike (n=34) in each trial of the (a) control, (b) competitor and (c) predator treatment.

6.4.1 Repeatability and stability of behavioural syndromes

Although repeatability was significant ($P < 0.05$) for the latency to attack within the control and competitor treatments, the repeatability estimate was low (0.12), together with a CI ascending from 0 within the control (Table 6.2).

	Behavioural measure	R	SE	95 % CI	P
(a)	Latency to attack prey	0.12	0.06	0.00 to 0.24	**0.011**
	Number of captured prey	0.19	0.08	0.05 to 0.35	**0.001**
	Number of unsuccessful attacks	0.10	0.09	0.00 to 0.32	0.094
	Swimming activity	0.07	0.05	0.00 to 0.09	0.086
(b)	Latency to attack prey	0.35	0.10	0.15 to 0.54	**0.001**
	Number of captured prey	0.44	0.13	0.18 to 0.68	**0.001**
	Number of unsuccessful attacks	0.00	0.10	0.00 to 0.32	0.660
	Swimming activity	0.07	0.07	0.00 to 0.23	0.192
(c)	Latency to attack prey	0.07	0.07	0.00 to 0.22	0.183
	Number of captured prey	0.21	0.13	0.03 to 0.53	**0.026**
	Number of unsuccessful attacks	0.00	0.29	0.00 to 0.85	0.788
	Swimming activity	0.08	0.07	0.00 to 0.25	0.138

Table 6.2. The repeatabilities (R) of behavioural measures in juvenile pike (n=34) within each experimental situation: (a) control (no risk), (b) competition (low risk), (c) predation (high risk). Latency to prey attack and swimming activity were log-transformed to achieve normality. Significant ($P < 0.05$) P-values are shown in bold.

The number of prey captured had significant P-values within all contexts, and although none of the CI overlapped with zero, the repeatability estimates and CI varied between contexts, with the competitor context having the highest effect size and CI. Repeatability analyses of behaviours across trials of each treatment conducted closest in time (i.e. temporal stability of behavioural syndrome), revealed significant P-values together with high effect sizes and CI for captured prey in trials 3 and 4 (Table 6.3.a-d).

Trials	Behavioural measure	R	SE	95 % CI	P
(a)	Latency to attack prey	0.05	0.08	0.00 to 0.26	0.310
	Number of captured prey	0.10	0.11	0.00 to 0.36	0.171
	Number of unsuccessful attacks	0.21	0.18	0.00 to 0.65	0.174
	Swimming activity	0.00	0.07	0.00 to 0.23	0.473
(b)	Latency to attack prey	0.17	0.11	0.00 to 0.39	0.062
	Number of captured prey	0.19	0.14	0.00 to 0.49	0.085
	Number of unsuccessful attacks	0.00	0.27	0.00 to 0.86	0.809
	Swimming activity	0.13	0.10	0.00 to 0.36	0.143
(c)	Latency to attack prey	0.23	0.11	0.00 to 0.44	**0.014**
	Number of captured prey	0.41	0.16	0.12 to 0.73	**0.003**
	Number of unsuccessful attacks	0.27	0.25	0.00 to 0.86	0.339
	Swimming activity	0.11	0.10	0.00 to 0.33	0.147
(d)	Latency to attack prey	0.50	0.10	0.28 to 0.66	**0.001**
	Number of captured prey	0.70	0.12	0.43 to 0.89	**0.001**
	Number of unsuccessful attacks	0.00	0.18	0.00 to 0.55	0.948
	Swimming activity	0.00	0.06	0.00 to 0.21	0.608
(e)	Latency to first attack	0.18	0.05	0.09 to 0.28	**0.001**
	Number of captured prey	0.30	0.09	0.14 to 0.49	**0.001**
	Number of unsuccessful attacks	0.03	0.04	0.00 to 0.12	0.129
	Swimming activity	0.10	0.03	0.00 to 0.12	**0.011**

Table 6.3. The repeatability (R) of behavioural measures in juvenile pike (n=34) across context using one trial of each treatment conducted closest in time: (a) trials 1 (n=3), (b) trials 2 (n=3), (c) trials 3 (n=3), (d) trials 4 (n=3), and (e) all trials (n=14). Latency to prey attack and swimming activity were log-transformed to achieve normality. Significant ($P < 0.05$) P-values are shown in bold.

Latency to attack was also found to be significant within trials 4, whereas in trials 3, the CI started from 0. Across all experiments, the number of prey captured and latency to attack were significantly repeatable with high CI and effect sizes, whereas swimming activity, although having a significant p-value, had a CI starting from 0 (Table 6.3.e).

Statistically significant correlations between treatments were found in the mean number of prey captured (Fig. 6.1), swimming activity (control and competitor, $r_s = 0.43$, $n = 34$, $P = 0.012$; control and predator, $r_s = 0.44$, $n = 34$, $P = 0.009$; and competitor and predator, $r_s = 0.37$, $n = 34$, $P = 0.030$), and mean latency to attack (control and competitor, $r_s = 0.51$, $n = 27$, $P = 0.002$; control and predator, $r_s = 0.48$, $n = 30$, $P = 0.005$, and competitor and predator, $r_s = 0.25$, $n = 34$, $P = 0.170$).

6.4.2 State-dependent behaviours

Initial mass, final mass and SGR were not correlated with any of the repeatable behavioural measures (i.e. number of captured prey, latency to prey attack and swimming activity) in any of the trials (all $P > 0.05$; e.g. low risk, Fig. 6.2).

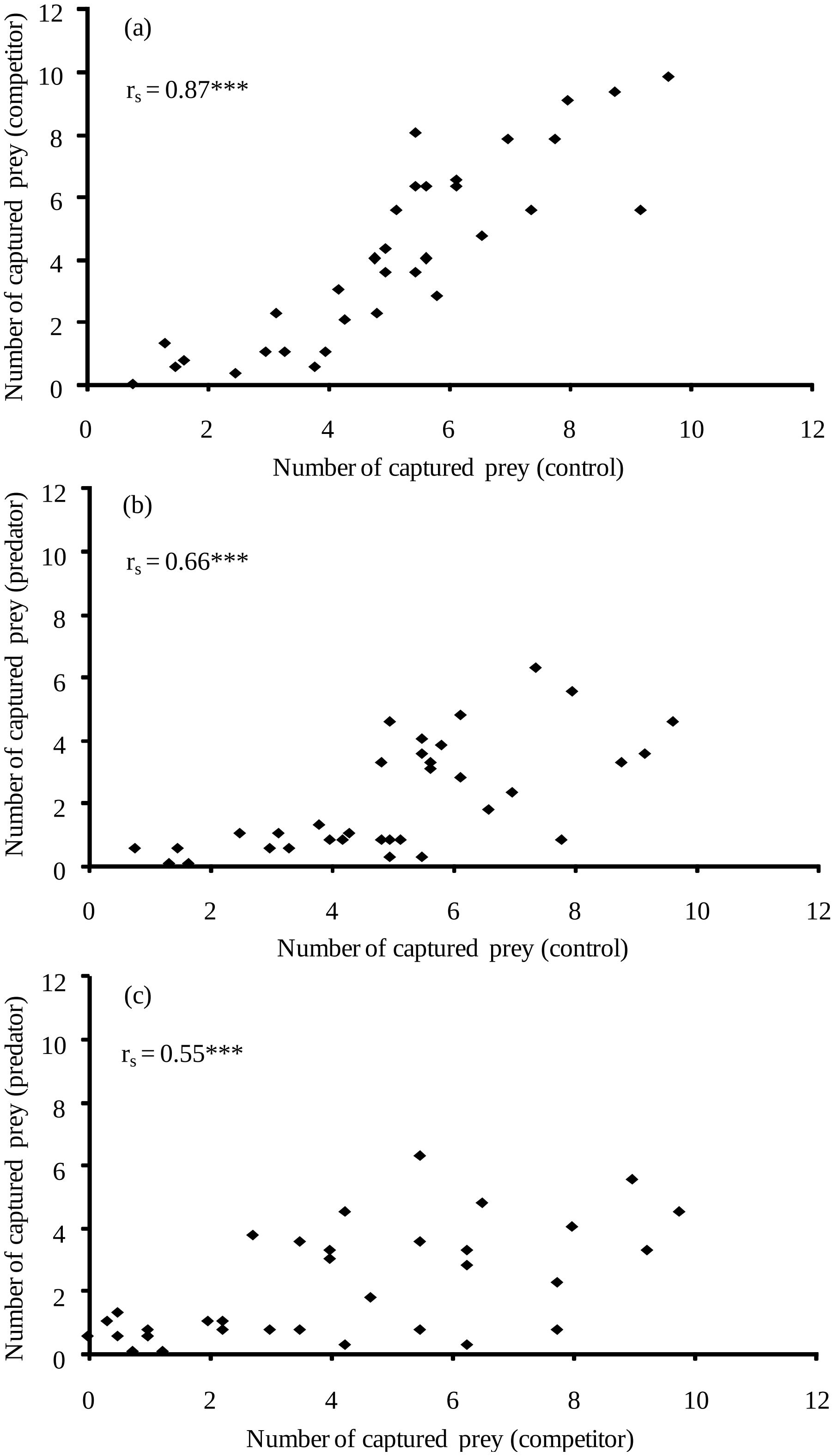

Figure 6.1. Mean number of prey captured per individual pike (n=34) in the experimental treatments. (a) Control versus competitor, (b) control versus predator, (c) competitor versus predator treatments. Correlations were investigated using Spearman's ranking tests (rs,*** $P < 0.001$).

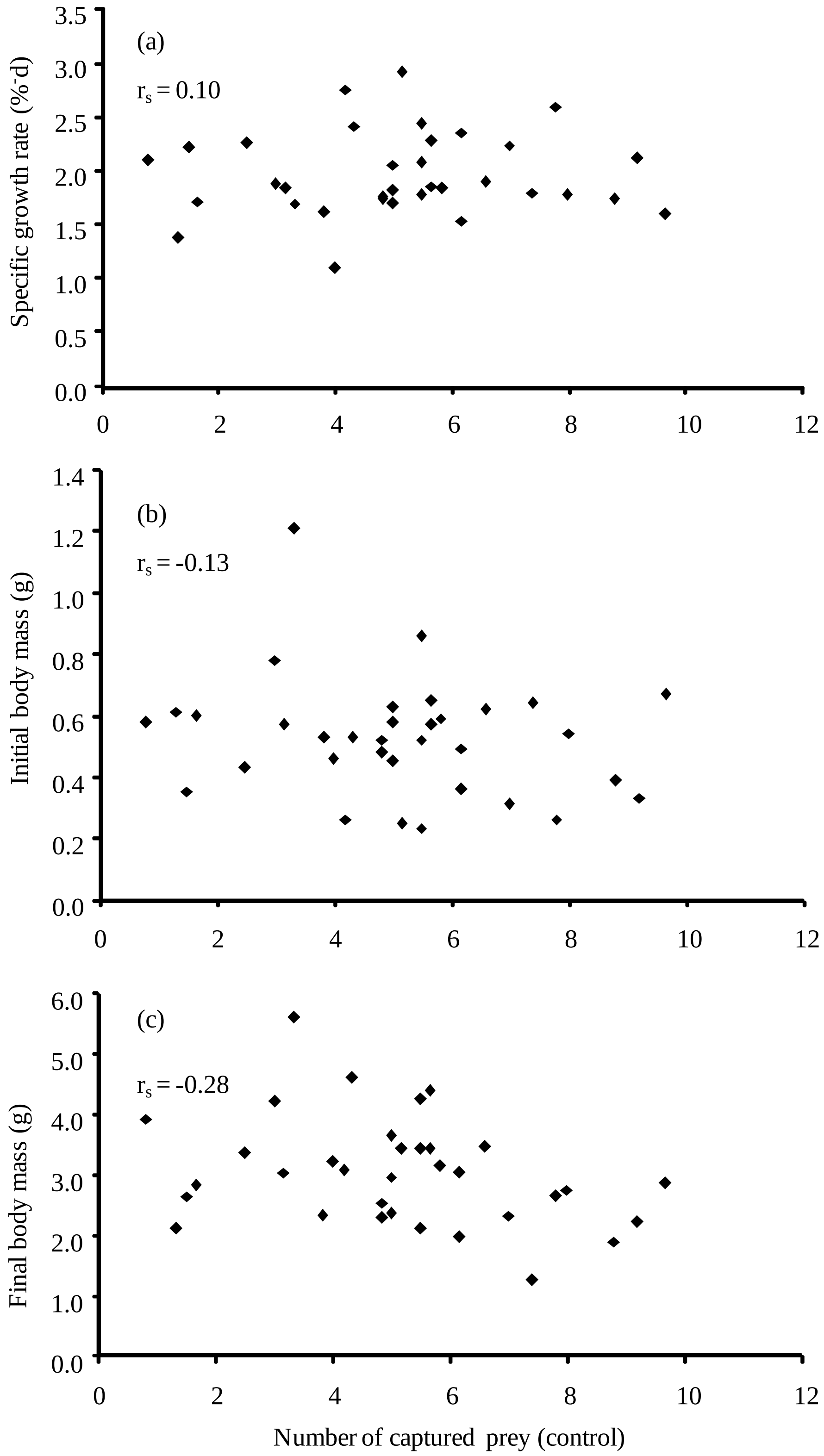

Figure 6.2. Mean number of prey captured in the control treatment per individual pike (n=34) and their metrics. (a) Specific growth rate, (b) initial body mass, (c) final body mass. Correlations were investigated using Spearman's ranking tests.

6.5 DISCUSSION

Consistent individual variation in foraging behaviour across time and risk levels was evident in the experiments, suggesting the presence of a behavioural syndrome within a solitary predator of wild origin. Analyses of between-situation consistency over time revealed temporal instability of the behavioural syndrome over the experimental period and no evidence to support the state-dependent personality hypothesis was found.

The general decrease in feeding activity with increased threat found is consistent with Engström-Öst and Lehtiniemi (2004) who report that pike exhibit threat-sensitivity by decreasing prey attacks and swimming activity with the degree of predation risk (Engström-Öst & Lehtiniemi 2004). Indeed, threat-sensitivity has been reported in a variety of vertebrate and invertebrate groups (Monclús et al. 2008), and is obviously an important behavioural strategy as an under-estimation of risk may be fatal for the individual whereas an over-estimation may lead to unnecessary decreases in feeding activity. Consistent and significant individual variation in feeding activity over time, supported by between-situation correlations, indicates that some individuals were bolder in their foraging behaviour than others. As latency of prey attack, a common measure of boldness in fish (Conrad et al. 2011), correlated significantly with the number of captured prey within all situations then prey capture was also considered an appropriate expression of boldness in the pike. Bold fish consistently continued to feed even during high predation risk (albeit at a lower rate), whilst others displayed consistently stronger risk-avoidance behaviour. The low but significant repeatabilities found here correspond to findings from a meta-analysis that showed significant behavioural repeatabilities are often low (Bell et al. 2009).

Many other studies of behavioural syndromes have conducted different experimental treatments using the same individuals on the same day (Bell 2005; Lee & Bereijikian 2008; Pronk et al. 2010). However, when little time has elapsed in between observations of individual behaviour in different contexts, individual consistency across observations may be a consequence of the individual motivational state. As the treatments were conducted independently of each other with 4 to 5 days between trials, the behavioural consistency detected is more likely to reflect a relatively stable, unchanging aspect of the fish's personality.

Both temporal stability of the behavioural syndrome, and consistency of individual behaviour that comprises the syndrome, have been suggested to affect the strength of the selection force on the syndrome (Lee & Bereijikian 2008; Stamps & Groothuis 2010). Although consistency of individual behaviours was found across all trials, analyses of one trial of each situation separately exposed discrepancies with non-significant repeatabilities versus strong repeatabilities in the first two and last two repeats respectively. As individual consistency was found within each situation, the non-significant repeatability may be due to low between-individual variation across situations at first. Individual behavioural variation might increase due to experiential factors (Stamps & Groothuis 2010), so that individual behaviour might have become more distinct over time increasing the size of the variation between individuals.

Theoretically, individuals that are bolder and consistently take more risks to acquire food should grow faster (Biro & Stamps 2008), and through a positive feedback, also be larger in body size (Luttbeg & Sih 2010). Growth differences have been found to persist even when individuals have been kept in isolation and fed *ad libitum* (Arendt 1997; Mangel & Munch 2005), for example, in lizards (Stamps et al. 1998), salamanders (Ragland & Carter 2004), turtles (Davenport & Scott 1993), and fish (Cui & Liu 1990; Martins et al. 2005; Mas-Muñoz et al. 2011). Here, however, the results revealed that despite some individuals repeatedly consuming more prey items during the experiments than others, these individuals did not achieve a higher growth rate during high food availability, nor was body mass related to the individual behaviour. The observed growth rates corresponded to the mean growth reported in their wild populations over a similar time scale during which size dimorphism has developed (Mann & Beaumont 1990). This suggests that individual growth differences do not occur as a consequence of individual behaviour alone but are likely to also be affected by a combination of spatial and temporal variation in the environment such as resource availability, competition level and/or predation pressure (Wolf et al. 2008; Adriaenssens & Johnsson 2009, 2011; Chapters 4 and 5). This is similar to the lack of correlation between behaviour and early growth rates found in rainbow trout fry when kept in a conventional hatchery-rearing environment (Conrad & Sih 2009). On the other hand, in sibling dorada (*Brycon moorei* Steindachner), kept in isolation and fed *ad libitum*, more aggressive individuals exhibited faster growth during the transition between food types (Baras & Lucas 2010). By comparison, the pike in the present study were fed one food type throughout the experimental period, thus this might have been a factor reducing the potential for individual growth variation. The non-significant relationship between behaviour and body mass indicates that any differences between hunger levels of smaller and larger fish was unlikely to have affected their behaviour.

The present experiments characterised the presence of a behavioural syndrome in a solitary predator species, with individuals maintaining their foraging behaviour through time within the different situations. The ecological relevance of intraspecific variation, including behaviour, is becoming increasingly evident (Conrad et al. 2011; Bolnick et al. 2011) and may be particularly important for populations of apex predators in their structuring effects on prey communities and food webs (Ritchie & Johnson 2009). Indeed, the assumption that all individuals from predatory species have similar effects in structuring prey communities is being increasingly challenged by studies showing differences in foraging mode between species in the same habitats (Carey & Wahl 2010). Such interspecific differences affect interactions between the predators and influence food web dynamics (Schmitz 2007). Thus, identifying behavioural differences at the individual level within a population may prove equally important in understanding the trophic dynamics in the ecosystems, and thus, there is a need to characterise appropriate behavioural syndromes in a wider range of species.

6.6 REFERENCES

Adriaenssens, B. & Johnsson, J. I. 2009. Personality and life-history productivity: consistent or variable association? *Trends in Ecology & Evolution*, 24, 179-180.

Adriaenssens, B. & Johnsson, J. I. 2011. Learning and context-specific exploration behaviour in hatchery and wild brown trout. *Applied Animal Behaviour Science*, 132, 90-99.

Arendt, J. D. 1997. Adaptive intrinsic growth rates: An integration across taxa. *Quarterly Review of Biology*, 72, 149-177.

Baras, E. & Lucas, M. 2010. Individual growth trajectories of sibling *Brycon moorei* raised in isolation since egg stage, and their relationship with aggressive behaviour. *Journal of Fish Biology*, 77, 985-997.

Bell, A. M. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology*, 18, 464-473.

Bell, A. M. 2007. Future directions in behavioural syndromes research. *Proceedings of the Royal Society B: Biological Sciences*, 274, 755-761.

Bell, A. M. & Sih, A. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, 10, 828-834.

Bell, A. M. & Stamps, J. A. 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, 68, 1339-1348.

Bell, A. M., Hankison, S. J. & Laskowski, K. L. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77, 771-783.

Biro, P. A. & Stamps, J. A. 2008. Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23, 361-368.

Biro, P. A., Abrahams, M. V., Post, J. R. & Parkinson, E. A. 2006. Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *Journal of Animal Ecology*, 75, 1165-1171.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C. & Vasseur, D. A. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26, 183-192.

Bry, C., Bonamy, F., Manelphe, J. & Duranthon, B. 1995. Early-life characteristics of pike, *Esox lucius*, in rearing ponds - temporal survival pattern and ontogenetic diet shifts. *Journal of Fish Biology*, 46, 99-113.

Budaev, S. & Brown, C. 2011. Personality traits and behaviour. In: *Fish Cognition and Behavior*, 2nd edn. (Ed. by C. Brown, K. Laland, & J. Krause), pp. 135-165. Wiley.

Carey, M. P. & Wahl, D. H. 2010. Interactions of multiple predators with different foraging modes in an aquatic food web. *Oecologia*, 162, 443-452.

Casselman, J. M. & Lewis, C. A. 1996. Habitat requirements of northern pike (*Esox lucius*). *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 161-174.

Conrad, J. L. & Sih, A. 2009. Behavioural type in newly emerged steelhead *Oncorhynchus mykiss* does not predict growth rate in a conventional hatchery rearing environment. *Journal of Fish Biology,* 75, 1410-1426.

Conrad, J. L., Weinersmith, K. L., Brodin, T., Saltz, J. B. & Sih, A. 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *Journal of Fish Biology,* 78, 395-435.

Cucherousset, J., Paillisson, J. M. & Roussel, J. M. 2007. Using PIT technology to study the fate of hatchery-reared YOY northern pike released into shallow vegetated areas. *Fisheries Research,* 85, 159-164.

Cui, Y. & Liu, J. 1990. Comparison of energy budget among six teleosts-IV. Individual differences in growth and energy budget. *Comparative Biochemistry and Physiology Part A: Physiology*, 97, 551-554.

Davenport, J. & Scott, C. R. 1993. Individual growth and allometry of young green turtles (*Chelonia mydas,* L.). *Herpetological Journal*, 3, 19-25.

Dingemanse, N. J. & Wolf, M. 2010. Recent models for adaptive personality differences: a review. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365, 3947-3958.

Engström-Öst, J. & Lehtiniemi, M. 2004. Threat-sensitive predator avoidance by pike larvae. *Journal of Fish Biology*, 65, 251-261.

Gabriel, P. O. & Black, J. M. 2010. Behavioural syndromes in Steller's jays: the role of time frames in the assessment of behavioural traits. *Animal Behaviour*, 80, 689-697.

Galarowicz, T. L. & Wahl, D. H. 2005. Foraging by a young-of-the-year piscivore: the role of predator size, prey type, and density. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 2330-2342.

Garamszegi, L. 2006. Comparing effect sizes across variables: generalization without the need for Bonferroni correction RID B-5089-2011. *Behavioral Ecology,* 17, 682-687.

Giles, N., Wright, R. M. & Nord, M. E. 1986. Cannibalism in pike fry, *Esox lucius* L - some experiments with fry densities. *Journal of Fish Biology*, 29, 107-113.

Gosling, S. D. 2001. From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, 127, 45-86.

Grimm, M. P. 1981a. The composition of northern pike (*Esox lucius* L) populations in 4 shallow waters in the Netherlands, with special reference to factors influencing 0+ pike biomass. *Fisheries Management*, 12, 61-76.

Grimm, M. P. 1981b. Intraspecific predation as a principal factor controlling the biomass of northern pike (*Esox lucius* L). *Fisheries Management*, 12, 77-79.

Houston, A. & McNamara, J. M. 1999. *Models of adaptive behaviour*. Cambridge University Press.

Ivanova, M. & Svirskay, A. 1995. Growth of juvenile pike, *Esox lucius*. *Journal of Ichtyology*, 35, 379-385.

Kaushik, S. J., Dabrowski, K. & Luquet, P. 1985. Experimental studies on some trophic relationships in juvenile pike, *Esox lucius* L. *Journal of Fish Biology*, 26, 171-180.

Lee, J. & Bereijikian, B. 2008. Stability of behavioral syndromes but plasticity in individual behavior: consequences for rockfish stock enhancement. *Environmental Biology of Fishes*, 82, 179-186.

Lehtiniemi, M. 2005. Swim or hide: predator cues cause species specific reactions in young fish larvae. *Journal of Fish Biology*, 66, 1285-1299.

Logue, D., Mishra, S., McCaffrey, D., Ball, D. & Cade, W. 2009. A behavioral syndrome linking courtship behavior toward males and females predicts reproductive success from a single mating in the hissing cockroach, *Gromphadorhina portentosa*. *Behavioral Ecology*, 20, 781-788.

Luttbeg, B. & Sih, A. 2010. Risk, resources and state-dependent adaptive behavioural syndromes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3977-3990.

Magnhagen, C. & Staffan, F. 2005. Is boldness affected by group composition in young-of-the-year perch (*Perca fluviatilis*)? *Behavioral Ecology and Sociobiology*, 57, 295-303.

Mangel, M. & Munch, S. B. 2005. A life-history perspective on short- and long-term consequences of compensatory growth. *American Naturalist*, 166, E155-E176.

Mangel, M. & Stamps, J. 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evolutionary Ecology Research*, 3, 583-593.

Mann, R. H. K. 1982. The annual food-consumption and prey preferences of pike (*Esox lucius*) in the river Frome, Dorset. *Journal of Animal Ecology*, 51, 81-95.

Mann, R. & Beaumont, W. 1990. Fast- and slow-growing pike, *Esox lucius* L., and problems of age-determinations from scales. *Aquaculture and Fisheries Management*, 21, 471-478.

Martins, C. I. M., Schrama, J. W. & Verreth, J. A. J. 2005. The consistency of individual differences in growth, feed efficiency and feeding behaviour in African catfish *Clarias gariepinus* (Burchell 1822) housed individually. *Aquaculture Research*, 36, 1509-1516.

Mas-Muñoz, J., Komen, H., Schneider, O., Visch, S. W. & Schrama, J. W. 2011. Feeding behaviour, swimming activity and boldness explain variation in feed intake and growth of sole (*Solea solea*) reared in captivity. *PLoS ONE*, 6, e21393.

Monclús, R., Palomares, F., Tablado, Z., Martínez-Fontúrbel, A. & Palme, R. 2008. Testing the threat-sensitive predator avoidance hypothesis: physiological responses and predator pressure in wild rabbits. *Oecologia*, 158, 615-623.

Moya-Larano, J. 2011. Genetic variation, predator-prey interactions and food web structure. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 1425-1437.

Nakagawa, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology*, 15, 1044-1045.

Nakagawa, S. & Cuthill, I. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, 82, 591-605.

Nakagawa, S. & Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, 85, 935-956.

Nilsson, P. A. & Bronmark, C. 1999. Foraging among cannibals and kleptoparasites: effects of prey size on pike behavior. *Behavioral Ecology*, 10, 557-566.

Pronk, R., Wilson, D. R. & Harcourt, R. 2010. Video playback demonstrates episodic personality in the gloomy octopus. *Journal of Experimental Biology*, 213, 1035-1041.

R development core team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raat, A. 1988. *Synopsis of biological data on the northern pike Esox lucius Linnaeus 1758.* FAO Fish. Synopsis.

Ragland, G. J. & Carter, P. A. 2004. Genetic covariance structure of growth in the salamander *Ambystoma macrodactylum*. *Heredity*, 92, 569-578.

Reale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82, 291-318.

Ritchie, E. G. & Johnson, C. N. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12, 982-998.

Schmitz, O. J. 2007. Predator diversity and trophic interactions. *Ecology*, 88, 2415-2426.

Schurch, R. & Heg, D. 2010. Life history and behavioral type in the highly social cichlid *Neolamprologus pulcher*. *Behavioral Ecology*, 21, 588-598.

Sih, A., Bell, A. & Johnson, J. C. 2004a. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19, 372-378.

Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. 2004b. Behavioral syndromes: An integrative overview. *Quarterly Review of Biology*, 79, 241-277.

Smith, B. R. & Blumstein, D. T. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, 19, 448-455.

Stamps, J. A. 1991. Why evolutionary issues are reviving interest in proximate behavioral mechanisms. *American Zoologist*, 31, 338-348.

Stamps, J. A. 2007. Growth-mortality tradeoffs and “personality traits” in animals. *Ecology Letters*, 10, 355-363.

Stamps, J. A. & Groothuis, T. G. G. 2010. Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 4029-4041.

Stamps, J. A., Mangel, M. & Phillips, J. A. 1998. A new look at relationships between size at maturity and asymptotic size. *American Naturalist*, 152, 470-479.

Toms, C. N., Echevarria, D. J. & Jouandot, D. J. 2010. A methodological review of personality-related studies in fish: focus on the shy-bold axis of behavior. *International Journal of Comparative Psychology*, 23, 1-25.

Wang, H. P., Hayward, R. S., Whitledge, G. W. & Fischer, S. A. 2003. Prey-size preference, maximum handling size, and consumption rates for redear sunfish *Lepomis microlophus* feeding on two gastropods common to aquaculture ponds. *Journal of the World Aquaculture Society*, 34, 379-386.

Ward, A., Thomas, P., Hart, P. & Krause, J. 2004. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, 55, 561-568.

Wilson, D. S. 1998. Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 353, 199-205.

Wilson, A. D. M. & McLaughlin, R. L. 2007. Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Animal Behaviour*, 74, 689-698.

Wilson, A. D. M. & Stevens, E. D. 2005. Consistency in context-specific measures of shyness and boldness in rainbow trout, *Oncorhynchus mykiss*. *Ethology*, 111, 849-862.

Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994. Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, 9, 442-446.

Wolf, M. & Weissing, F. J. 2010. An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3959-3968.

Wolf, M., van Doorn, G. S. & Weissing, F. J. 2008. From the cover: evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences*, 105, 15825-15830.

Ziliukiene, V. & Ziliukas, V. 2006. Feeding of early larval pike *Esox lucius* L. reared in illuminated cages. *Aquaculture*, 258, 378-387.

Chapter 7

Absence of a context-general behavioural syndrome in a solitary predator

7.1 ABSTRACT

The correlation of seemingly unrelated behaviours into behavioural syndromes has been established in a variety of species and taxa. However, most studies report on short-term behavioural correlations without insight into individual consistency or temporal stability of the behavioural syndrome. Here, the individual repeatability of single behaviours, and the presence and temporal stability of a context-general behavioural syndrome, is examined in pike. Behavioural measurements on the same individuals were measured independently through time and across three contexts: aggression towards a competitor, exploration of a novel environment and boldness under predation risk. There was no indication of a temporally stable behavioural syndrome, consisting of boldness, activity and exploration, nor were individuals consistent in the separate behaviours, contradicting the general assertion of its taxonomic prevalence. Furthermore, the study did not provide support for size or growth dependent behaviour in this size-dimorphic species in conditions of limited food availability. The Chapter highlights the importance of independent multiple observations of individual behaviours across time or contexts when measuring behavioural repeatability and co-variation.

7.2 INTRODUCTION

Consistent differences in individual behaviour across multiple observations at the population level have been observed in a variety of species and taxa

(Gosling 2001; Sih et al. 2004a; Bell et al. 2009). Among individual variation, the focus is often on the co-variation of behaviours, either across situations within a context (e.g. within a feeding context under different levels of predation risk) or across different contexts (e.g. feeding, mating), defined as context-specific and context-general behavioural syndromes respectively (Sih et al. 2004a,b; Reale et al. 2010; Stamps & Groothuis 2010). The latter is considered to be of particular evolutionary interest as it implies the co-evolution of functionally distinct individual behaviours (Stamps 1991; Sih et al. 2004a).

Boldness, exploration and aggression constitute the most commonly reported context-general behavioural syndromes, and although positive correlations between these different behaviours are generally reported (Bell 2007a; Smith & Blumstein 2010; Conrad et al. 2011), both species- and population specific deviations exist. For example, no correlation between aggression and boldness was found in nine-spined stickleback (*Pungitus pungitus* L.) (Herczeg et al. 2009), whereas a positive correlation was apparent in three spined stickleback (*Gasterosteus aculeatus* L.) originating from habitats with predator presence (Bell 2005; Dingemanse et al. 2007). Most studies on behavioural syndromes have tested the behaviours within the same day or over a small number of consecutive days. Such short-term behavioural correlations are frequently assumed to signify longer-term patterns without insight into individual consistency or ontogenetic stability of the behavioural syndrome (Sinn et al. 2010). Indeed, the correlation of individual behaviours at different points in time defines a stable behavioural syndrome, thus disregarding whether some individuals remain consistently more bold, aggressive, exploratory or active than others (i.e. maintenance of their rank order within single behaviours) (Bell & Stamps 2004; Sih et al. 2004a). The importance of such individual consistency for the strength of behavioural syndromes has recently been raised (Logue et al. 2009; Stamps & Groothuis 2010), with some concern over behavioural syndromes that lack the demonstration of individual stability being spurious (Logue et al. 2009).

Studies on context-general behavioural syndromes have tended to focus on species that have social traits such as parental care or dominance structures (Sih et al. 2004a; Reale et al. 2007; Conrad et al. 2011). Thus, the detection of behavioural syndromes in solitary animals has rarely been documented, and so the general view of the scope of behavioural syndromes seems biased. Pike is a solitary predator with a despotic-type distribution as a consequence of competitive exclusion through agonistic behaviour, such as cannibalism and kleptoparasitism (i.e. stealing of others' captured prey) (Nilsson & Brönmark 1999; Hawkins et al. 2005).

Although the majority of theoretical models explain the occurrence of individual behavioural consistencies by differences in individual state, such as body size and age (Wolf & Weissing 2010), few empirical studies exist that have explicitly tested this (Dingemanse & Wolf 2010). Since pike can display significant size dimorphism with, for example, a 60% difference in mean size attained between slow and fast growing individuals at the end of their first year of life (Mann & Beaumont 1990; Chapter 3), it is an excellent model species to explore size-dependent behavioral syndromes. In this chapter, the presence of a context-general behavioural syndrome and its effect on individual growth rate and body size in juvenile pike is tested.

The individual repeatability of single behaviours, and the presence and temporal stability of a context-general behavioural syndrome, is examined through recording of repeated and independent behavioural measurements on the same individuals across three contexts: aggression towards a competitor, exploration of a novel environment and boldness under predation risk. When deciding the contexts which best represent certain personality traits in a species of interest, a careful consideration of species-specific behaviours has been advised (Bell 2007; Toms et al. 2010; Conrad et al. 2011). Juvenile pike encounter strong predation and competitive pressure by conspecifics in their nursery habitats (Grimm 1981; Mann 1982), there is a trade-off between feeding to grow fast and avoid predation (due to piscivorous gape limitation), and anti-predator avoidance is essential for increasing the survival probabilities of individual juveniles (Lehtiniemi 2005). Boldness has previously been measured in this species as repeatable foraging behaviour under predation risk in pike (Nyqvist et al. 2012). Whilst the general behaviour of pike is strongly motivated by food, competitor and/or predator pressures, an appropriate context to measure exploration was considered to involve obscured food in a novel environment. With intra-cohort interactions thought to be strong in juvenile pike, measuring antagonistic acts (e.g. bites) and proximity to a competitor (similar sized pike) would be indicative of aggression. The observed behaviours will then be related to growth rate (as a fitness proxy) and body size (as the individual state). It is hypothesised that (i) individuals will behave consistently within the behavioural contexts; (ii) pike will exhibit a context-general behavioural syndrome where bold individuals take consistently increased risk in predator presence, higher aggression towards a competitor and have increased exploration rates in a novel environment; and (iii) under limited food supply, the bold/aggressive/exploratory behavioural type is positively correlated with growth rate or/and body size.

7.3 MATERIALS AND METHODS

7.3.1 Collection of study fish

YOY pike were collected in a tributary of the River Frome between 26 and 28 May 2010. Details on the collection and housing of the fish, and research ethics, are provided in Section 2.2.1 and 2.3 respectively. The fish were kept in isolation and fed with evenly sliced earthworm once per day by hand for at least 22 days prior to the first experiment. The feeding procedure consisted of giving sequential portions of five slices, and new slices were added only if the previous portion had been eaten. As an *ad libitum* feeding regime was found not to generate considerable variations in growth in juvenile pike kept in isolation (Nyqvist et al. 2012), the food was available for a maximum of 2 h, after which the remaining food items were removed. As juvenile pike have been shown to feed throughout the day with the greatest intensity at night (Ziliukiene & Ziliukas 2006), together with high evacuation rates of ingesta (Kaushik et al. 1985), a feeding time of 2 hours was considered as limiting. Pike of age 1+ (160-180 mm fork length) were used as a predator in the experiments and were caught from the same site on 31 May 2010. See Section 2.21 for details on the collection and housing of these fish.

7.3.2 Experimental protocol

Thirty-four juvenile pike (initial mass, $W_i = 1.24 \pm 0.11$ g, mean ± SE) were used as the experimental focal fish (hereafter referred to as focal fish). Individual behaviour was measured repeatedly across three experimental contexts (*i.e.* treatments): i) exploration of a novel environment; ii) aggression towards a competitor (similar-sized conspecific); and iii) feeding under risk of a predator (larger conspecific). Each treatment was repeated four times (each repeat is hereafter referred to as a trial), thus 12 trials were conducted in total. Five days elapsed between trials, and the trials were conducted in the sequence they were listed above. Each trial, during which the 34 individuals were tested, was completed in two days (between 9:00 and 18:00 h). Individuals were starved for 24 h prior to experiments to ensure similar hunger levels.

The experimental protocol meant each focal fish was removed from their keeping tank by scooping using a 0.5 L beaker and transferred to an experimental tank with the same temperature and oxygen levels as that of the holding tanks, and acclimatised for 30 minutes. Each assay using single fish lasted 10 minutes and was recorded using a digital video camera (Sony SDR-S26). The order of assessment (time and day) of individual pike in each trial was randomised. At the conclusion of the individual assays, the fish was placed back in their individual holding tanks by scooping, and the water in the experimental tank replaced with fresh conditioned and aerated water. Each fish was weighed two days after the completion of each ‘foraging under risk of a predator’ trial. All trials were done between 20 June and 17 October 2010 (119 days). All films were subsequently analysed blind with respect to fish identity and in a randomised order by the same person.

Behavioural context 1: Exploration of a novel environment

The experimental tank (40 x 40 x 30 cm high), with a water depth of 10 cm, consisted of two equal sized compartments; a ‘simple side’ without any features and a ‘complex side’ with five features consisting of plastic plants, rocks, and a petri dish containing gravel and one slice of *D. veneta*. The two compartments were separated by a removable divider and after acclimatisation in the simple side, the divider was gently lifted half-way out of the tank enabling the fish to access the complex side. All sides of the tank were covered to prevent other visual stimuli. The camera was mounted over the ‘complex’ side of the tank, so recording the behaviour of pike in the new area (top view). A grid (5 x 5 cm squares) was placed underneath the tank for quantifying fish movement from the videos (Fig. 7.1a). The following metrics were quantified (i) latency of the fish to move into the ‘complex’ side of the tank; (ii) time spent in new area; (iii) number of squares traversed; and (iv) latency to the first attack on prey. Individuals that did not move into the new area were given latency times of 10 minutes so as not to remove the least explorative animals. Here, latency to emerge in a novel environment is termed ‘exploratory behaviour’ following frameworks by Reale et al. (2007) and Conrad et al. (2011). No effect of time of day of the experiments was found on any of the behavioural variables measured in the focal fish (ANOVA, all $P > 0.05$).

Behavioural context 2: Aggression towards a competitor

The experimental tank (30 x 20 x 20 cm high) with a water depth of 10 cm contained a 1-L transparent glass beaker that was placed on one side of the tank. After the acclimatisation period, a competitor of similar size (± 5 mm; conspecific) from the same population was placed into the beaker, and lateral filming commenced (Fig. 7.1b). All the other three sides of the tank were covered to prevent other visual stimuli. From the videos, the following metrics were quantified: (i) latency to attack the competitor; (ii) number of attacks at the competitor; (iii) time spent within one body length of the competitor, and (iv) time spent orienting towards the competitor. Individuals that did not attack a competitor were given latency times of 10 minutes so as not to remove the animals that were least likely to attack. A competitor was not used twice in a day. No effect of time of day of the experiments or competitor individual used was found on any of the behavioural variables measured in the focal fish (ANOVA, all P > 0.05).

Behavioural context 3: Boldness in the presence of a predator

The experimental tank (40 x 40 x 30 cm high) was divided into two parts by a glass wall and a removable opaque divider. The larger pike (‘predator’) was placed in one side of the tank (water depth 20 cm) to acclimatise an hour prior to the experiments and the focal fish in the other side (water depth 10 cm). The opaque divider was gently removed and the focal fish was left for five minutes to detect the predator before the start of the experiment, when three slices of *D. veneta* were gently dropped along the middle of the glass divider towards the predator side. All the other sides of the tank were covered to prevent other visual stimuli. The camera was mounted above the compartment containing the focal fish (top view) (Fig. 7.1.c). Predator detection was evident from the videos with pike freezing while facing the predator, and all fish detected the predator prior to the start of the experiment. From the video recordings, the following metrics were quantified: (i) latency to first attack on prey; (ii) number of attacks; (iii) time spent within one body length of the predator; and (iv) time spent orienting towards the predator. Three predator pike were used, and they were kept in their experimental tanks throughout the experimental day. Focal fish were assigned randomly to the predator fish. Individuals that did not attack prey were given latency times of 10 minutes so as not to remove animals least likely to attack prey. No effect of time of day of the experiments or predator individual used was found on any of the behavioural variables measured in the focal fish (ANOVA, all P > 0.05).

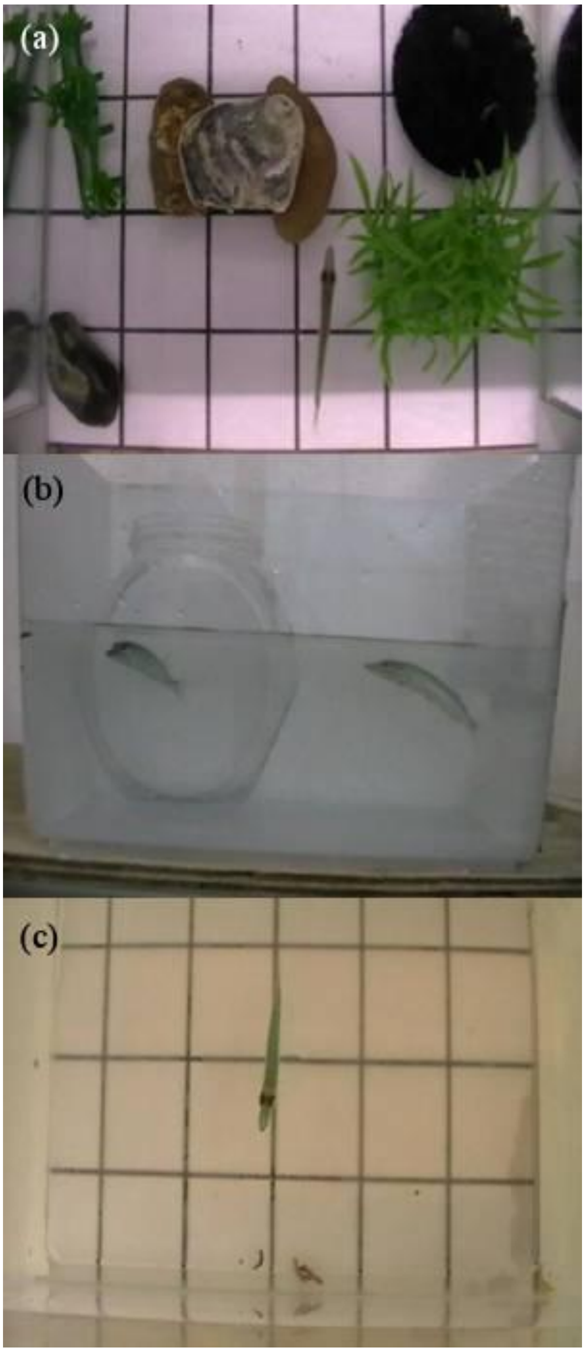

Figure 7.1. View of experimental contexts: (a) exploration of a novel environment, (b) aggression towards a conspecific, and (c) boldness under risk of predation.

7.3.3 Data and statistical analysis

The specific growth rate (SGR) expressed as a change of weight over time of each individual pike was determined at intervals, and over the whole experimental period (119 days). SGR was calculated as per Section 2.4. To assess how inter-individual variation of each behavioural measure of the four trials within contexts and overall SGR and BM, CV was calculated (Section 2.4).

Individual behavioural consistency was determined by calculating the repeatability (Section 2.4) of the different behavioural measures across the four trials of each experimental context. The number of squares traversed, number of bites at the competitor and number of prey attacks (predator context) constituted ‘count’ data and were analysed using the Poisson multiplicative overdispersion model fitted by PQL (penalized quasi-likelihood) estimation on the original scale. Data on latency to first attack (predator and competitor contexts) were log-transformed to attain normal distributions and analysed using the restricted maximum likelihood model. Both models use a randomization procedure for significance tests. The repeatability analyses were conducted using R 2.12.1 (“R development core team (2009). To compare repeatability estimates, we compared effect sizes and the 95 % CIs, in addition to determining whether the confidence intervals overlapped with zero (Nakagawa 2004; Garamszegi 2006; Nakagawa & Cuthill 2007).

Separate principal component analyses (PCA) were conducted to summarise the behavioural measurements for each repeated trial into component scores. In all trials of each context, the behavioural variables loaded onto one main principal component with an eigenvalue greater than 1 (Kaiser-Guttman) that explained 39-82 % of the variance in observed data (Table 7.1). This generated a total of four component scores for every individual in each of the three contexts. Therefore, correlations across contexts were analysed four times per individual. As component scores were not all normally distributed, the non-parametric Spearman’s correlation ranking test (r_s) was used. In addition, the behavioural variables were averaged (mean) for each context, and analysed for between-context correlations. Finally, correlations between components scores, or mean behavioural variables, initial and final mass, and SGR were analysed. The sequential Bonferroni procedure was used to adjust for multiple correlations. All behavioural variables were tested for normality using the

Kolmogorov–Smirnov test and subsequently log transformed where needed. These analyses were conducted in STATISTICA, version 7.0.

	Behavioural measure	**1**	**2**	**3**	**4**
a)	Latency to enter	0.91	0.81	0.96	0.85
	Time in new area	-0.90	-0.88	-0.93	-0.90
	Number of squares traversed	-0.88	-0.79	-0.79	-0.85
	Latency to prey attack	0.27	0.86	0.94	0.79
	Cumulative %	62.51	69.86	82.49	71.96
b)	Latency to bite	-0.78	-0.83	0.81	0.81
	Number of bites	0.43	0.61	-0.60	—
	Time spent oriented to competitor	0.87	0.57	-0.92	-0.88
	Time near competitor	0.66	0.60	-0.56	-0.53
	Cumulative %	49.64	43.62	54.17	57.31
c)	Latency to prey attack	-0.90	-0.95	-0.93	-0.95
	Number of attacks	0.89	0.96	0.90	0.97
	Time spent oriented to predator	0.05	-0.03	-0.14	-0.20
	Time near predator	0.25	0.22	-0.33	0.04
	Cumulative %	41.78	47.04	45.19	47.13

Table 7.1. PCA component loadings for juvenile pike *E. lucius* behavioural variables and total variance explained for each of the four trials in a) new environment, b) competitor and c) predator contexts.

7.4 RESULTS

The final BM of the individuals (n = 34) ranged from 1.4 to 14.3 g, with a mean (± SE) of 4.3 (± 0.5), g displaying a CV of 57.5 % (initial mass, CV = 51.2 %). There was a significant correlation between initial and final BM ($r_s = 0.72$, $P < 0.0001$), indicating that individual rank-order in size was maintained through the experimental period. The mean (± SE) SGR was 0.77 (± 0.04) % d^{-1} with a moderate CV of 27.3%.

Results from the behavioural tests showed high individual variation in most behavioural measures with an overall mean CV of 83% (Table 7.2).

Behavioural measures within contexts were relatively consistent across the four trials. In the new area context, latency to enter and time spent in the new area decreased and increased respectively with trial, whereas the other measures varied slightly without a temporal association (Table 7.2a). The low CV for latency to prey attack, especially in the first trial, was due to few individuals attacking, and so most individuals had a latency of 10 minutes (Table 7.2a). Although individuals varied greatly in the time spent oriented to the competitor (CV = 120-184 %), the mean values decreased overall with time (Table 7.2b). In contrast, the time spent oriented to the predator was lower in the first compared to the subsequent trials (Table 7.2c).

7.4.1 Within-context repeatability (individual stability)

Repeatability analyses of individual behaviours within the ‘presence of a predator’ context (context 3) showed a significant individual consistency for latency to prey attack. However, even if the effect size was higher compared to all other measures, the lower 95 % CI overlapped with 0 for latency to prey attack (Table 7.3). No behavioural variables were significantly repeatable in either the novel environment or competitor contexts (contexts 1 & 2 respectively; Table 7.3).

	1		2		3		4	
Behavioural measures	Mean ± SE	CV (%)	Mean ± SE	CV (%)	Mean ± SE	CV (%)	Mean ± SE	CV (%)
a) New environment								
Latency to enter	482 ± 44.9	52	423.4 ± 37.7	51	434.1 ± 34.6	47	403 ± 38.3	52
Time in new area	81.5 ± 26.9	184	103.5 ± 26.8	149	139.8 ± 30.9	129	151.1 ± 33.1	120
Number of squares traversed	2.9 ± 1	195	3.8 ± 1.2	176	7.7 ± 3	224	4.8 ± 1.2	139
Latency to prey attack	595.4 ± 3.5	3	545.7 ± 22.6	24	485.6 ± 28.2	34	566.9 ± 15.4	15
b) Competitor								
Latency to orient to stimulus	119.1 ± 31.8	156	113.8 ± 35.4	176	184.2 ± 43.5	136	201.7 ± 40.1	109
Number of bites	2.5 ± 0.5	107	1.3 ± 0.3	130	0.2 ± 0.1	240	0	0
Time oriented to stimulus	212.3 ± 26.2	72	211.9 ± 22.8	61	156.2 ± 24	88	139.7 ± 23.2	91
Time near stimulus	310.3 ± 30.2	57	373.5 ± 28.5	43	372.2 ± 21.0	32	331.6 ± 32.4	54
c) Predator								
Latency to prey attack	392.4 ± 48.1	67	293.9 ± 50	98	374 ± 48.1	74	512.1 ± 37.5	39
Number of attacks	0.7 ± 0.25	186	1.2 ± 0.23	109	0.8 ± 0.2	145	0.3 ± 0.14	245
Time oriented to predator	287.1 ± 37.2	71	490.6 ± 23.6	28	459.6 ± 22.6	28	442.0 ± 31.4	38
Time near predator	234.2 ± 36.2	85	430.3 ± 28.5	38	391.2 ± 32.1	47	364.7 ± 35.6	53

Table 7.2. Mean behavioural measurements (± SE) and CVs of juvenile pike (n=34) in each trial of the (a) new environment, (b) competitor and (c) predator treatment.

	Behavioural measure	R	SE	95 % CI	P
a)	Latency to enter (s)	0.02	0.07	0.00 to 0.25	0.443
	Latency to prey attack (s)	0.00	0.15	0.00 to 0.51	0.875
	Number of squares	0.00	0.14	0.00 to 0.43	0.887
	Time in new area (s)	0.00	0.05	0.00 to 0.17	0.647
b)	Latency to attack (s)	0.05	0.06	0.00 to 0.20	0.253
	Number of bites	0.00	0.11	0.00 to 0.33	0.701
	Time spent oriented to competitor (s)	0.01	0.05	0.00 to 0.16	0.390
	Time near competitor (s)	0.00	0.05	0.00 to 0.16	0.709
c)	Latency to prey attack (s)	0.16	0.09	0.00 to 0.34	**0.036**
	Number of attacks	0.02	0.09	0.00 to 0.30	0.438
	Time spent oriented to predator (s)	0.06	0.07	0.00 to 0.25	0.221
	Time near predator (s)	0.00	0.05	0.00 to 0.16	0.649

Table 7.3. The repeatabilities (R) of behavioural measures in juvenile pike *E. lucius* (n=34) within each experimental context: a) new environment b) competitor and c) predator. Significant ($P < 0.05$) P-values are shown in bold.

7.4.3 Between-context correlations (behavioural syndrome)

No significant correlations were found between component scores of the different contexts across time when using the four repeated trials of each context separately (Table 7.4). Correlation analyses of mean behavioural measures between contexts did not reveal any significant associations either (after Bonferroni corrections).

Trial	Context	Aggression	Boldness	BM (g)	SGR (% day^{-1})
1	Exploration	0.02	0.01	-0.09	-0.51*
	Aggression	1.00	-0.17	0.18	0.10
	Boldness	-0.17	1.00	-0.25	0.11
2	Exploration	-0.16	0.14	-0.06	-0.03
	Aggression	1.00	-0.18	0.08	-0.02
	Boldness	-0.18	1.00	0.31	0.04
3	Exploration	0.19	0.05	0.48**	0.01
	Aggression	1.00	-0.04	0.53**	0.00
	Boldness	-0.04	1.00	-0.07	0.04
4	Exploration	-0.02	0.30	0.37	0.15
	Aggression	1.00	0.26	-0.29	0.00
	Boldness	0.26	1.00	-0.23	0.02

Table 7.4. Spearman’s correlations between the component scores of the four repeated trials of each behaviour, body mass (BM) and SGR in juvenile pike *E. lucius*. * $P < 0.05$ and ** $P < 0.01$ (significant correlation after the sequential Bonferroni procedure ($P < 0.01$).

7.4.4 Size or growth-dependent behaviour

None of the component scores correlated with initial or final body mass (after Bonferroni corrections), but a significant correlation was found between the first exploration score and SGR (Table 7.4). Among correlations between the average individual behavioural measures and body mass/SGR, a significant association was found between time spent in the new area and final mass (Table 7.5).

	Behavioural measure	Initial mass (g)	Final mass (g)	SGR
a)	Latency to enter (s)	-0.27	-0.18	0.09
	Latency to attack (s)	0.08	0.00	0.06
	Number of squares	-0.20	-0.20	-0.10
	Time in new area (s)	-0.39*	-0.55**	-0.14
b)	Latency to bite (s)	-0.12	-0.06	0.26
	Number of bites	-0.08	-0.03	0.07
	Direction towards competitor (s)	-0.02	0.13	0.03
	Time near competitor (s)	0.32	0.12	-0.29
c)	Latency to attack (s)	0.17	0.43	0.45*
	Number of attacks	0.19	-0.02	-0.11
	Direction towards predator (s)	0.25	0.08	-0.09
	Time near predator (s)	0.35	0.34	0.03

Table 7.5. Spearman's rank correlations between mean behavioural measurements and initial and final body size in a) new environment, b) competitor and c) predator contexts of juvenile pike *E. lucius*. * $P < 0.05$ and ** $P < 0.01$ (significant correlation after the sequential Bonferroni procedure ($P < 0.01$).

7.5 DISCUSSION

There was little experimental evidence to suggest individual stability in juvenile pike behaviour, with only latency to prey attack within the predator context indicating individual repeatability. As none of the individual PCA scores correlated across contexts, the prediction that a general contextual behavioural syndrome exists in juvenile pike can be rejected. As few and sporadic associations between individual behaviour and body size or growth were detected, the experiments failed to find support for size or growth dependent behaviour in this size-dimorphic species.

Repeatability of individual behaviour requires relatively low within-individual variance in combination with high inter-individual variance (Bell et al. 2009; Nakagawa & Schieltzeth 2010). As most behavioural measures had high CVs, indicating high inter-individual variance, the low repeatabilities are most likely due to high within-individual variance. This demonstrates individual plasticity in these behaviours. Considering that survival of juvenile pike in their natural nursery habitats is largely determined by the trade-off between feeding and predation avoidance (Engström-Öst & Lehtiniemi 2004; Lehtiniemi 2005), exploratory and aggressive behaviours (measured under limiting or no opportunity to feed, respectively) are perhaps trivial. Individual consistency in these behaviours may therefore not have evolved in this species. This is supported by the model of Wolf et al. (2007) suggesting that the evolution of personality traits is favoured by life-history trade-offs. The importance of positive feedback (e.g. increased food intake or avoiding risks) on the experience of an individual's performance may play a role in generating consistent behaviours (Wolf et al. 2008; Wolf & Weissing 2010). If the behaviour has no positive feedbacks (e.g. increased food intake or avoiding risks), which ultimately affect fitness or fitness proxies (e.g. survival, growth), then there is no stimulus for individuals to remain consistent in the behaviour. Furthermore, if fitness does not associate with consistent behavioural types, frequency-dependent selection of behavioural types is highly unlikely (Wolf & Weissing 2010), resulting in behavioural plasticity.

While there are indications in wild pike populations of individual differences in habitat use (Knight et al. 2008), movement (Kobler et al. 2009) and migration from nursery habitats (Mann & Beaumont 1990; Cucherousset et al. 2009), the results presented here revealed that individual differences in exploration of new environments were not consistent in juveniles. This was in contrast to the invasive mosquito fish (*Gambusia affinis* Baird & Girard) that displayed significant individual repeatability in the exploration of novel areas (Cote et al. 2010). As a small live-bearing species that are aggregative, they are thus very different to solitary-living juvenile pike. In the cooperatively breeding cichlid (*Neolamprologus pulcher* Trewavas & Poll), the occurrence of consistent individual differences in exploration was suggested to reflect different breeding strategies, with the more exploratory fish dispersing to breed independently, whereas less exploratory individuals displaying a higher degree of territory maintenance inherited the breeding position in the home territory (Bergmuller & Taborsky 2010). In contrast, a context with limiting feeding opportunities, as in the exploration experiment, may be an unsuitable approach for studying consistent individual behaviours in the juvenile stages of species where the most important activity is feeding while avoiding threats.

As pike is generally a solitary animal (except during the spawning period), consistent individual aggressive or social behaviour towards conspecifics, other than perhaps during cannibalism, appears not to be important in juveniles. Nilsson et al. (2006) found that pike decreased attack frequencies and consumption rates while foraging in the presence of conspecifics, but no direct agonistic behaviour was observed. These results suggested that to pinpoint consistent individual differences in responses to a conspecific, the presence of a feeding opportunity is required. In contrast, aggression has been found to be a personality trait in many small, social, nest-building or territorial fish species, such as the cooperatively breeding cichlid (*N. pulcher*) (Riebli et al. 2011), territorial male Caribbean damselfish (*Stegastes leucostictus* Müller & Troschel) (Snekser et al. 2009), and male swordtails (*Xiphophorus* sp.) (Magellan & Kaiser 2010). In these species, the function of aggression has been studied in adults as a way to gain access to mates and the behavioural measurements included attacks against conspecifics. In brown trout parr (*Salmo trutta* L.), individual consistency in aggression was identified through measurements of the total time near and the number of bites towards a conspecific intruder (Adriaenssens & Johnsson 2010). Consistency in individual aggression is obviously important in species that establish dominance hierarchies or defending territories, which would explain its absence in pike.

In addition to the lack of individual behavioural consistency, the pike were also characterised by a lack of behavioural correlations between functionally-different contexts. With one trial being conducted weekly, the three contexts, which were tested for correlations, had a time interval of 1 and 2 weeks. In comparison, many other studies of behavioural syndromes have conducted the experiments on the same day (e.g. Bell 2005; Lee &

Bereijikian 2008; Pronk et al. 2010). As discussed in Chapter 6, such multiple tests that are carried out on the same individuals are temporally independent. The state of the fish may influence the behavioural consistency, for example, if a fish is hungry, this could influence both its exploratory and foraging behaviour, causing them to co-vary. Therefore, the importance of independent multiple observations of individual behaviour across time or contexts when measuring behavioural repeatability and co-variation should be emphasised.

With the lack of both individual consistency and behavioural syndromes reported here, it was perhaps not surprising that there was no association between behaviour and growth. In many other studies reporting on such an association in fish, the individuals have been kept in groups, thus allowing for effects of competition or dominance hierarchies to impact individual growth (e.g. Vøllestad & Quinn 2003; Adriaenssens & Johnsson 2010). The pike could not be kept in groups due to the risk of cannibalism (Bry et al. 1995) and so this does suggest a competitive environment may be necessary to induce the association between growth and behavioural traits and syndromes.

The ecological and evolutionary importance of individual behavioural variation is often used to highlight the importance of behavioural syndromes with reference to fitness consequences of individual consistency (e.g. Smith & Blumstein 2008). Smith & Blumstein (2010) stressed the importance of studying the fitness consequences of correlated behaviours to understand the ecological and evolutionary consequences of their variation. As results from studies in behavioural syndromes vary and few studies on fitness consequences of broad syndromes have been conducted (Logue et al. 2009; Smith & Blumstein 2010), it is thus difficult to draw conclusions on its significance. Here, there was no indication of the existence of a behavioural syndrome, consisting of boldness, aggression and exploration, including repeatability of separate behaviours in a solitary living predator species, contradicting the general assertion of its taxonomic prevalence. To improve our understanding of the evolutionary and ecological importance of behavioural syndromes, there is now a need to disentangle the empirical work conducted so far regarding the type of species studied, and the extent and effect of variations in behavioural measurements.

7.6 REFERENCES

Adriaenssens, B. & Johnsson, J. I. 2010. Shy trout grow faster: exploring links between personality and fitness-related traits in the wild. *Behavioral Ecology*, 22, 135-143.

Baras, E. & Lucas, M. 2010. Individual growth trajectories of sibling *Brycon moorei* raised in isolation since egg stage, and their relationship with aggressive behaviour. *Journal of Fish Biology*, 77, 985-997.

Bell, A. M. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology*, 18, 464-473.

Bell, A. M. 2007. Future directions in behavioural syndromes research. *Proceedings of the Royal Society B: Biological Sciences*, 274, 755-761.

Bell, A. M. & Stamps, J. A. 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, 68, 1339-1348.

Bell, A.M., Hankison, S.J. & Laskowski, K.L. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77, 771–783.

Bergmuller, R. & Taborsky, M. 2010. Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, 25, 504-511.

Biro, P. A. & Stamps, J. A. 2008. Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23, 361-368.

Biro, P. A., Abrahams, M. V., Post, J. R. & Parkinson, E. A. 2006. Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *Journal of Animal Ecology*, 75, 1165-1171.

Bry, C., Bonamy, F., Manelphe, J. & Duranthon, B. 1995. Early-life characteristics of pike, *Esox lucius*, in rearing ponds - temporal survival pattern and ontogenic diet shifts. *Journal of Fish Biology*, 46, 99-113.

Conrad, J. L., Weinersmith, K.L., Brodin, T., Saltz, J. B. & Sih, A. 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *Journal of Fish Biology*, 78, 395-435.

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T. & Sih, A. 2010. Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). 277, 1571-1579.

Cucherousset, J., Paillisson, J. M., Cuzol, A. & Roussel, J. M. 2009. Spatial behaviour of young-of-the-year northern pike (*Esox lucius* L.) in a temporarily flooded nursery area. *Ecology of Freshwater Fish*, 18, 314-322.

Dingemanse, N. J. & Wolf, M. 2010. Recent models for adaptive personality differences: a review. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365, 3947-3958.

Dingemanse, N., Wright, J., Kazem, A., Thomas, D., Hickling, R. & Dawnay, N. 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology*, 76, 1128-1138.

Engström-Öst, J. & Lehtiniemi, M. 2004. Threat-sensitive predator avoidance by pike larvae. *Journal of Fish Biology*, 65, 251-261.

Gosling, S. D. 2001. From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, 127, 45-86.

Grimm, M. P. 1981. Intraspecific predation as a principal factor controlling the biomass of northern pike (*Esox lucius* L). *Fisheries Management*, 12, 77-79.

Hawkins, L., Armstrong, J. & Magurran, A. 2005. Aggregation in cannibals: interactions between habitat and density in pike (*Esox lucius*). *Journal of Fish Biology*, 67, 265-265.

Herczeg, G., Gonda, A. & Merila, J. 2009. Predation mediated population divergence in complex behaviour of nine-spined stickleback (*Pungitius pungitius*). *Journal of Evolutionary Biology*, 22, 544-552.

Kaushik, S. J., Dabrowski, K. & Luquet, P. 1985. Experimental studies on some trophic relationships in juvenile pike, *Esox lucius* L. *Journal of Fish Biology*, 26, 171-180.

Knight, C., Gozlan, R. & Lucas, M. 2008. Can seasonal home-range size in pike *Esox lucius* predict excursion distance? *Journal of Fish Biology*, 73, 1058-1064.

Kobler, A., Klefoth, T., Mehner, T. & Arlinghaus, R. 2009. Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? *Oecologia*, 161, 837-847.

Koch, F. & Wieser, W. 1983. Partitioning of energy in fish: can reduction of swimming activity compensate for the cost of production? *Journal of Experimental Biology*, 107, 141 -146.

Lee, J. & Bereijikian, B. 2008. Stability of behavioral syndromes but plasticity in individual behavior: consequences for rockfish stock enhancement. *Environmental Biology of Fishes*, 82, 179-186.

Lehtiniemi, M. 2005. Swim or hide: predator cues cause species specific reactions in young fish larvae. *Journal of Fish Biology*, 66, 1285-1299.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation - a review and prospectus. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 68, 619-640.

Logue, D., Mishra, S., McCaffrey, D., Ball, D. & Cade, W. 2009. A behavioral syndrome linking courtship behavior toward males and females predicts reproductive success from a single mating in the hissing cockroach, *Gromphadorhina portentosa*. *Behavioral Ecology*, 20, 781-788.

Magellan, K. & Kaiser, H. 2010. Male aggression and mating opportunity in a poeciliid fish. *African Zoology*, 45, 18-23.

Mann, R. H. K. 1982. The annual food-consumption and prey preferences of pike (*Esox lucius*) in the river Frome, Dorset. *Journal of Animal Ecology*, 51, 81-95.

Mann, R. & Beaumont, W. 1990. Fast- and slow-growing pike, *Esox lucius* L., and problems of age-determinations from scales. *Aquaculture and Fisheries Management*, 21, 471-478.

Nakagawa, S. & Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, 85, 935-956.

Nilsson, P. A. & Brönmark, C. 1999. Foraging among cannibals and kleptoparasites: effects of prey size on pike behavior. *Behavioral Ecology*, 10, 557-566.

Nilsson, P. A., Turesson, H. & Brönmark, C. 2006. Friends and foes in foraging: intraspecific interactions act on foraging-cycle stages. *Behaviour*, 143, 733-745.

Nyqvist, M.J., Gozlan, R.E., Cucherousset, J. & Britton, R. 2012. Behavioural syndrome in a solitary predator is independent of body size and growth rate. *PLoS ONE*, 7: e31619.

Pronk, R., Wilson, D. R. & Harcourt, R. 2010. Video playback demonstrates episodic personality in the gloomy octopus. *Journal of Experimental Biology*, 213, 1035-1041.

R development core team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82, 291-318.

Reale, D., Dingemanse, N. J., Kazem, A. J. N. & Wright, J. 2010. Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 365, 3937-3946.

Reinbold, D., Thorgaard, G. H. & Carter, P. A. 2009. Reduced swimming performance and increased growth in domesticated rainbow trout, *Oncorhynchus mykiss*. *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 1025-1032.

Rennie, M. D., Collins, N. C., Shuter, B. J., Rajotte, J. W. & Couture, P. 2005. A comparison of methods for estimating activity costs of wild fish populations: more active fish observed to grow slower. *Canadian Journal of Fisheries and Aquatic Sciences,* 62, 767-780.

Riebli, T., Avgan, B., Bottini, A., Duc, C., Taborsky, M. & Heg, D. 2011. Behavioural type affects dominance and growth in staged encounters of cooperatively breeding cichlids. *Animal Behaviour,* 81, 313-323.

Sih, A., Bell, A. & Johnson, J. C. 2004a. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19, 372-378.

Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. 2004b. Behavioral syndromes: An integrative overview. *Quarterly Review of Biology*, 79, 241-277.

Sinn, D., Moltschaniwskyj, N., Wapstra, E. & Dall, S. 2010. Are behavioral syndromes invariant? Spatiotemporal variation in shy/bold behavior in squid. *Behavioral Ecology And Sociobiology,* 64, 693-702.

Smith, B. R. & Blumstein, D. T. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology,* 19, 448-455.

Smith, B. & Blumstein, D. 2010. Behavioral types as predictors of survival in Trinidadian guppies (*Poecilia reticulata*). *Behavioral Ecology*, 21, 919-926.

Snekser, J., Leese, J., Ganim, A. & Itzkowitz, M. 2009. Caribbean damselfish with varying territory quality: correlated behaviors but not a syndrome. *Behavioral Ecology*, 20, 124-130.

Stamps, J. A. 1991. Why evolutionary issues are reviving interest in proximate behavioral mechanisms. *American Zoologist*, 31, 338-348.

Stamps, J. A. 2007. Growth-mortality tradeoffs and “personality traits” in animals. *Ecology Letters*, 10, 355-363.

Stamps, J. A. & Groothuis, T. G. G. 2010. Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 4029-4041.

Toms, C. N., Echevarria, D. J. & Jouandot, D. J. 2010. A methodological review of personality-related studies in fish: focus on the shy-bold axis of behavior. *International Journal of Comparative Psychology*, 23, 1-25.

Vøllestad, L. A. & Quinn, T. P. 2003. Trade-off between growth rate and aggression in juvenile coho salmon, *Oncorhynchus kisutch*. *Animal Behaviour*, 66, 561-568.

Wilson, A. D. M., Godin, J. G. J. & Ward, A. J. W. 2010. Boldness and reproductive fitness correlates in the Eastern Mosquitofish, *Gambusia holbrooki*. *Ethology*, 116, 96-104.

Wolf, M., Sander van Doorn, G., Leimar, O. & Weissing, F.J. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447, 581-585.

Wolf, M., Sander van Doorn, G. & Weissing, F.J. 2008. Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 15825-15830.

Wolf, M. & Weissing, F. J. 2010. An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3959-3968.

Ziliukiene, V. & Ziliukas, V. 2006. Feeding of early larval pike *Esox lucius* L. reared in illuminated cages. *Aquaculture*, 258, 378-387.

Chapter 8

General discussion

8.1 INTRODUCTION

Over the last twenty years, the increasing detection of the occurrence of animal personalities and behavioural syndromes has led to a renewed recognition of the evolutionary and ecological importance of behavioural variation. Theory to explain the occurrence of consistent individual behavioural variation (in contrast to behavioural plasticity) has focused on state-dependency, where the behaviour of an individual is influenced by its state (e.g. body size). Behavioural variation has also been hypothesised to precede state variation and through positive feedbacks, initial individual consistent behavioural variation causes differences in state (Wolf & Weissing 2010). In addition, theories associating consistent growth differences with personality traits have been presented (Stamps 2007). Our understanding of behavioural causes of size dimorphism remains weak (Blanckenhorn 2005) and there have been few studies investigating the relationship between individual behavioural consistency and growth variations in size dimorphic populations. This thesis aimed to identify behavioural causes and consequences of size dimorphism by disentangling the relationship in pike between individual behavioural variation at different levels (personality, movement, and dispersal), and growth and size variability.

Firstly, an investigation of the growth trajectories of individuals within the River Frome pike population revealed that early intrapopulation growth variation had lifetime consequences for individual body sizes, suggesting that early growth is an important driver of sexual size dimorphism in this species (Chapter 3). Consequently, the subsequent data chapters focused on the juvenile stage, with the field studies involving fish between 0+ and 2+

years (Chapters 4-5), and the experimental studies focusing on the initial six months of life (Chapters 6-7).

The outputs of the field studies revealed that juvenile pike in the side-channels of the River Frome exhibited consistent individual variation in movement within age-classes. The larger-sized individuals in an age class exhibited a higher level of movement, with this unrelated to their trophic niche and growth rate (Chapter 4). A comparison between pike dispersing from nursery habitats with those staying showed that whilst dispersing individuals had lower trophic values and body sizes, those that successfully settled in the river (i.e. recaptured in the river at a later point) benefited from their dispersal by subsequently increasing their growth and trophic position (Chapter 5). The experimental work revealed consistent foraging behaviour in the juvenile pike over time and across situations of different risk levels (low, intermediate and high; Chapter 6). However, individual behaviours did not relate to their growth, nor was it a function of body size, thus showing no evidence in support of the state-dependent behavioural model. Furthermore, no evidence for a context-general behavioural syndrome was found in juvenile pike (Chapter 7).

In this Chapter, the main outputs from across the different chapters are discussed and their significance evaluated. Finally, conclusions on the extent to which the aim of this thesis was attained and suggestions for future research directions are presented.

8.2 GROWING APART: DEVELOPMENT OF SEXUAL SIZE DIMORPHISM IN PIKE

The pike population that was studied in the River Frome showed SSD, with significant differences in body size between the sexes at most ages, where females attained larger sizes than males. However, the data also showed large individual size variations within the sexes. In most species, sexual differences in growth and development are underpinned by genetics (Badyaev 2002), but a strong environmental effect has also been suggested (Blanckenhorn 2005). For example, variation in growth is mediated generally by food availability, with this influenced at the individual level through foraging ability and competition (Blanckenhorn 2005). The absence of interspecific competition and/ or predation pressure, together with high intraspecific density (or competition and the availability of open niches) provides an opportunity for individual specialisation on alternative prey or habitats and causes the population to diverge (Robinson & Wilson 1994; Skulason & Smith 1995). Several studies have highlighted the relationship between dwarf and normal forms in a population and their trophic position (Hindar & Jonsson 1982; Chouinard et al. 1996; Guiguer et al. 2002). Dwarf forms are commonly found to inhabit alternative niches of lower value resources, which depends on the habitat available (Lu & Bernatchez 1999; Winfield et al. 2002). Growth polymorphism is then thought to be a consequence of local environment and resource conditions (Saint-Laurent et al. 2003; Andersson et al. 2005). Intra-specific habitat segregation, together with a difference in food availability, requires different foraging efficiencies, which is thought to be the main cause of the development of morphs (Ehlinger & Wilson 1988; Skulason & Smith 1995; Robinson et al. 1996; Svanbäck & Eklöv 2003). For example, grasshoppers feeding on harder plants develop larger heads and mandibles (Thompson 1992), and planktivorous fish generally have more slender bodies than benthivorous fish (Webb 1984). In Arctic charr, structurally simple habitats (e.g. the pelagic zone) with high zooplankton densities give rise to individuals with slender bodies when compared to individuals from structurally complex habitats (e.g. the benthic zone) where zooplankton availability is lower (Andersson et al. 2005). In European perch, individuals with deeper bodies were found to have faster growth in the littoral zone, while individuals with a more streamlined body grew faster in the pelagic zone (Hjelm et al. 2001; Svanbäck & Eklöv 2002). While most studies on the development of polymorphism focus on different forms or morphs (Smith & Skulason 1996; Andersson et al. 2005), fewer studies have addressed similar questions from the resource partitioning perspective relating to SSD. After identifying in Chapter 3 that intraspecific growth variation and the divergence between sexes takes place during early life, the following chapters aimed at identifying proximate behavioural mechanisms related to resource use for SSD in juveniles.

8.3 INDIVIDUAL VARIATION: CAN INDIVIDUAL BEHAVIOUR EXPLAIN THE DEVELOPMENT OF SIZE DIMORPHISM?

8.3.1 Does size-dependent juvenile movement, dispersal and trophic niche indicate interference competition?

Individual variation in the spatial behaviour of juvenile pike was size related, indicating a behavioural cause of size dimorphism. Consistency in individual variation in movement was positively size-dependent, which might be due to risks associated with moving in this cannibalistic species. Dispersal from the ditches was, however, found to be negatively size-dependent, i.e. smaller pike dispersed while larger pike remained in the ditches, a counter-intuitive finding that may indicate that smaller pike were competitively excluded from the ditches by their larger conspecifics. This fits in with size-dependent intimidation, interference behaviour or social stress which has been reported in adult pike (Nilsson & Brönmark 1999; Nilsson et al. 2006; Edeline et al. 2010). Nilsson & Brönmark (1999) demonstrated that prey size increases the duration of prey manipulation and handling, which attracts conspecifics and increases the risk of falling victim to cannibals or kleptoparasites. Prey handling duration can therefore inflict major fitness costs. As larger pike have a larger gape-size, which enables handling of larger prey, the results of Nilsson (2006) also infer size-influenced interference behaviour. Small pike have also been found to spatially avoid larger conspecifics, creating a size-influenced distribution among pike individuals (Nilsson 2006). Most recently, Edeline et al. (2010) showed that an increase in pike density caused a social stress response in the pike with a negatively size-dependent effect on the energetic status and body growth rate. These findings provide evidence for the importance of size-dependent interference in pike, supporting the inference made in the present study of interference-driven dispersal. Larger individuals may, through interference, gain higher access to resources by negatively affecting the foraging behaviour and habitat use of smaller individuals (Vanbuskirk 1992; Post et al. 1999; Aljetlawi & Leonardsson 2002). Larger individuals can also consume a larger size range of prey than smaller conspecifics (Wilson 1975).

Possible mechanisms underpinning interference competition in pike include constant intimidation, which occurs when the mere presence of a strong competitor (slightly larger pike) causes weaker individuals to increase avoidance behaviour to avoid kleptoparasitism or attack, reducing their foraging activity (Persson 1988; Nilsson & Brönmark 1999; Griffiths & Armstrong 2002). With the lower trophic positions and body sizes of pike dispersing, this is a likely mechanism. Filtering interference, whereby weaker competitors only access those resources undetected or ignored by stronger individuals (Wilson 1974), may also be a possibility in pike. Direct aggressive interactions, during which individuals fight over prey and strong interferers are more successful (Sirot 2000), is less probable to be the cause of interference competition in pike. Fighting would likely have caused physical injuries and marks on the body to the pike, but these were not observed on any of the pike captured.

In animal communities, species often avoid detrimental effects of interference competition by segregation in either time or space (Morris 1999). The appearance of a dominant competitor may not only induce higher avoidance behaviour but also reduce an individual’s willingness to use an area, thus excluding it from the area. Habitat exclusion due to interference competition has mostly been shown to occur between different species. For example, Bohn & Amundsen (2001) found that during an invasion of vendace (*Coregonus albula* L.), white fish (*Coregonus lavaretus* L.) changed its habitat from pelagic to littoral areas. Similarly, evidence for habitat exclusion of arctic foxes (*Alopes lagopus* L.) by red foxes (*Vulpes vulpes* L.) has been found during years of low food abundance in northern Sweden (Tannerfeldt et al. 2002). The subordinate species or individuals within a population may depart due to risk of mortality caused by starvation, or risk predation if they stay. Interference competition may therefore have important consequences on the distribution of foragers and can lead to competitive exclusion (Armstrong & McGehee 1980; Rutten et al. 2010).

The subsequent faster growth of dispersers in the main river highlights the importance of habitat complexity in affecting the development of size dimorphism. Indeed, different dispersal patterns may relate to the heterogeneity or fragmentation of the habitat (Matthysen 2002; Dale et al. 2005). In a homogenous habitat, subordinate pike (smaller individuals with lower foraging or competitive ability) would have no alternative habitat to move to. Indeed, SSD in pike has been more commonly reported in rivers (e.g. Masters et al. 2005; Vehanen et al. 2006) compared to lakes (e.g. Lorenzoni et al. 2002; Kobler et al. 2009). This indicates the importance of a heterogeneous environment for the development of SSD in pike. Interestingly, in the lacustrine, adult pike population studied by Kobler et al. (2009), individual movement and habitat use associated positively with access to prey quality. This was suggested to reduce intraspecific competition in the preferred habitats, but differences in habitat use did not relate to growth rate. Increased levels of activity to feed have been related to decreased growth rates in a number of species (e.g. Koch & Wieser 1983; Rennie et al. 2005; Reinbold et al. 2009). Such a growth-foraging activity trade-off provides an alternative theory to explain growth-and size independent behaviour. The role habitat complexity plays in generating inter-population differences in growth and size variability remains poorly understood.

8.3.2 Do behavioural syndromes explain size dimorphism in pike?

A behavioural syndrome, shown as repeatable foraging behaviour across risk situations, was detected in the juvenile pike, for which foraging under risk is considered an appropriate indication of boldness (Nyqvist et al. 2012). However, no evidence for a context-general behavioural syndrome of exploration, aggression and boldness was found. The strong repeatability of individual foraging behaviour, in contrast to its absence in contexts with limited feeding opportunity, may be due to pike being a highly predatory species. The reported trade-off in pike larvae between predator avoidance and feeding activity to out-grow the predator prey sizes (Engström-Öst & Lehtiniemi 2004) highlights the importance of individual variation in risk-taking during foraging, i.e. it is as a significant behavioural trait. This supports the hypothesis that the development of personality traits relates to the acquisition of food resources, as mediated by consistent individual differences in life history productivity, such as growth (Biro & Stamps 2008). Nevertheless, there was no relationship between behaviour and growth in either experimental study, despite different feeding regimes. In the first study, individuals were fed *ad libitum* between experimental sessions, while feeding was restricted (max. 2 hours feeding per day) in the second study. Although individual variation in growth rates has been found to occur in many species fed *ad libitum* (Mangel & Stamps 2001), this was not the case for these juvenile pike. The restricted feeding regime during the second experimental study decreased the overall mean (± SE) SGR to 0.77 (± 0.04) from 1.96 (± 0.06) % day^{-1} in the first experimental study, where individuals were fed *ad libitum*. Individual variation in SGR, however, differed between the experiments (2009, CV = 19.6%; 2010, CV = 27.3%), indicating that the limited feeding increased growth variations. Nevertheless, few relationships were detected between growth and body size, and behaviours assayed in the second set of experiments. As the contexts and types of behaviour that were measured differed between the years, together with differences in their repeatabilities, it is difficult to directly compare the relationship between growth and behaviour. The association between personality traits and life history productivity (e.g. growth) advanced by Biro & Stamps (2008), which is based on the widespread reports of consistent growth rates among individuals (Stamps 2007), assumes that individuals that show fast growth should consistently be more willing to take risks to feed. This has been suggested to be valid only for homogeneous environments (e.g. captive conditions), where directional selection can result in stable associations between personality and life history productivity (Adriaenssens & Johnsson 2009). Instead, Adriaenssens & Johnsson (2009) proposed that in the presence of variable natural selection pressures in heterogeneous habitats, the association is more dynamic. Indeed, dominance hierarchies formed among fish in the laboratory may differ from those formed in complex natural environments (Milinski & Parker 1991). In brown trout juveniles, the growth rate of aggressive dominant individuals in relation to subordinates decreased when the habitat complexity increased (Höjesjö et al. 2004). Even physiological correlates of dominance have been found to differ between natural and laboratory populations of brown trout (Sloman et al. 2008). Höjesjö et al. (2004) suggest that fluctuating selective pressures in response to environmental complexity act to maintain behavioural variation in natural populations and allow subordinate and dominant strategies to coexist. Also studying brown trout, Adriaenssens & Johnsson (2010) found that although aggression and exploration behaviours measured in the laboratory constituted a behavioural syndrome, the behaviours did not affect performance in the wild, nor did aggression predict social dominance in the wild. Adriaenssens & Johnson (2010) therefore raised concern over using laboratory measured behaviours to predict fitness consequences in the wild. Indeed, in a meta-analysis of fitness consequences of personality, the degree of association between reproductive success and personality traits was reduced when only wild animals were included (Smith & Blumstein 2008). Furthermore, Archard & Braithwaite (2010) point out that although laboratory conditions are designed to resemble conditions in the wild, this is rarely the case in reality given that predation pressures are removed, food is provided reducing foraging efforts, and individuals are treated against diseases. A link between size dimorphism and personality traits in pike may therefore be revealed through studying them in their natural habitat.

8.3.3 Is individual variation in movement and dispersal underpinned by the behavioural syndrome?

A growing number of studies show that consistent behavioural differences between individuals have a genetic basis and are the target of selection in natural environments (Sih et al. 2004b; Smith & Blumstein 2008; Dochtermann & Roff 2010). In addition, behavioural syndromes have been found to affect several ecological processes and are therefore considered to be ecologically important (Reale et al. 2007; Sih et al. 2012). For example, behavioural variation within a species can affect species interactions, with bolder predators having a larger impact on prey densities, or on a broader range of prey species (Riechert 1991; Ioannou et al. 2008), whereas bold prey suffers heavier predation (Sih et al. 2003). Bolder, more aggressive or sociable individuals have also been found to be more heavily parasitized (Kortet et al. 2010). Furthermore, inter-individual variation in behaviour can also affect the population's response to environmental disturbance, for example, bolder and more aggressive individuals of brown trout are more likely to be captured than shy and less aggressive individuals (Biro et al. 2004). The remaining individuals have a lower impact on their prey and are less likely to out-compete other species (Sih et al. 2012).

Evidence from several studies suggests that individual variation in movement and dispersal is likely to be caused by the underlying behavioural type and behavioural syndromes (Fraser et al. 2001; Reale et al. 2007; Cote et al. 2010b). For example, Fraser et al. (2001) measured boldness in Trinidad killifish in laboratory experiments followed by their release in the field and showed that bolder individuals dispersed longer distances, but this was independent of size or sex. A similar laboratory–field study using mosquitofish (*G. affinis*) revealed that sociability was an important indicator of dispersal distance, with more asocial individuals dispersing further (Cote et al. 2010a). In root voles (*Microtus oeconomus* Pallas), dispersers displayed social behaviour towards unfamiliar males at a younger age, were faster explorers and more active than residents; however, the behavioural differences between dispersers and residents were temporary (Hoset et al. 2011). Recently, state-dependent links between individual differences in exploration and dispersal has been reported in great tits (*Parus major* L.), where the relationship was found to be stronger in smaller individuals (Quinn et al. 2011), supporting the state-dependent personality models (Wolf & Weissing 2010).

While movement and dispersal was size-dependent in pike, providing a behavioural link to the development of size dimorphism, the behavioural syndrome detected experimentally was independent of body size and growth. The importance of intraspecific competition in driving dispersal was inferred by its negative size dependency. A study by Caldow et al. (1999) suggests that individual variation in foraging efficiency is of great importance for determining competitive ability. They found the use of separate feeding habitats of different quality to be related to individual variation in foraging efficiency in oystercatchers *Haematopus ostralegus* (L.), but not to variation in dominance. Indeed, a difference in trophic position between individuals may be underpinned by individual consistency in foraging behaviour across risk. As pike were not found to exhibit consistency in exploration or aggression, these behaviours are unlikely to underpin mechanisms leading to differences in dispersal. Furthermore, personality dependent dispersal has been suggested to be influenced by species interactions in the source habitat (Sih et al. 2012). As predation risk may generate prey dispersal, more cautious, less aggressive prey might leave to get away from predators (Sih et al. 2012). This could also be applicable within a cannibalistic species consisting of shy and bold individuals. Indeed, Hawkins et al. (2005) showed through a series of laboratory experiments, that pike kept in isolation preferred shallow water habitats, but when kept in pairs in the same habitat, one pike occupied shallow (considered dominant), while the other (subordinate) occupied deep water. The dominant pike was found to occasionally enter the deep water, but this did not affect the position of the subordinate pike (Hawkins et al. 2005). The authors suggest that the subordinate did not move to shallow waters due to increased risk of attack. This also indicates that individual variation in movement and dispersal found here may be underpinned by personality.

8.4 CONCLUSIONS AND FUTURE DIRECTIONS

The overall aim of this thesis to identify the behavioural causes of size dimorphism was achieved through demonstrating size-dependent spatial behaviour and trophic ecology in juvenile life stages of a wild size dimorphic population. Although personality traits related to foraging under different risk situations under experimental conditions, no relation to growth or size was found. These findings therefore indicate that intraspecific interactions such as size-dependent interference competition play a key role in maintaining intraspecific size variation and trophic polymorphism in the wild population. The competitive ability of individuals may, however, be underpinned by variation in boldness to forage under risk. Furthermore, the non-significant relationship between boldness and growth suggested that the heterogeneous environment plays a significant role in providing the potential for habitat and resource segregation to occur and so subsequently, enables the divergent growth.

Further experimental work is required to elucidate the relationship between individual competitive ability and the development of size variations and size dimorphism. One possible approach includes initially measuring individuals foraging under risk to determine boldness followed by keeping individuals in groups to assess their competitive ability and interference behaviour. Their growth rates would then be monitored to elucidate whether group living (i.e. constant competitive pressure) leads to the development of size dimorphism. A combined experimental-field study involving initially assessing individuals' boldness or competitive ability under laboratory conditions followed by their release back in their natural habitat could be conducted to directly test whether size-dependent dispersal is driven by boldness/competitive ability. Here, the experimental part of the study would need to be conducted under a short time frame so as not affect individuals' behaviour in the wild when released. Combined experimental-field studies have the potential to demonstrate direct ecological consequences of behavioural variation (Fraser et al. 2001; Cote et al. 2010a).

Despite the River Frome pike population exhibiting size dimorphism, when kept in isolation in the laboratory, such a bimodal size distribution did not develop. As highlighted by Adriaenssens & Johnsson (2009), predictions of consequences in wild populations of personality traits measured in the laboratory should be taken with caution as laboratory conditions cannot fully represent the conditions in the wild. Measuring personality traits in the wild is difficult, as conditions cannot be controlled and could therefore vary between individuals. Thus, to test for a relationship between behavioural type (bold/shy) and the development of size dimorphism, the best approach would again be a combined laboratory-field study. As the fish could not be released back into the wild due to legislative restrictions relating to fish stocking activities in the present study site, an alternative to releasing into the wild using River Frome pike would require using isolated and artificial channels. However, such a site was not available during the present study. As few studies on personality have been conducted on size dimorphic species, this avenue of research would enable a wider research gap to be closed involving state-dependent personality models.

While this thesis has focused on the behavioural causes of SSD in juveniles, more research into the ecological consequences of SSD in adults is needed. Intra-SSD has been reported for pike, especially in males, and is believed to have significant consequences on the behaviour and reproductive fitness of individuals (Knight 2006). Although it has been suggested that male alternative reproductive tactics (MARTs) occur in pike, with small males exhibiting protandry and sneaking behaviour on the reproductive site (Knight 2006), this has not yet been proved. These tactics are thought to maximise reproductive fitness and compensate for small size during male-male competition or/and female mate selection (Morbey & Ydenberg 2001). In species with indeterminate growth, the age of sexual maturity has also been found to be lower in smaller sized individuals due to the trade-off between resource allocation to growth or reproduction (Kozlowski 1992; Heino & Kaitala 1999). Although small males that undertake sneaking have generally been considered to be low-quality males who are unable to attract a female themselves (Goncalves et al. 2003), in reviewing evidence, Reichard et al. (2007) suggested that females may actually seek to mate with sneaker males. This is because sneaking may be a means by which females increase fertilisation rates, and fitness and genetic diversity among the offspring (Reichard *et al*. 2007). Ultimately, the presence of SSD may only be important if there is an implication for reproductive fitness. To improve our understanding of the life-time consequences of SSD by using pike as a model, an assessment of age and size at reproductive maturity is necessary. Subsequently, the relationship between age and size at maturity and the expression of MARTs and female mate-selection needs to be ascertained. The combined application of fixed and portable PIT antennae would allow the arrival of pike to the spawning sites to be determined, and the movement of individuals on the spawning ground and their mating strategies to be observed. The use of genetic (e.g. microsatellite-based) analyses to determine parentage of fertilised eggs (Chakraborty et al. 1988; Jones et al. 2001) could then reveal the relationship between reproductive success and size-dependent reproductive behavioural strategies. This would enable a determination of life-time fitness consequences of variable body sizes, which would contribute greatly to the understanding of SSD.

8.5 REFERENCES

Adriaenssens, B. & Johnsson, J. I. 2009. Personality and life-history productivity: consistent or variable association? *Trends in Ecology & Evolution*, 24, 179-180.

Adriaenssens, B. & Johnsson, J. I. 2010. Shy trout grow faster: exploring links between personality and fitness-related traits in the wild. *Behavioral Ecology*, 22, 135-143.

Aljetlawi, A. & Leonardsson, K. 2002. Size-dependent competitive ability in a deposit-feeding amphipod, *Monoporeia affinis*. *Oikos*, 97, 31-44.

Andersson, J., Bystrom, P., Persson, L. & De Roos, A. M. 2005. Plastic resource polymorphism: effects of resource availability on Arctic char (*Salvelinus alpinus*) morphology. *Biological Journal of the Linnean Society*, 85, 341-351.

Archard, G. A. & Braithwaite, V. A. 2010. The importance of wild populations in studies of animal temperament. *Journal of Zoology*, 281, 149-160.

Armstrong, R. & McGehee, R. 1980. Competitive-exclusion. *American Naturalist*, 115, 151-170.

Badyaev, A. V. 2002. Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends in Ecology & Evolution*, 17, 369-378.

Biro, P.A., Abrahams, M. V., Post, J. R. & Parkinson, E. A. 2004. Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society B-Biological Sciences*, 271, 2233–2237.

Biro, P. A. & Stamps, J. A. 2008. Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23, 361-368.

Blanckenhorn, W. U. 2005. Behavioral causes and consequences of sexual size dimorphism. *Ethology*, 111, 977-1016.

Bohn, T. & Amundsen, P. 2001. The competitive edge of an invading specialist. *Ecology*, 82, 2150-2163.

Caldow, R., Goss-Custard, J., Stillman, R., Durell, S., Swinfen, R. & Bregnballe, T. 1999. Individual variation in the competitive ability of interference-prone foragers: the relative importance of foraging efficiency and susceptibility to interference. *Journal of Animal Ecology*, 68, 869-878.

Chakraborty, R., Meagher, T. R. & Smouse, P. E. 1988. Parentage analysis with genetic markers in natural populations. I. The expected proportion of offspring with unambiguous paternity. *Genetics*, 118, 527-536.

Chouinard, A., Pigeon, D. & Bernatchez, L. 1996. Lack of specialisation in trophic morphology between genetically differentiated dwarf and normal forms of lake whitefish (*Coregonus clupeaformis* Mitchill) in Lac de l'Est, Quebec. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 74, 1989-1998.

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T. & Sih, A. 2010a. Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). 277, 1571-1579.

Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. 2010b. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 4065 -4076.

Dale, S., Lunde, A. & Steifetten, O. 2005. Longer breeding dispersal than natal dispersal in the ortolan bunting. *Behavioral Ecology*, 16, 20-24.

Dochtermann, N. A. & Roff, D. A. 2010. Applying a quantitative genetics framework to behavioural syndrome research. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 4013–4020.

Edeline, E., Haugen, T. O., Weltzien, F. A., Claessen, D., Winfield, I. J., Stenseth, N. C. & Vøllestad, L. A. 2010. Body downsizing caused by non-consumptive social stress severely depresses population growth rate. *Proceedings of the Royal Society B-Biological Sciences*, 277, 843-851.

Ehlinger, T. & Wilson, D. 1988. Complex foraging polymorphism in bluegill sunfish. *Proceedings of the National Academy of Sciences of the United States of America*, 85, 1878-1882.

Engström-Öst, J. & Lehtiniemi, M. 2004. Threat-sensitive predator avoidance by pike larvae. *Journal of Fish Biology*, 65, 251-261.

Fraser, D., Gilliam, J., Daley, M., Le, A. & Skalski, G. 2001. Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *American Naturalist*, 158, 124-135.

Goncalves, D., Fagundes, T. & Oliveira, R. 2003. Reproductive behaviour of sneaker males of the peacock blenny. *Journal of Fish Biology,* 63, 528-532.

Griffiths, S. & Armstrong, J. 2002. Kin-biased territory overlap and food sharing among Atlantic salmon juveniles. *Journal of Animal Ecology*, 71, 480-486.

Guiguer, K., Reist, J., Power, M. & Babaluk, J. 2002. Using stable isotopes to confirm the trophic ecology of Arctic charr morphotypes from Lake Hazen, Nunavut, Canada. *Journal of Fish Biology*, 60, 348-362.

Hawkins, L., Armstrong, J. & Magurran, A. 2005. Aggregation in cannibals: interactions between habitat and density in pike (*Esox lucius*). *Journal of Fish Biology*, 67, 265-265.

Heino, M. & Kaitala, V. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology*, 12, 423-429.

Hindar, K. & Jonsson, B. 1982. Habitat and food segregation of dwarf and normal arctic charr (*Salvelinus alpinus*) from vangsvatnet lake, western Norway. *Canadian Journal of Fisheries and Aquatic Sciences*, 39, 1030-1045.

Hjelm, J., Svanbäck, R., Byström, P., Persson, L. & Wahlström, E. 2001. Diet-dependent body morphology and ontogenetic reaction norms in Eurasian perch. *Oikos*, 95, 311-323.

Höjesjö, J., Johnsson, J. I. & Bohlin, T. 2004. Habitat complexity reduces the growth of aggressive and dominant brown trout (*Salmo trutta*) relative to subordinates. Behavioral Ecology and Sociobiology, 56, 286- 289.

Hoset, K. S., Ferchaud, A.-L., Dufour, F., Mersch, D., Cote, J. & Le Galliard, J.-F. 2011. Natal dispersal correlates with behavioral traits that are not consistent across early life stages. *Behavioral Ecology*, 22, 176-183.

Ioannou, C. C., Payne, M. & Krause, J. 2008. Ecological consequences of the bold–shy continuum: the effect of predator boldness on prey risk. *Oecologia*,157, 177–182.

Jones, A. G., Walker, D., Kvarnemo, C., Lindström, K. & Avise, J. C. 2001. How cuckoldry can decrease the opportunity for sexual selection: Data and theory from a genetic parentage analysis of the sand goby, *Pomatoschistus minutus*. *Proceedings of the National Academy of Sciences*, 98, 9151 -9156.

Knight, C. 2006. Utilisation of off-river habitats by lowland river fishes. PhD thesis, University of Durham, UK.

Kobler, A., Klefoth, T., Mehner, T. & Arlinghaus, R. 2009. Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? *Oecologia*, 161, 837-847.

Koch, F. & Wieser, W. 1983. Partitioning of energy in fish: can reduction of swimming activity compensate for the cost of production? *Journal of Experimental Biology*, 107, 141 -146.

Kortet, R., Hedrick, A. V. & Vainikka, A. 2010. Parasitism, predation and the evolution of animal personalities. *Ecology Letters*, 13, 1449–1458.

Kozlowski. 1992. Optimal allocation of resources to growth and reproduction - implications for age and size at maturity. *Trends in Ecology & Evolution*, 7, 15-19.

Lorenzoni, M., Corboli, M., Dorr, A. J. M., Mearelli, M. & Giovinazzo, G. 2002. The growth of pike (*Esox lucius* Linnaeus, 1798) in Lake Trasimeno (Umbria, Italy). *Fisheries Research*, 59, 239-246.

Lu, G. & Bernatchez, L. 1999. Correlated trophic specialization and genetic divergence in sympatric lake whitefish ecotypes (*Coregonus clupeaformis*): Support for the ecological speciation hypothesis. *Evolution*, 53, 1491-1505.

Mangel, M. & Stamps, J. 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evolutionary Ecology Research*, 3, 583-593.

Masters, J., Hodder, K., Beaumont, W., Gozlan, R., Pinder, R., Kenward, J. & Welton, S. 2005. Spatial behaviour of pike *Esox lucius* L. in the River Frome, UK. In: *Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe.*, (Ed. by M. Spedicato, G. Lembo, & G. Marmulla), pp. 179-190.

Matthysen, E. 2002. Boundary effects on dispersal between habitat patches by forest birds (*Parus major*, *P. caeruleus*). *Landscape Ecology*, 17, 509-515.

Milinski, M. & Parker, G. A. 1991. Competition for resources. In: Behavioural Ecology. 3rd edn (Ed. by J. R. Krebs & N. B. Davies), pp. 137-168. Oxford: Blackwell.

Morbey, Y. E. & Ydenberg, R. C. 2001. Protandrous arrival timing to breeding areas: a review. *Ecology Letters*, 4, 663-673.

Morris, D. 1999. Has the ghost of competition passed? *Evolutionary Ecology Research*, 1, 3-20.

Nilsson, P. A. 2006. Avoid your neighbours: size-determined spatial distribution patterns among northern pike individuals. *Oikos*, 113, 251-258.

Nilsson, P. A. & Brönmark, C. 1999. Foraging among cannibals and kleptoparasites: effects of prey size on pike behavior. *Behavioral Ecology*, 10, 557-566.

Nilsson, P. A., Turesson, H. & Brönmark, C. 2006. Friends and foes in foraging: intraspecific interactions act on foraging-cycle stages. *Behaviour*, 143, 733-745.

Nyqvist, M.J., Gozlan, R., Cucherousset, J. & Britton, J.R. 2012. Behavioural syndrome in a solitary predator is independent of body size and growth rate. *PLoS ONE*, 7: e31619.

Persson, L. 1988. Asymmetries in competitive and predatory interactions in fish populations. In: *Size-structured populations: ecology and evolution*, (Ed. by B. Ebenman & L. Persson), Berlin: Springer-Verlag.

Post, J., Parkinson, E. & Johnston, N. 1999. Density-dependent processes in structured fish populations: Interaction strengths in whole-lake experiments. *Ecological Monographs*, 69, 155-175.

Quinn, J. L., Cole, E. F., Patrick, S. C. & Sheldon, B. C. 2011. Scale and state dependence of the relationship between personality and dispersal in a great tit population. *Journal of Animal Ecology*, 80, 918-928.

Reale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82, 291-318.

Reichard, M., Le Comber, S. C. & Smith, C. 2007. Sneaking from a female perspective. *Animal Behaviour*, 74, 679-688.

Reinbold, D., Thorgaard, G. H. & Carter, P. A. 2009. Reduced swimming performance and increased growth in domesticated rainbow trout, *Oncorhynchus mykiss*. *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 1025-1032.

Rennie, M. D., Collins, N. C., Shuter, B. J., Rajotte, J. W. & Couture, P. 2005. A comparison of methods for estimating activity costs of wild fish populations: more active fish observed to grow slower. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 767-780.

Riechert, S. E. 1991. Prey abundance vs diet breadth in a spider test system. *Evolutionary Ecology*, 5, 327–338.

Robinson, B. W. & Wilson, D. S. 1994. Character release and displacement in fishes - a neglected literature. *American Naturalist*, 144, 596-627.

Robinson, B., Wilson, D. & Shea, G. 1996. Trade-offs of ecological specialization: An intraspecific comparison of pumpkinseed sunfish phenotypes. *Ecology*, 77, 170-178.

Rutten, A. L., Oosterbeek, K., van der Meer, J., Verhulst, S. & Ens, B. J. 2010. Experimental evidence for interference competition in oystercatchers, *Haematopus ostralegus*. I. Captive birds RID C-6687-2011 RID B-1613-2009. *Behavioral Ecology*, 21, 1251-1260.

Saint-Laurent, R., Legault, M. & Bernatchez, L. 2003. Divergent selection maintains adaptive differentiation despite high gene flow between sympatric rainbow smelt ecotypes (*Osmerus mordax* Mitchill). *Molecular Ecology*, 12, 315-330.

Sih, A., Kats, L. B. & Maurer, E. F. 2003. Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. *Animal Behaviour*, 65, 29–44.

Sih, A., Cote, J., Evans, M., Fogarty, S. & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, 15, 278-289.

Sirot, E. 2000. An evolutionarily stable strategy for aggressiveness in feeding groups. *Behavioral Ecology*, 11, 351-356.

Skulason, S. & Smith, T. B. 1995. Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution*, 10, 366-370.

Sloman, D., Baker, D., Winberg, S. & Wilson, R.W. 2008. Are there physiological correlates of dominance in natural trout populations? Animal Behaviour, 76, 1279-1287.

Smith, B. R. & Blumstein, D. T. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, 19, 448-455.

Smith, T. B. & Skulason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics*, 27, 111-133.

Stamps, J. 2007. Growth-mortality tradeoffs and ‘personality traits’ in animals. *Ecology Letters*, 10, 355-363.

Svanbäck, R. & Eklöv, P. 2002. Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. *Oecologia*, 131, 61-70.

Svanbäck, R. & Eklöv, P. 2003. Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? *Oikos*, 102, 273-284.

Tannerfeldt, M., Elmhagen, B. & Angerbjorn, A. 2002. Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia*, 132, 213-220.

Thompson, D. 1992. Consumption rates and the evolution of diet-induced plasticity in the head morphology of *Melanoplus femurrubrum* (Orthoptera, Acrididae). *Oecologia*, 89, 204-213.

Vanbuskirk, J. 1992. Competition, cannibalism, and size class dominance in a dragonfly. *Oikos*, 65, 455-464.

Vehanen, T., Hyvärinen, P., Johansson, K. & Laaksonen, T. 2006. Patterns of movement of adult northern pike (*Esox lucius* L.) in a regulated river. *Ecology of Freshwater Fish*, 15, 154-160.

Webb, P. 1984. Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist*, 24, 107-120.

Wilson, D. S. 1974. Prey capture and competition in the ant lion. *Biotropica*, 6, 187-193.

Wilson, D. S. 1975. The adequacy of body size as a niche difference. *American Naturalist*, 109, 769-784.

Winfield, I., Bean, C. & Hewitt, D. 2002. The relationship between spatial distribution and diet of Arctic charr, *Salvelinus alpinus*, in Loch Ness, UK. *Environmental Biology of Fishes*, 64, 63-73.

Wolf, M. & Weissing, F. J. 2010. An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3959-3968.

APPENDIX I

Table of PIT tagged pike

Date at first capture	PIT ID	FL (mm) at first capture	BM (g) at first capture	Year of birth	Sex	First catch location	Capture method	Number of recaptures
09/12/2008	1	178.0	39.9	2008		RW	e/f	0
09/12/2008	2	170	41	2008	F	RW	e/f	3
09/12/2008	3	175	39.6	2008		RW	e/f	0
09/12/2008	4	217	68	2008		FR	e/f	0
09/12/2008	5	145	25	2008		FR	e/f	0
09/12/2008	6	167	31.2	2008		FR	e/f	0
09/12/2008	7	194	51	2008		FR	e/f	1
09/12/2008	8	147	24.2	2008		FR	e/f	0
09/12/2008	9	207	64	2008		FR	e/f	1
09/12/2008	10	159	27	2008		FR	e/f	0
09/12/2008	11	162	29.9	2008		RU	e/f	1
09/12/2008	12	177	38	2008		RU	e/f	0
09/12/2008	13	253	122	2007	M	RU	e/f	0
09/12/2008	14	220	71	2008		RU	e/f	1
16/01/2009	15	203	69	2008		RW	e/f	3
16/01/2009	16	204	68	2008		RW	e/f	0
16/01/2009	17	176	43	2008		RW	e/f	1
16/01/2009	18	144	29	2008		RW	e/f	0
16/01/2009	19	166	34	2008		RW	e/f	0
16/01/2009	20	168	37	2008		RW	e/f	1
16/01/2009	21	196	60	2008		RW	e/f	0
16/01/2009	22	168	32	2008		RW	e/f	0
16/01/2009	23	229	95	2008		RW	e/f	0
16/01/2009	24	212	66	2008		RW	e/f	1
16/01/2009	25	308	217	2007	M	FR	e/f	0
16/01/2009	26	142	20	2008		FR	e/f	3
16/01/2009	27	437	640	2005	M	RU	e/f	0
16/01/2009	28	404	500	2007	M	RU	e/f	0
16/01/2009	29	177	44	2008		RU	e/f	0
16/01/2009	30	156	26	2008		RU	e/f	0
16/01/2009	31	158	27	2008		RU	e/f	0
16/01/2009	32	288	183	2007	F	RU	e/f	0
16/01/2009	33	346	340	2007	M	RU	e/f	0

16/01/2009	34	152	25	2008		RU	e/f	2
16/01/2009	35	213	76	2008		FR	e/f	0
16/01/2009	36	194	53.8	2008		FR	e/f	0
16/01/2009	37	220	71.9	2008		FR	e/f	1
16/01/2009	38	194	51.3	2008		FR	e/f	1
16/01/2009	39	175	35.1	2008		FR	e/f	0
24/02/2009	40	206	62.6	2008		RW	e/f	0
24/02/2009	41	170	40	2008		RW	e/f	1
24/02/2009	42	178	44	2008		RW	e/f	0
24/02/2009	43	120	13.3	2008		RW	e/f	0
24/02/2009	44	410	520	2007	F	RW	e/f	0
24/02/2009	46	211	76	2008		FR	e/f	0
24/02/2009	47	181	47	2008		FR	e/f	0
24/02/2009	48	185	42	2008		FR	e/f	0
24/02/2009	49	200	56	2008		FR	e/f	1
24/02/2009	50	480	820	2006		FR	e/f	0
24/02/2009	51	401	780	2005	M	RU	e/f	1
24/02/2009	52	376	440	2007	F	RU	e/f	0
24/02/2009	53	170	24	2008		RU	e/f	3
24/02/2009	54	190	58	2008		RU	e/f	2
24/02/2009	55	190	53	2008		RU	e/f	2
24/02/2009	6129	744	3480	2002	M	FR	e/f	1
25/02/2009	56	218		2008		MF	e/f	1
25/02/2009	57	211	67.4	2008		MF	e/f	0
25/02/2009	58	173	43.2	2008		MF	e/f	0
25/02/2009	59	535	1240	2005	M	MF	e/f	1
25/02/2009	60	605	2000	2005	F	MF	e/f	1
25/02/2009	61	218	70	2008		MF	e/f	0
25/02/2009	62	515	1120	2005	M	MF	e/f	0
25/02/2009	63	200	57.3	2008		MF	e/f	0
25/02/2009	64	230	91	2008		MF	e/f	0
25/02/2009	65	210	97	2008		MF	e/f	0
25/02/2009	66	208	58.8	2008		MF	e/f	0
25/02/2009	67	215	86.2	2008		MF	e/f	0
25/02/2009	68	565	1420	2005	M	MF	e/f	0
25/02/2009	69	579	1400	2005	M	MF	e/f	0
25/02/2009	70	505	900	2006	F	MF	e/f	1
25/02/2009	71	250	111.1	2008		MF	e/f	0
25/02/2009	72	215	69	2008		MF	e/f	0
25/02/2009	73	193	49.6	2008		MF	e/f	0
25/02/2009	74	170	39.1	2008		MF	e/f	0
25/02/2009	75	595	1420	2006	F	MF	e/f	0
25/02/2009	76	208	59.5	2008		MF	e/f	0

25/02/2009	77	212	67.3	2008		MF	e/f	0
25/02/2009	78	195	56.2	2008		MF	e/f	0
25/02/2009	79	189	46	2008		MF	e/f	1
25/02/2009	80	195	44	2008		MF	e/f	0
25/02/2009	81	196	63.3	2008		MF	e/f	0
25/02/2009	82	190	56.1	2008		MF	e/f	0
25/02/2009	83	193	53.5	2008		MF	e/f	0
25/02/2009	84	208	68.9	2008		MF	e/f	0
25/02/2009	85	152	26.9	2008		MF	e/f	0
25/02/2009	86	202	62.9	2008		MF	e/f	0
25/02/2009	87	234	101.5	2008		MF	e/f	0
25/02/2009	3629	835	6180	2000	F	MF	e/f	0
25/02/2009	6112	635	2320	2003	M	MF	e/f	2
25/02/2009	6126	810	4400	2001	F	MF	e/f	1
25/02/2009	8340	810	4200	2002	F	MF	e/f	0
03/03/2009	88	530	1240	2005	M	MF	a	0
03/03/2009	89	695	2700	2003	M	MF	a	0
03/03/2009	90	578	2100	2006	F	MF	a	1
03/03/2009	91	905	6060	2002	F	MF	a	0
03/03/2009	92	657	2400	2003	F	MF	a	0
07/03/2009	93	520	1200	2006	F	MF	a	1
07/03/2009	94	740	4300	2002	F	MF	a	0
07/03/2009	95	8370	5700	2001	F	MF	a	0
09/03/2009	96	584	1450	2004	F	MF	a	0
09/03/2009	97	709	2800	2004	M	MF	a	1
12/03/2009	98	590	1468	2004		MF	a	0
19/03/2009	99	133	15	2008		RW	e/f	0
19/03/2009	100	162	30	2008		RW	e/f	1
19/03/2009	101	264	106	2008	M	FR	e/f	1
19/03/2009	102	220	70	2008	M	FR	e/f	0
19/03/2009	103	159	29	2008		FR	e/f	0
19/03/2009	104	194	51	2008		FR	e/f	0
19/03/2009	105	229	87	2008		FR	e/f	0
19/03/2009	106	174	38	2008		FR	e/f	1
19/03/2009	107	144	21	2008		FR	e/f	0
19/03/2009	108	160	30	2008	M	FR	e/f	3
19/03/2009	109	159		2008		MF	e/f	0
24/03/2009	110	194	55	2008		RU	e/f	0
24/03/2009	111	199	65	2008		RU	e/f	1
24/03/2009	112	716	3010	2004	M	RU	e/f	0
24/03/2009	113	205	59	2008	M	MF	e/f	0
24/03/2009	114	212	78	2008	M	MF	e/f	0
24/03/2009	115	460	905	2003	F	MF	e/f	0

24/03/2009	116	755	3409	2005	F	MF	e/f	0
24/03/2009	117	134	16	2008		MF	e/f	0
09/07/2009	118	328	278	2007	F	MF	e/f	0
09/07/2009	119	272	159	2008		MF	e/f	0
09/07/2009	120	300	216	2008		MF	e/f	0
09/07/2009	121	205	88.5	2008		MF	e/f	0
09/07/2009	122	715	3400	2004		MF	e/f	0
10/07/2009	123	244	133	2008	F	MS	e/f	0
10/07/2009	124	371	0.8	2008	M	MS	e/f	0
10/07/2009	125	364	373	2008	M	MS	e/f	0
10/07/2009	126	386	508	2008	M	MS	e/f	0
10/07/2009	127	364	391	2008	F	MS	e/f	0
10/07/2009	128	315	261	2008	M	MS	e/f	0
10/07/2009	129	299	207	2008		MS	e/f	0
25/08/2009	130	152	24.2	2009		RU	e/f	1
15/10/2009	131	200	56.5	2009		RW	e/f	1
15/10/2009	132	181	39.5	2009		FR	e/f	1
15/10/2009	133	376	460	2008	M	RU	e/f	0
15/10/2009	134	205	54	2009		RU	e/f	2
15/10/2009	135	125	13.7	2009		RU	e/f	0
15/10/2009	136	164	32	2009		RU	e/f	0
29/10/2009	137		1720	2003	M	MF	a	0
29/10/2009	138		1020	2006	F	MF	a	0
10/11/2009	139	716	3520	2004	M	MF	a	0
24/02/2010	140	221	88	2009		RW	e/f	0
24/02/2010	141	177	35.4	2009		FR	e/f	0
24/02/2010	142	300	205	2007	M	FR	e/f	0
24/02/2010	143	138	18	2009		FR	e/f	3
24/02/2010	144	257	118	2009		FR	e/f	1
24/02/2010	145	154	25.3	2009		RU	e/f	1
24/02/2010	146	229	91.4	2009		RU	e/f	0
24/02/2010	147	157	25.3	2009		RU	e/f	0
24/02/2010	148	205	64.6	2009		RU	e/f	2
24/02/2010	149	181	47.2	2009		RU	e/f	0
24/02/2010	150	175	36.3	2009		RU	e/f	2
24/02/2010	151	219	72	2009		RU	e/f	0
24/02/2010	152	225	77.5	2009		RU	e/f	1
24/02/2010	153	130	15.1	2009		RU	e/f	0
24/02/2010	154	149	23.1	2009		RU	e/f	0
24/02/2010	155	182	40.2	2009		RU	e/f	0
24/02/2010	156	417	508	2007	M	RU	e/f	0
24/02/2010	157	181	40.4	2009		RU	e/f	0
24/02/2010	158	240	104.1	2009		RU	e/f	0

24/02/2010	159	165	37	2009		RU	e/f	0
24/02/2010	160	170	42.4	2009		RU	e/f	1
24/02/2010	161	146	21.9	2009		RU	e/f	0
24/02/2010	162	301	213	2008		RU	e/f	1
24/02/2010	163	197	59.1	2009		RU	e/f	0
24/02/2010	164	224	77.5	2009		RU	e/f	0
24/02/2010	165	154	29.9	2009		RU	e/f	1
24/02/2010	166	150	30.3	2009		RU	e/f	0
27/02/2010	167	730	3180	2004		MF	a	0
04/03/2010	168	397	505	2008	M	MF	e/f	1
04/03/2010	169	820	4300	2005	F	MF	e/f	0
10/06/2010	170	292	196	2009	F	MS	e/f	0
23/06/2010	171	485	1060	2008	M	MF	e/f	0
23/06/2010	172	243	115.2	2009		MF	e/f	0
23/06/2010	173	385	500	2006	F	MF	e/f	0
23/06/2010	174	294	219	2009		MF	e/f	0
23/06/2010	175	620	2740	2006	M	MF	e/f	0
08/07/2010	176	237	98.2	2009		RU	fn	0
12/07/2010	177	173	35.7	2009		RU	fn	3
22/07/2010	178	177	38	2009		FR	fn	1
03/08/2010	179	289	174	2009		MS	e/f	1
18/08/2010	180	278	168	2009		RU	e/f	1
18/08/2010	181	274	152	2009		RU	e/f	0
18/08/2010	182	279	178	2009		RU	e/f	1
18/08/2010	183	249	122	2009		RU	e/f	1
18/08/2010	184	258	123	2009		RU	e/f	0
18/08/2010	185	233	103	2009		RU	e/f	2
18/08/2010	186	214	83.6	2009		RU	e/f	0
20/08/2010	187	105	8.8	2010		FR	e/f	0
26/08/2010	188	376	376	2009	M	FR	fn	0
31/08/2010	189	144	21.8	2010		RU	fn	2
31/08/2010	190	305	217	2008		RU	fn	1
02/09/2010	191	180	37.8	2010		RU	fn	2
03/09/2010	192	140	21.4	2010		MS	e/f	0
05/09/2010	193	111	9.8	2010		FR	fn	0
09/09/2010	194	286	177.5	2009		RU	fn	1
10/09/2010	195	240	97	2009		RU	fn	2
13/09/2010	196	157	29.5	2010		RU	fn	0
24/09/2010	197	186	24.6	2010		RU	fn	0
27/09/2010	198	98	9.1	2010		FR	fn	2
28/09/2010	199	166	37.8	2010		MF	e/f	0
28/09/2010	200	172	36.7	2010		MF	e/f	0
28/09/2010	201	165	36.5	2010		MF	e/f	0

28/09/2010	202	418	520	2009		MF	e/f	1
30/09/2010	203	105	7.8	2010		FR	e/f	0
30/09/2010	204	107	7	2010		RU	fn	0
08/10/2010	205	247	112	2009		RU	fn	1
08/10/2010	207	205	63	2010		MS	e/f	0
08/10/2010	208	195	51.8	2010		MS	e/f	0
08/10/2010	209	211	67	2010		MS	e/f	1
12/10/2010	210	216	75	2010		MF	e/f	0
22/10/2010	211	250	115	2009		RU	e/f	1
22/10/2010	212	242	98.5	2009		RU	e/f	0
22/10/2010	213	237	95	2009		RU	e/f	0
22/10/2010	214	144	20	2010		RU	e/f	0
22/10/2010	215	138	17	2010		RU	e/f	1
22/10/2010	216	246	108	2009		RU	e/f	2
22/10/2010	217	203	63	2010		RU	e/f	2
22/10/2010	218	97	6	2010		RU	e/f	0
22/10/2010	219	111	9.4	2010		RU	e/f	1
22/10/2010	220	248	120	2009		RU	e/f	1
24/11/2010	221	725	3260	2006	F	MF	e/f	0
24/11/2010	222	810	4580	2006	F	MF	e/f	0
24/11/2010	223	585	1600	2008	M	MF	e/f	0
24/11/2010	224	360	145	2009	F	MF	e/f	0
24/11/2010	225	420	480	2009	M	MF	e/f	0
24/11/2010	226	419	640	2009	F	MF	e/f	0
24/11/2010	227	482	1800	2008	M	MF	e/f	0
24/11/2010	228	444	650	2009	F	MF	e/f	0
24/11/2010	229	367	376	2009	M	MF	e/f	0
24/11/2010	230	700		2004	M	MF	e/f	0
24/03/2011	241	127		2010		RU	e/f	0
24/03/2011	242	136	16.3	2010		RU	e/f	0
24/03/2011	243	338	306	2009	M	RU	e/f	0
24/03/2011	244	213	74.5	2010		RU	e/f	0
24/03/2011	245	234	108	2009		RU	e/f	1
24/03/2011	246	113	10	2010		RU	e/f	1
24/03/2011	247	118	12.7	2101		FR	e/f	0
15/06/2011	249	125	41.4	2010		RU	fn	0
15/06/2011	250	178	44.4	2010		RU	fn	0
17/06/2011	251	227	93	2010		FR	fn	0
25/06/2011	252	276	168.6	2010		RU	fn	0
27/06/2011	253	251	116.2	2010		RU	fn	0
27/06/2011	254	218	69.3	2010		RU	fn	0
04/07/2011	255	231	95.9	2010		RU	e/f	1
04/07/2011	256	234	101.4	2010		RU	e/f	0

04/07/2011	257	297	197	2010	RU	e/f	1
18/07/2011	258	149	26.5	2010	FR	fn	0
20/07/2011	760	71	2.8	2011	RU	fn	0

Sex: M=male, F=female, Site: FR=Flood relief, RW=Railway ditch, RU= Rushton ditch, Capture methods: e/f=electric fishing, a=angling, fn=fyke netting.

APPENDIX II

Table of dates of tracking sessions and number of detected pike in each ditch during the tracking surveys

Tracking survey	Date of tracking	Rushton	Flood relief	Railway
Spring 2009	14/03/2009	8	15	10
	23/03/2009	6	19	10
	30/03/2009	11	18	9
	02/04/2009	6	17	3
	06/04/2009	6	20	8
	09/04/2009	8	17	9
	11/04/2009	8	17	6
	14/04/2009	9	18	8
	16/04/2009	8	17	9
	18/04/2009	9	16	8
	20/04/2009	8	17	7
	22/04/2009	5	14	7
	26/04/2009	10	15	5
	02/05/2009	7	18	5
	04/05/2009	8	16	5
	19/05/2009	6	13	5
	31/05/2009	6	11	4
Spring 2010	11/03/2010	20	4	2
	07/04/2010	11	10	2
	12/04/2010	20	8	2
	14/04/2010	16	7	1
	18/04/2010	20	6	2
	21/04/2010	16	3	1
	23/04/2010	7	8	2
	25/04/2010	7	4	2
	27/04/2010	9	5	3
	01/05/2010	4	5	2
	11/05/2010	4	7	0
	14/05/2010	8	5	3
	27/05/2010	8	4	2

Winter 2010/2011	05/01/2011	11	2
	25/01/2011	14	3
	27/01/2011	13	4
	29/01/2011	16	2
	30/01/2011	17	4
	05/02/2011	18	5
	07/02/2011	20	4
	09/02/2011	16	4
	14/02/2011	18	2
	17/02/2011	12	2
	05/03/2011	19	4
	08/03/2011	19	4

APPENDIX III

FULL OUTPUTS OF GLMs AND GLMMs FROM CHAPTER 5

Table A3-5.1. Results of GLMs on the effects of capture date, year (2009, 2010, 2011) and habitat (river/ditch) on the FL and TP of pike of ages 0+ to 2+.

Age	Parameter	Source of variation	SS	df	F	P
0+	FL	Intercept	314436.90	1	331.04	**<0.0001**
		Capture date	2378.45	1	2.50	0.118
		Year	3531.67	1	3.72	0.058
		Habitat	27243.23	1	28.68	**<0.0001**
		Year x Habitat	11873.83	1	12.50	**0.001**
		Error	63639.03	67		
	TP	Intercept	131.92	1	793.31	**<0.0001**
		Capture date	0.36	1	2.17	0.146
		Year	0.34	1	2.06	0.156
		Habitat	5.41	1	33.12	**<0.0001**
		Year x Habitat	0.79	1	4.76	**0.033**
		Error	11.47	69		
1+	FL	Intercept	392509.93	1	135.39	**<0.0001**
		Capture date	17971.22	1	6.20	**0.015**
		Year	40950.04	2	7.07	**0.001**
		Habitat	66174.32	1	22.84	**<0.0001**
		Year x Habitat	12036.82	2	2.08	0.132
		Error	246238.67	85		
	TP	Intercept	75.10	1	547.00	**<0.0001**
		Capture date	0.01	1	0.05	0.819
		Year	0.25	2	0.90	0.410
		Habitat	2.48	1	18.05	**<0.0001**
		Year x Habitat	1.63	2	5.92	**0.004**
		Error	11.53	84		

2+	FL	Intercept	164498.12	1	52.59	**<0.0001**
		Habitat	8145.05	1	2.60	0.135
		Capture date	5022.85	1	1.61	0.231
		Error	34407.62	11		
	TP	Intercept	165363.84	1	57.22	**<0.0001**
		Capture date	5086.42	1	1.76	0.209
		Habitat	91944.03	1	31.82	**<0.0001**
		Error	34679.17	12		

Table A3-5.2. Results of GLMs on the effects of capture date, age (in summer and autumn 2010: 0+ to 2+: in 2011: 1+ to 2+) and dispersal status (stayer/disperser) on the FL and TP of pike sampled in summer 2010, autumn 2010 and summer 2011.

Period	Parameter	Source of variation	SS	df	F	P
Summer 2010	TP	Intercept	5.87	1	71.86	**<0.0001**
		Capture date	0.32	1	3.92	**0.06**
		Age	1.33	2	8.15	**0.0013**
		Dispersal status	1.23	1	15.12	**0.0004**
		Age x dispersal status	0.02	2	0.12	0.89
		Error	2.78	34		
	FL	Intercept	3151.29	1	1.89	0.18
		Capture date	3202.70	1	1.93	0.17
		Age	297821.33	2	89.51	**<0.0001**
		Dispersal status	2272.62	1	1.37	0.25
		Age x dispersal status	5458.55	2	1.64	0.21
		Error	53235.78	32		
Autumn 2010	TP	Intercept	0.03	1	0.48	0.50
		Capture date	0.01	1	0.13	0.72
		Age	0.74	2	5.19	**0.013**
		Dispersal status	0.11	1	1.57	0.22
		Age x dispersal status	0.36	2	2.50	0.10
		Error	1.78	25		
	FL	Intercept	992.82	1	0.16	0.69
		Capture date	2661.67	1	0.42	0.52
		Age	53600.47	2	4.26	**0.026**
		Dispersal status	3036.83	1	0.48	0.49
		Age x dispersal status	7039.23	2	0.56	0.58
		Error	157404.44	25		
Summer 2011	TP	Intercept	4.42	1	26.40	**<0.0001**
		Capture date	0.02	1	0.11	0.74
		Age	0.04	1	0.21	0.65
		Dispersal status	0.01	1	0.08	0.78
		Age x dispersal status	0.02	1	0.13	0.72
		Error	3.18	19		
	FL	Intercept	19761.73	1	10.38	**0.0045**
		Capture date	1277.46	1	0.67	0.42
		Age	7099.29	1	3.73	0.07
		Dispersal status	15.48	1	0.01	0.93
		Age x dispersal status	1440.37	1	0.76	0.40
		Error	36164.60	19		

Table A3-5.3. Results of GLMs on the effects of age, TP, FL and interactions terms with age on the timing of dispersal of pike captured in the fyke nets in 2010 (including separately for summer and autumn 2010) and summer 2011.

Period	Source of variation	SS	df	F	P
2010	Intercept	955.27	1	0.69	0.416
n=32	Age	49.03	2	0.02	0.983
	TP	1445.41	1	1.04	0.319
	FL	11406.24	1	8.18	**0.009**
	Age x TP	721.41	2	0.26	0.774
	Age x FL	1619.37	2	0.58	0.567
	Error	32056.51	23		
Summer 2010	Intercept	1078.98	1	2.89	0.123
n=18	Age	1029.98	2	1.38	0.300
	TP	586.14	1	1.57	0.242
	Length/mm	850.76	1	2.28	0.165
	Age x TP	890.97	2	1.19	0.347
	Age x FL	1336.49	2	1.79	0.222
	Error	3360.33	9		
Autumn 2010	Intercept	287.85	1	1.48	0.277
n=14	Age	254.64	2	0.66	0.558
	TP	0.35	1	0.00	0.968
	FL	231.94	1	1.20	0.324
	Age x TP	95.81	2	0.25	0.790
	Age x FL	183.19	2	0.47	0.649
	Error	969.69	5		
Summer 2011	Intercept	38.75	1	0.26	0.627
n=13	Age	18.63	2	0.06	0.939
	TP	0.91	1	0.01	0.940
	FL	1.29	1	0.01	0.929
	Age x FL	88.50	2	0.30	0.751
	Error	885.66	6		

Table A3-5.4. Results of a GLM on the effects of FL, day of capture, change in TP, age, dispersal status (recaptured in ditch or river), and the interactions age x dispersal status on the specific growth rate of pike initially captured in the ditch.

Parameter	Source of variation	SS	df	F	P
SGR	Intercept	0.12	1	25.05	**<0.0001**
	FL	0.05	1	11.41	**0.002**
	Day of capture	0.04	1	7.36	**0.010**
	Change in TP	0.00	1	0.88	0.354
	Age	0.00	1	0.51	0.478
	Dispersal status	0.02	1	4.56	**0.040**
	Age x Dispersal status	0.00	1	0.28	0.603
	Error	0.17	36		

* Day of capture was log-transformed.