

UNIVERSITY OF SOUTHAMPTON

COMPETITIVE INTERACTIONS IN STREAM FISH
COMMUNITIES

Andrew John Henry Davey

Thesis submitted for the degree of Doctor of Philosophy

Biodiversity and Ecology Division
School of Biological Sciences
Faculty of Science

August 2003

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

BIODIVERSITY AND ECOLOGY DIVISION

Doctor of Philosophy

COMPETITIVE INTERACTIONS IN STREAM FISH
COMMUNITIES

by Andrew John Henry Davey

The aim of this thesis was to investigate the causes and consequences of competitive interactions in stream fish. Two small benthic fish, bullheads Cottus gobio and stone loach Barbatula barbatula, were used as a model system. The research combined manipulative field and laboratory experiments with field surveys to examine the biological mechanisms underlying intraspecific and interspecific interactions.

Growth in body size of adult bullheads was negatively density dependent. Individuals grew faster when densities of invertebrate prey were experimentally elevated above ambient levels, indicating that bullheads were food limited. Parallel dietary shifts were observed in response to manipulation of both bullhead density and resource availability, suggesting that exploitation competition for preferred prey (Gammarus pulex) was the primary mechanism responsible for density dependent growth. Evidence was sought, but not found, for interference competition. Density dependent growth at the adult stage may potentially regulate bullhead populations if it affects fecundity and survival.

Habitat use of bullheads was strongly influenced by the availability of shelter. Occupation of shelters was density dependent as a result of both exploitation and interference competition and individual shelter use was positively correlated with body size and movement rate. Shelter use did not affect individual growth in body size, but there was some evidence that unsheltered fish attempted to emigrate. In the field, larger fish utilised coarser substrates. Laboratory experiments suggested that this microhabitat partitioning was caused by intraspecific competition between size classes and that the strength of competition may be modulated by light intensity. Thus, competition for shelter appears to drive the spatial distribution of fish in the field.

There was little evidence for interspecific competition between bullheads and stone loach. Habitat and dietary partitioning mediated by behavioural and morphological differences appeared to moderate any potential competitive interactions, whilst growth of stone loach was enhanced by bullheads. The mechanism underlying this facilitation is unclear. Contrasting foraging behaviours resulted in different contributions by each predator species to top-down effects on community structure. Bullheads and stone loach generally functioned independently, with combined effects simply the sum of the impacts of the component species in isolation.

The results are discussed in a broader context with reference to the regulation of population size, maintenance of species diversity and structure of stream ecosystems.

CONTENTS

ABSTRACT	ii
CONTENTS	iii
LIST OF TABLES	vi
LIST OF FIGURES	vii
LIST OF PLATES	viii
ACKNOWLEDGEMENTS	ix
1 GENERAL INTRODUCTION	1
1.1 INTRODUCTION	1
1.2 COMPETITION: THEORETICAL BACKGROUND	2
1.2.1 Definitions	2
1.2.2 Intraspecific competition	3
1.2.3 Interspecific competition	4
1.3 COMPETITION IN STREAM FISH	5
1.3.1 Introduction	5
1.3.2 Intraspecific competition	6
1.3.3 Interspecific competition	10
1.4 EXPERIMENTAL APPROACH	14
1.5 MODEL SYSTEM	15
1.5.1 Species	16
1.5.2 Chalk streams	18
1.5.3 Advantages of this model system	20
1.6 AIMS AND OBJECTIVES	21
2 MECHANISMS OF DENSITY DEPENDENCE IN BULLHEADS	22
2.1 ABSTRACT	22
2.2 INTRODUCTION	23
2.3 METHODS	25
2.3.1 Study site	25
2.3.2 Experimental enclosures	26
2.3.3 Experimental design and protocol	26
2.3.4 Data collection	30
2.3.5 Statistical analysis	30
2.4 RESULTS	31
2.4.1 Experiment 1: testing for density dependence	31
2.4.2 Experiment 2: distinguishing exploitation and interference competition	33
2.5 DISCUSSION	36
2.5.1 Timing of density dependence in the life cycle	37
2.5.2 Mechanisms of density dependence	38
2.5.3 Implications for population dynamics	39
2.5.4 Conclusions	40

3	MODELLING DYNAMICS OF SHELTER USE IN BULLHEADS: THE EFFECT OF INTRASPECIFIC COMPETITION	41
3.1	ABSTRACT	41
3.2	INTRODUCTION	42
3.3	METHODS	44
3.3.1	Markov chain model of shelter use dynamics	44
3.3.2	Field experiment	47
3.3.3	Statistical analysis	49
3.4	RESULTS	51
3.4.1	Strength of competition	51
3.4.2	Individual-level responses	51
3.4.3	Population-level responses	57
3.5	DISCUSSION	59
3.5.1	Behavioural mechanisms of shelter use	59
3.5.2	Consequences for population-level processes	61
3.5.3	Conclusions	63
4	PATTERNS AND PROCESS OF MICROHABITAT SELECTION IN A CHALK STREAM FISH COMMUNITY	64
4.1	ABSTRACT	64
4.2	INTRODUCTION	65
4.3	METHODS	67
4.3.1	Field survey	67
4.3.2	Laboratory experiment	70
4.4	RESULTS	73
4.4.1	Field survey	73
4.4.2	Laboratory experiment	80
4.5	DISCUSSION	82
4.5.1	Interspecific microhabitat partitioning	82
4.5.2	Ontogenetic habitat shifts in bullheads	84
4.5.3	Conclusions	86
5	INTERSPECIFIC INTERACTIONS BETWEEN STONE LOACH AND BULLHEADS	87
5.1	ABSTRACT	87
5.2	INTRODUCTION	88
5.3	METHODS	89
5.3.1	Study site	89
5.3.2	Experimental enclosures	89
5.3.3	Experimental design	90
5.3.4	Experimental protocol	90
5.3.5	Statistical analysis	92
5.4	RESULTS	93
5.4.1	Stone loach	93
5.4.2	Bullheads	94
5.5	DISCUSSION	96

6	CONTRASTING AND ADDITIVE EFFECTS OF ECOLOGICALLY SIMILAR PREDATORS	99
6.1	ABSTRACT	99
6.2	INTRODUCTION	100
6.3	METHODS	102
	6.3.1 Study site	102
	6.3.2 Experimental enclosures	102
	6.3.3 Experimental design	102
	6.3.4 Experimental protocol	103
	6.3.5 Statistical analysis	104
6.4	RESULTS	105
	6.4.1 Invertebrates	105
	6.4.2 Epilithic algae	109
	6.4.3 Fish diets	110
6.5	DISCUSSION	110
	6.5.1 Predator effects	110
	6.5.2 Contrasting effects of similar predators	112
	6.5.3 Multiple predator effects	114
	6.5.4 Conclusions	115
7	GENERAL DISCUSSION	116
7.1	INTRODUCTION	116
7.2	LIMITATIONS OF PRESENT STUDY	116
7.3	SYNTHESIS OF MAIN FINDINGS	118
	7.3.1 Intraspecific competition among bullheads	118
	7.3.2 Interspecific competition between bullheads and stone loach	120
7.4	IMPLICATIONS FOR STREAM FISH ECOLOGY	121
	7.4.1 Intraspecific competition	121
	7.4.2 Interspecific competition	124
7.5	WIDER PERSPECTIVES	126
7.6	CONCLUDING REMARKS	127
	APPENDIX A	129
	REFERENCES	130

LIST OF TABLES

2.1	Prey consumption of bullheads in experiment 1	33
2.2	Prey consumption of bullheads in experiment 2	33
3.1	Markov chain state space for $K = 2$ and $S = 4$	46
3.2	Results of GLM for mean probability of shelter use, growth in mass, growth in TL and movement rate of bullheads	56
4.1	Modified Wentworth scale for stream substratum classification	69
4.2	Results of principal components analysis of microhabitat availability in the Brandy Stream	75
4.3	ANOVA of arcsine-transformed proportion of juvenile bullheads occupying cobbles in laboratory aquaria	82
4.4	ANOVA of arcsine-transformed proportion of adult bullheads occupying cobbles in laboratory aquaria	82
5.1	Prey consumption of stone loach and bullheads held in enclosures with and without heterospecifics	95
6.1	Two-way ANCOVA of log-transformed invertebrate densities in cage enclosures stocked with and without bullheads and stone loach	106
6.2	Repeated-measures two-way ANOVA of chlorophyll-a biomass density of epilithic algae in cage enclosures stocked with and without bullheads and stone loach	110
6.3	Dietary composition of bullheads and stone loach	111

LIST OF FIGURES

2.1	Experimental design to separate the effects of exploitation and interference competition	28
2.2	Relationship between stocking density of bullheads and their subsequent performance	32
2.3	Growth in mass and TL of bullheads during experiment 2	34
2.4	Prey consumption of bullheads in experiment 2	35
3.1	Flow-through stream enclosures used to experimentally manipulate shelter density and fish density <i>in situ</i>	48
3.2	Mean proportion of bullheads occupying shelter and mean proportion of shelters occupied as a function of fish density and shelter density in cage enclosures	52
3.3	Duration of shelter occupation and instantaneous probability of departure from shelter of individually-marked bullheads in cage enclosures.	53
3.4	Longitudinal distribution of sheltered and unsheltered bullheads in cage enclosures.	53
3.5	Probability of shelter use of large bullheads relative to that of smaller bullheads as a function of shelter availability	54
3.6	Probability of movement of sheltered and unsheltered bullheads in cage enclosures.	55
3.7	Change in number of bullheads occupying shelter over time	55
3.8	Mean growth in mass and TL of bullheads stocked into enclosures at a range of densities under high and low shelter availability	57
3.9	Mean movement rate of bullheads in cage enclosures as a function of fish density and shelter density	58
4.1	Experimental design used to investigate microhabitat use of juvenile and adult bullheads in relation to light intensity, fish density and size-class composition	72
4.2	Availability of PCA 1 habitat in the Brandy Stream, and habitat use and habitat preference of bullheads and stone loach	76
4.3	Availability of PCA 2 habitat in the Brandy Stream, and habitat use and habitat preference of bullheads and stone loach	77

4.4	Availability of PCA 3 habitat in the Brandy Stream, and habitat use and habitat preference of bullheads and stone loach	78
4.5	Mean size of substrate used by juvenile and adult bullheads along a shade gradient	79
4.6	Mean light intensity in laboratory aquaria and on the Brandy Stream	80
4.7	Mean habitat use of juvenile and adult bullheads held in laboratory tanks under three different stocking conditions crossed with two levels of light intensity	81
5.1	Growth in body size of stone loach and bullheads alone and with heterospecifics	94
6.1	Densities of macroinvertebrates in cage enclosures stocked with and without bullheads and stone loach	108
6.2	Mean chlorophyll-a biomass density of epilithic algae in cage enclosures stocked with and without bullheads and stone loach	109

LIST OF PLATES

1	Study organisms: bullheads and stone loach	17
2	Cage enclosures on the Brandy Stream	27

ACKNOWLEDGEMENTS

This project was funded by a Fisheries Society of the British Isles Studentship. I would like to thank my supervisors Patrick Doncaster, Steve Hawkins and George Turner for their help and guidance. This work would not have been possible without the support of Winchester College, who kindly gave me permission to work on the River Itchen. Bill Beaumont, Simon Cain and the Forestry Commission also provided access to field sites. I am particularly grateful to Tim Ball, Nicky Barson, Sarah Crofts, Jean Lou Dorne, James Fraser, Mairi Knight, Steve Law, Nigel Massen, Ole Seehausen, Alan Smith and Nick Smith who all gave up their time to help me in the field. Thanks also to Phil Belfield, Terry Langford, Alex McCormac, Mark Sankey and Richard Thompson for loan of equipment, Tas Crowe and Paula Moschella for help and advice, James Peat and Pisces Conservation for photos and Rick Trenchard for constructing fieldwork equipment. The Markov chain modelling work was carried out in collaboration with Owen Jones (Faculty of Mathematical Studies). Constructive comments from Jeremy Greenwood greatly improved earlier versions of the manuscript. Finally, I would like to thank Kirsty Greenwood for her unfailing support and encouragement.

- 1 -

GENERAL INTRODUCTION**1.1 INTRODUCTION**

Attempts to explain the distribution and abundance of species have been, and continue to be, a central theme in ecology. Competition is a fundamental process shaping ecological communities (Elton 1927; Nicholson 1933; Hutchinson 1957; Connell 1961; Tilman 1982; Law & Watkinson 1989). Competitive interactions within and between species for resources in limited availability can act to regulate population abundance (Murdoch 1994), limit species diversity (MacArthur & Levins 1967) and modify trophic interactions (Sih *et al.* 1998). Since the effects of competition are manifested at the individual level, the exact consequences for higher levels of ecological organisation will depend upon the mode, strength and symmetry of competition (Keddy 1989; Sutherland 1996). In stream fish, competition for food, shelter and foraging space has the potential to influence spatial distribution of animals (Fraser & Sise 1980), population dynamics (Elliott 1985) and community structure (Baltz *et al.* 1982) via effects on habitat use, growth, fecundity and survival of individual fish. Scientific understanding of competition in this system is, however, surprisingly cursory due to a lack of robust empirical evidence from field experiments (Connell 1983; Schoener 1983; but see Le Cren 1965; Fausch & White 1981; Resetarits 1997; Jenkins *et al.* 1999).

The aim of this thesis is to investigate the processes of competition acting to structure stream fish communities. Two small benthic fish species in chalk streams, bullheads *Cottus gobio* and stone loach *Barbatula barbatula*, were used as a model system to test for intraspecific and interspecific competition amongst adult fish and elucidate the underlying biological mechanisms. This chapter begins by reviewing the theoretical background to intraspecific and interspecific competition, critically evaluating the evidence for competition in stream fish across multiple scales of organisation, highlighting key research priorities and describing the shortcomings of descriptive studies and natural experiments. I then describe the benefits of adopting an experimental approach, introduce the model system and set out in detail the objectives of this study.

1.2 COMPETITION: THEORETICAL BACKGROUND

1.2.1 Definitions

Competition may be defined as the interaction between individuals in which one organism has a negative effect on another by consuming, or controlling access to, a resource that is limited in availability (Keddy 1989). In the strictest sense, competition causes the population growth of one or all species involved to be adversely affected as a consequence of reduced individual fitness (number of offspring produced that later reach reproductive maturity) (Law & Watkinson 1989). In practice, fitness is difficult to measure directly, so resource use, growth in body size, reproductive output or survival are more often used as proxy measures indicating individual performance (MacNally 1983). Since the effects of competition are manifested at the individual level (Keddy 1989; Sutherland 1996), the exact consequences for population dynamics and community structure will depend upon the mode (Fretwell & Lucas 1970; Fretwell 1972; Doncaster 1999), strength (Hassell *et al.* 1976; Roughgarden 1979) and symmetry (Lomnicki 1978; Persson 1985) of competition.

Competition may occur through a variety of mechanisms (Schoener 1983), which can be broadly grouped into two basic modes, exploitation and interference (Park 1962).

Exploitation competition (also known as scramble competition, Nicholson 1954) is an indirect process in which individuals affect others by reducing the availability of resources through consumption. Interference competition (or contest competition, Nicholson 1954) describes direct, behavioural interactions between individuals that reduce the gain of resources independently of changes in resource density. The strength, or intensity, of competition refers to the sum effects of all competitors on the performance of a population or individual (Keddy 1989). Although competing individuals may have equal effects on each other, competitive interactions may be asymmetric as a result of size or species-specific differences in competitive ability.

Competitive interactions are classified as intraspecific or interspecific, according to whether the competing individuals are conspecifics or heterospecifics. This simple classification has dominated the study of competition to date and shaped the development of theoretical models of competition.

1.2.2 Intraspecific competition

Given unlimited resources, a population can have a constant growth rate per capita, yielding exponential growth. In nature, however, populations do not grow indefinitely. Thomas Malthus was one of the first to propose that competition for limited resources is an important force checking the growth of animal and plant populations (Malthus 1798). The concept of competition was later developed by Charles Darwin, who identified it as a crucial process driving evolution through natural selection (Darwin 1859). In ecological time, intraspecific competition for limiting resources causes individual fitness, per capita growth rate and hence overall population growth rate, to decline as population density increases. Negative density dependence in per capita demographic rates thus results in fast population growth at low densities and slow or negative population growth at high densities. The outcome is that fluctuations in population abundance are bounded and population size is stabilised or regulated (Nicholson 1933; Murdoch 1994). For continuously breeding populations, this negative feedback is modelled deterministically by the logistic growth equation:

$$\frac{dN}{dt} = rN \left(\frac{K - N}{K} \right) \quad (1.1)$$

where N = population size, t = time, r = intrinsic per capita rate of population growth and K = maximal value of N . In this model, K is the population size at which the environment becomes saturated with organisms and population growth is zero. This equilibrium density about which the population is regulated is known as the carrying capacity.

This simple model of intraspecific competition assumes symmetrical interactions amongst individuals in a homogeneous population. In practice, competitive ability may be a function of, for example, age or body size (Connell 1983; Persson 1985), leading to highly asymmetrical interactions between age- or size-classes (Schoener 1983). Strong intraspecific competition in size-structured populations may limit recruitment of juveniles to the adult population. This process is particularly important in organisms which change markedly size during ontogeny, such as fish (Werner & Gilliam 1984), molluscs (Boaventura *et al.* 2003) and other animals with indeterminate growth.

The extent to which population abundance is determined by intraspecific competition has been the subject of considerable debate (Andrewartha & Birch 1954; Nicholson 1954; Turchin 1999). Although competition can strongly influence population size, competition will be sporadic or absent if population growth is checked by periodic bouts of density independent mortality (Wiens 1984; DeAngelis & Waterhouse 1987). Competition is therefore predicted to be more pervasive in stable environments with low stochastic disturbance events (Wiens 1977), and in *K*-selected species that have low fecundity and high survival (MacArthur & Wilson 1967; Pianka 1970).

1.2.3 Interspecific competition

In addition to competition from conspecifics, heterospecifics can also have a negative effect on individual performance. The effect of interspecific competition on population growth is commonly represented by the Lotka-Volterra models (Volterra 1926; Lotka 1932), which extend the logistic growth equation to consider the growth of two competing species (1 and 2) by incorporating competition coefficients (α) that measure the per capita competitive effect of heterospecifics relative to the per capita effect of conspecifics:

$$\frac{dN_1}{dt} = r_1 \cdot N_1 \left(\frac{K_1 - N_1 - \alpha_{12}N_2}{K_1} \right) \quad (1.2)$$

$$\frac{dN_2}{dt} = r_2 \cdot N_2 \left(\frac{K_2 - N_2 - \alpha_{21}N_1}{K_2} \right) \quad (1.3)$$

where α_{12} = per capita impact on growth of species 1 by species 2, relative to impact of 1 on itself, and α_{21} = per capita impact on growth of species 2 by species 1, relative to impact of 2 on itself.

The realised growth rate of each species is then determined both by its own population size and that of the other species. These coupled equations predict that interspecific competition can result in one species competitively excluding the other. Consequently interspecific competition is thought to be an important mechanism limiting local (alpha) species diversity (Keddy 1989). Co-existence is possible, however, when intraspecific

competition is stronger than interspecific competition (ie: $\alpha_{12}, \alpha_{21} < 1$), and when $\alpha_{21} > 1$ if $K_2 \gg K_1$ (or vice versa) (Gause 1934; Doncaster *et al.* 2003).

Early experimental studies of interspecific competition between congeners confirmed that competition from one species can drive the other to extinction (Tansley 1917; Gause 1934). It was therefore postulated that two species cannot co-exist in nature without some difference in resource use between them - the competitive exclusion principle (Gause 1934; Hardin 1960). From this idea arose the theory of limiting similarity, which proposed that species can co-exist up to some critical level of similarity, beyond which competitive exclusion occurs as a result of intense interspecific competition (MacArthur & Levins 1967; Abrams 1983). Interspecific competition is intuitively expected to be most severe between closely related species because of their greater similarity in resource use (Darwin 1859), but despite mathematical attempts to relate ecological similarity (niche overlap) to intensity of interspecific competition (MacArthur & Levins 1967), there appears to be no definitive relationship between resource use and competitive strength (Colwell & Futuyma 1971; Sale 1974; Keddy 1989).

On ecological timescales, (i.e. within a single generation), species that engage in interspecific competition are predicted to diverge in resource use (Lack 1946). Dynamic resource partitioning in response to bouts of severe competition may facilitate species co-existence (Schoener 1986). Over evolutionary timescales, interspecific competition may result in morphological character displacement (Schluter & McPhail 1992), but since the evolutionary effect of interspecific competition (the ghost of competition past, Connell 1980) cannot be observed directly, its influence in shaping communities cannot be proved or disproved.

1.3 COMPETITION IN STREAM FISH

1.3.1 Introduction

Competition has long attracted the attention of fish biologists attempting to explain observed patterns of population abundance and community composition (Lindroth 1955; Larkin 1956; Chapman 1966). Density dependent responses are common in aquaculture studies, and anglers frequently perceive interspecific competition to be a problem (Mann *et al.* 1989). Furthermore, the intensive habitat manipulation and culling operations often carried out by fishery managers to maximise the production of target species are underpinned by the notion that competition for resources is limiting local carrying capacity (Larkin 1956; Riley & Fausch 1995). Despite this, knowledge of the influence of competition in structuring wild fish communities is limited. This is due in a large part to a lack of robust empirical evidence from field experiments (Connell 1983; Schoener 1983).

1.3.2 Intraspecific competition

1.3.2.1 Strength and timing of competition

Compared to other animal groups, relatively little is known about the role of intraspecific competition in fish population dynamics (Sinclair 1989; Shepherd & Cushing 1990). The majority of empirical studies on intraspecific competition in stream fish have employed natural or manipulative experiments to investigate individual-level responses to changes in fish density. A variety of response variables have been used as indicators of performance, with the most compelling evidence for competition coming from studies that either measure changes in fitness directly by monitoring fecundity and survival, or parameters that are closely linked to these, such as growth rates or relative condition (Le Cren 1965, 1975; Fox 1978a; Harvey & Nakamoto 1997; Schlosser 1998; Armstrong *et al.* 1999; Jenkins *et al.* 1999; Jensen *et al.* 2000; Grenouillet *et al.* 2001; Keeley 2001; Matthews *et al.* 2001). Intraspecific competition may also affect the spatio-temporal distribution of individual fish through changes in emigration rate (Keeley 2001), habitat use (Heggenes 1988; Freeman & Stouder 1989; Greenberg *et al.* 1997; Mullen & Burton 1998; Bult *et al.* 1999) or temporal activity patterns (Alanara *et al.* 2001). The significance of these shifts in behaviour or resource use for population dynamics is, however, uncertain. At the population level, field studies have attempted to detect density dependence in demographic rates from repeated population surveys. If individuals are aged, then it is possible to follow

the fate of a particular cohort through time and to correlate survival or recruitment during a particular time increment to initial density. This approach has found evidence for intraspecific competition in a number of stream fish populations (Mortensen 1977a; Bohlin 1978; Elliott 1984, 1985; Solomon 1985; Crisp 1993; Elliott & Hurley 1998; Jonsson *et al.* 1998; Nordwall *et al.* 2001; Cattaneo *et al.* 2002). For example, dome-shaped stock-recruitment curves indicate strong density dependence in populations of migratory brown trout *Salmo trutta* in a Lake District stream (Elliott 1985).

Although intraspecific competition has been demonstrated clearly in some systems, however, competition is generally not thought to be an important and widespread process in stream fish populations. Firstly, competitive interactions are predicted to be weak in animals such as fish that display high fecundity and high mortality during early life stages (Sinclair 1989; Townsend *et al.* 2003). Secondly, the inherent variability and unpredictable nature of the lotic environment suggests that stochastic factors might have a strong, possibly overriding, influence on community structure (Starrett 1951; Le Cren 1965). Many fish species show high inter-annual variation in recruitment success and subsequent year class strength, which may be caused by relatively minor fluctuations in water temperature or discharge (Mills & Mann 1985; Coon 1987; Jensen & Johnsen 1999; Grenouillet *et al.* 2001; Nunn *et al.* 2003). Furthermore, extreme discharge events such as floods and droughts can have substantial negative impacts on fish. Floods (spates) can cause high mortality (John 1964; Hoopes 1975; Harrell 1978; Matthews 1986; Chapman & Kramer 1991), and may also have short-term sub-lethal effects by reducing foraging success (Hill & Grossman 1993), growth (Jensen & Johnsen 1999) or abundance of food (Kido 1996). Droughts adversely affect water quality through elevated water temperatures and reduced levels of dissolved oxygen and both high mortality and reduced growth rates have been reported in severe drought years (Brooker *et al.* 1977; Cowx *et al.* 1984; Elliott *et al.* 1997). Under some circumstances, therefore, high density independent mortality may limit fish populations below the level at which resources become limiting (Horwitz 1978; Grossman *et al.* 1982; Moyle & Vondracek 1985).

The stage in the life cycle at which competition occurs has important implications for the strength and nature of population regulation (Sinclair 1989). Theoretical studies suggest that if fish populations are regulated, it will be caused primarily by density dependent

mortality of young fish. For example, individual-based modelling of fish growth predicts that exploitation competition for prey resources will cause density dependent growth and mortality at a critical body-mass corresponding to the juvenile life stage (Cowan *et al.* 2000). It has also been suggested, however, that populations could be regulated at the adult stage via density dependence in individual growth rate (Shepherd & Cushing 1990). This mechanism is potentially very powerful because fecundity and survival are strongly correlated with body size in fish (Mann 1971; Sogard 1997). Sublethal effects of competition may therefore also influence population dynamics. Empirical studies support the prediction that intraspecific competition occurs almost exclusively at the early juvenile stage, with growth and survival of adult fish being density independent (Mortensen 1977b; Elliott 1985; Jonsson *et al.* 1998). The majority of work to date concerns salmonids; it is therefore difficult to assess the prevalence and timing of intraspecific competition in stream fish as a whole. This thesis aims to correct this bias by investigating intraspecific competitive interactions amongst adult fish (Chapters 2 to 4).

1.3.2.2 Mechanisms of intraspecific competition

Foraging space, food, and shelter are commonly cited as potential limiting factors for freshwater fish (Larkin 1956; Chapman 1966), but knowledge of the exact mechanisms by which intraspecific competition translates into density dependence in per capita demographic rates is limited.

Territorial competition for foraging space in drift-feeding species can be observed easily and directly and is therefore the best studied mechanism of competition in stream fish. Drift-feeding involves catching invertebrates as they drift downstream in the water column. Individual fish select optimal drift-feeding microhabitats by trading off prey encounter rate, foraging efficiency and energetic costs of holding position (Hill & Grossman 1993). This foraging strategy results in intense competition for the best drift-feeding stations. Interactions between conspecifics are often size-structured, with dominant fish displacing smaller individuals from preferred habitats (Greenberg *et al.* 1997; Jonsson *et al.* 1999; Vehanen *et al.* 1999), resulting in spatial segregation between size classes. Under the influence of this dominance hierarchy, subdominant individuals may suffer reduced foraging efficiency (Greenberg *et al.* 1997) or emigrate to avoid competition (Chapman 1962; Keeley 2001). Territorial behaviour among juveniles has been suggested to regulate

salmonid populations via density dependent mortality and emigration (Elliott 1985, 1990; Grant & Kramer 1990).

Availability of food may influence the severity of territorial competition by affecting territory size (Keeley 2000) and emigration rates (Chapman 1966; Keeley 2001), but there is limited evidence that stream fish compete for food directly. Density dependent mortality in juvenile fish is thought to involve an interaction between food supply and predation, whereby exploitation competition for food at high fish density reduces individual growth and prolongs the critical period during which fish are vulnerable to gape-limited predators (Sinclair 1989; Shepherd & Cushing 1990). However, there have been no empirical studies on stream fish that support this hypothesis. Stream fish can significantly reduce densities of invertebrate prey through predation (see Wooster 1994; Dahl & Greenberg 1996; Shurin *et al.* 2002 for reviews) suggesting that exploitation competition might be an important mechanism of intraspecific competition. Shadow competition has been shown in drift feeding salmonids (Elliott 2002) but to date there is little other evidence that stream fish are food limited (Boss & Richardson 2002) or that consumption of prey is density dependent (Forrester *et al.* 1994). The hypothesis that predation by fish results in exploitation competition for benthic invertebrate prey is tested experimentally in Chapter 2.

Shelter is important for many fish as a refuge from predation (Gregory & Griffith 1996b; MacKenzie & Greenberg 1998; Allouche 2002). Shelter use is commonplace amongst benthic species, but other species, such as Atlantic salmon, also utilise shelter (Cunjak 1988; Fraser *et al.* 1995). Supplementing shelter can increase individual growth and population density of fish in the field, suggesting that availability is limiting (Saunders & Smith 1962; Eklöv & Greenberg 1998), but knowledge of how intraspecific competition affects shelter use and how competition for shelter affects population level processes and spatial distribution of fish, is limited. Shelter use may be density dependent (Armstrong & Griffiths 2001) as a result of fish defending shelters against intruders (Gregory & Griffith 1996a; Mullen & Burton 1998). Interference competition for shelter could also occur as a result of aggressive or avoidance behaviours, but has not been examined to date.

Individual fish that fail to find a shelter are likely to be more vulnerable to predation and may suffer reduced somatic growth as a result of increased stress (Fischer 2000). Chapter

dynamics of bullheads and considers the individual and population-level consequences of density dependent shelter use. Chapter 4 goes on to examine the consequences of intraspecific competition for habitat use of fish in the field.

1.3.3 Interspecific competition

1.3.3.1 Individual level effects

The effects of interspecific competition at the individual level are highly variable. In some cases, fish have been reported to alter habitat use (Fausch & White 1981; Finger 1982; Fausch & White 1986; Kennedy & Strange 1986b; Rodriguez 1995; Taylor 1996), shelter use (Baltz *et al.* 1982; Greenberg 1988; Harwood *et al.* 2002) and foraging behaviour (Katano *et al.* 2000) in the presence of heterospecifics. These short-term behavioural changes may translate into reduced prey consumption (Dewald & Wilzbach 1992), growth (Dewald & Wilzbach 1992; Harvey & Nakamoto 1996) or survival (Le Cren 1965; Kennedy & Strange 1986a; Resetarits 1997). In contrast, other workers have found little or no evidence for interspecific competition (Schlosser & Toth 1984; Grossman & Boule 1991; Kocik & Taylor 1995; Grossman *et al.* 1998; Rincon & Grossman 1998; Glova 1999). The true prevalence of interspecific competition cannot be assessed because a bias towards the study of species that are likely to compete, and under-reporting of null results, mean that the frequency of competition is likely to be exaggerated to an unknown extent (Keddy 1989; Townsend *et al.* 2003).

Inconsistent effects of interspecific competition have been explained by variation in ecological similarity and evolutionary history. Firstly, interspecific competition is thought to be more common between closely related and morphologically similar species because of greater similarity in resource use (MacArthur & Levins 1967; Abrams 1983). Niche overlap is generally higher between congeneric or confamilial species pairs of fish (Ross 1986) and strong competition is frequently reported amongst ecologically similar species (Le Cren 1965; Fausch & White 1986; Kennedy & Strange 1986a). However, phylogenetic relatedness does not necessarily indicate strong competitive interactions (Schlosser & Toth 1984) and species with contrasting morphologies and distinct phylogenies may also show strong interspecific competition (Baltz *et al.* 1982; Resetarits 1995; Hesthagen & Heggenes 2003). The hypothesis that species with similar resource use engage in interspecific competition is tested in Chapter 5. Secondly, competition has been predicted

to be more intense among species that have evolved in allopatry than those with a long history of sympatry (Hairston 1980). Fine scale resource partitioning within guilds (Ross 1986; Winemiller 1991) has prompted the suggestion that co-existence of closely related species is the result of evolutionary divergence in response to past interspecific competition (but see Connell 1980 for a cautionary tale). In contrast, where species have been introduced recently to new environments, and have no history of co-evolution with the native fauna, strong competition is frequently the outcome (Ross 1991). For example, the introduction of brown trout has resulted in competitive displacement of native species in New Zealand (McIntosh *et al.* 1992), Australia (Ault & White 1994) and North America (Dewald & Wilzbach 1992).

1.3.3.2 Population and community level effects

Despite an abundance of experimental studies demonstrating effects of interspecific competition on individual fish, evidence that interspecific competition influences population dynamics and community structure is more equivocal. Negative covariation in the abundance or occurrence of pairs of species has been found in some studies (Andreasson 1969b; Baltz *et al.* 1982; Ault & White 1994; Fausch *et al.* 1994; McIntosh *et al.* 1994; Taylor 1996) but not others (Degerman & Sers 1993; Oberdorff *et al.* 1998; Jorgensen *et al.* 1999). Drawing conclusions from such studies is made difficult by potentially confounding effects of abiotic environmental variables on spatial variation in abundance (Underwood 1986) and low power of such techniques to detect subtle competitive interactions acting at a local scale (Fausch *et al.* 1994). Negative associations between species appear more likely to be detected using quantitative data from small sampling units (Baltz *et al.* 1982; Fausch *et al.* 1994; Taylor 1996), suggesting that the sensitivity of these tests may be dependent upon the spatial resolution of investigation.

Community structure may be influenced by diffuse competition as well as by pair-wise species interactions (Keddy 1989). Evidence for diffuse competition has been sought by regressing population abundance against local (alpha) species diversity, testing for a decoupling of total fish number or biomass from species diversity (density compensation *sensu* MacArthur *et al.* 1972), and seeking evidence for saturation in local-regional species richness relationships. Community and guild scale analyses such as these allow direct evaluation of the role of competition in community structuring which is difficult to

achieve using more conventional approaches (Naslund *et al.* 1998). They have, however, found little evidence for competitive structuring (Degerman & Sers 1993; Angermeier & Winston 1995; Hugueny & Paugy 1995; Taylor 1996; Oberdorff *et al.* 1998) which may be because there is none, because the approach lacks sufficient resolution, or because positive and negative interactions cancel each other out (Schluter 1984). Thus, although interspecific competition may influence performance of individual fish, there is limited evidence to suggest that interspecific competition is important at higher levels of ecological organisation.

Interspecific competition may affect not only the population dynamics of the competing species, but also have consequences for lower trophic levels. Predation by stream fish is important in structuring communities of benthic invertebrates and algae (Power 1992; Dahl & Greenberg 1996). Changes in habitat use, foraging behaviour or prey selection caused by heterospecifics may result in quantitative or qualitative changes in prey consumption and lead to non-additive multiple predator effects on lower trophic levels (Sih *et al.* 1998). The influence of interspecific competition on predation impacts of bullheads and stone loach is investigated in Chapter 6.

1.3.3.3 Mechanisms of interspecific competition

Interspecific competition proceeds by the same fundamental mechanisms as intraspecific competition. Drift-feeding species show a high similarity in microhabitat use (Heggenes *et al.* 1999) and interspecific competition for the best drift-feeding stations can be intense (Kalleberg 1958). Highly aggressive species such as brown trout displace subdominant species such as Atlantic salmon *Salmo salar*, grayling *Thymallus thymallus* and brook trout *Salvelinus fontinalis* from preferred foraging microhabitats (Kalleberg 1958; Jones 1975; Fausch & White 1981; Egglishaw & Shackley 1982; Kennedy & Strange 1982, 1986b; Rodriguez 1995; Greenberg 1999). Territorial competition for foraging space may reduce foraging efficiency. For example Dewald & Wilzbach (1992) showed that prey capture rates of both brook trout and brown trout were higher when kept alone than when together. Similarly, fish compete with heterospecifics for shelter, with the competitively superior species displacing the other from shelter (Baltz *et al.* 1982; Greenberg 1988; Harwood *et al.* 2002). Evidence for interspecific competition for food is less clear. High interspecific dietary overlap among stream fishes has led to speculation that species

compete for food (Hartley 1948; Maitland 1965; Mann & Orr 1969; Gray *et al.* 1997). No definitive relationship exists, however, between niche overlap and competitive strength (Colwell & Futuyma 1971; Sale 1974) and consequently, without some assessment of resource availability (or evidence for limitation), high niche overlaps do no more than indicate potential for competition (Prejs & Prejs 1987). Thus, although predation by stream fish is known to exert strong top-down effects on densities of benthic invertebrate prey (Wooster 1994; Dahl & Greenberg 1996), there is no experimental evidence that one species can affect the prey intake and performance of a sympatric predator species through exploitation competition.

Clearly, habitat and shelter use and foraging behaviour of fish can be affected by heterospecifics, but the consequences for individual growth, and in turn population dynamics, are frequently not known. Species may diverge in dietary composition during seasonal periods of food depression by shifting to under-utilised food sources or switching foraging tactics (Zaret & Rand 1971; Magalhães 1993; Gray *et al.* 1997; Nakano *et al.* 1999). These niche shifts have been suggested to moderate interspecific competition, at least in the short term, by partitioning resources between species, and could be an important mechanism of co-existence in stream fish (Nakano *et al.* 1999). The extent to which flexible behaviour is able to ameliorate interspecific competition remains largely unknown. Chapter 4 of this thesis explores the capacity for habitat partitioning to spatially segregate potential competitors whilst Chapter 5 describes exploitation competition for food amongst two benthic fish species and provides an experimental demonstration of resource partitioning.

A final point to note is that interspecific actions are not always negative (Connell 1983; Bertness & Callaway 1994; Bruno *et al.* 2003). Facilitation can occur, for example, when predator mediated changes in behaviour or microhabitat use of prey enhance the foraging efficiency of a second predator species by increasing prey availability (Matsuda *et al.* 1993; Sih *et al.* 1998). Enhanced growth or survival (Soluk & Collins 1988; Soluk 1993; Losey & Denno 1998; Eklov & van Kooten 2001) as a result of indirect trophic interactions can cancel out the effects of competition, or occur sequentially at different stages of a life cycle giving rise to complex size-structured interspecific interactions (Bruno *et al.* 2003).

1.4 EXPERIMENTAL APPROACH

The majority of studies of competitive interactions to date have attempted to infer competition from observed patterns of resource use in the field (MacArthur & Levins 1967) or exploited natural changes in the density of competitors in space or time to compare fitness under different competitive scenarios (natural experiments *sensu* Diamond 1986). Descriptive studies of resource partitioning and niche overlap are, at best, only partial tests of competition however because they cannot indicate whether shared resources are limiting nor assess the consequences for demographic parameters (Schoener 1986; Prejs & Prejs 1987). Natural experiments have also been criticised because they often lack controls for environmental variation and therefore cannot determine with certainty whether a niche shift or ecological release by a species is due to the absence of its competitor or simply an artefact of differences between streams or sites (Underwood 1986).

A lack of robust, empirical evidence from well designed field experiments has contributed to the prolonged debate about the importance of competition in structuring ecological communities (Schoener 1982; Underwood 1986). The shortcomings of descriptive approaches and natural experiments highlight the need for carefully designed experiments to provide more rigorous tests of competition and to elucidate the mechanisms involved (Colwell & Fuentes 1975; Bender *et al.* 1984; Gurevitch *et al.* 1992). This study therefore takes a largely experimental approach to the study of competitive interactions in stream fish, using cage enclosures to manipulate fish density, species composition and resource availability *in situ*.

Manipulative field experiments of competition involve directly removing or adding individuals, species or resources under natural or semi-natural conditions and determining the consequent changes in density, behaviour and performance of focal individuals (see Tansley 1917; Connell 1961; Abramsky *et al.* 1998 for examples). Manipulative experiments overcome the drawbacks of natural experiments by holding constant all extraneous variables except the factor of interest, and are therefore an efficient method of distinguishing cause and effect in complex ecological systems (Connell 1983; Gurevitch *et*

al. 1992). Experiments represent a shift from pattern- to process-orientated research, and focus on developing mechanistic models of competitive interactions. The fact that competition occurs between individuals and not populations suggests that research should concentrate on understanding small-scale processes before attempting to explain large-scale patterns and phenomena (Sutherland 1996). Indeed, knowing how competition occurs provides a better understanding of the factors affecting spatial and temporal variation in the strength of competition, and aids the development of predictive models. Manipulative experiments are generally considered to be the best way of testing suspected mechanistic interactions since they allow observations to be made at the individual level and can be used to identify both the critical limiting resource and the mode of competition (Schoener 1983).

Whilst competition may be demonstrated clearly under simplified laboratory conditions, experiments conducted in the field test whether competition operates in the presence of possibly overriding extrinsic factors (Schoener 1983). An experimental approach has been widely used in a variety of systems such as rocky shores (Connell 1961; Underwood 1978), terrestrial plants (Tansley 1917; Tilman 1982) and desert rodents (Mitchell *et al.* 1990; Abramsky *et al.* 1998) but less so in streams due to the practical difficulties involved (see reviews in Connell 1983; Schoener 1983). Field enclosures have been used widely in freshwater ecology to manipulate components of the stream environment *in situ* and are therefore ideally suited to investigate competitive interactions amongst small benthic fish.

1.5 MODEL SYSTEM

Many aspects of ecology are similar across species and environments, but certain organisms are much easier to study than others. For this reason scientists frequently test hypotheses using simple, idealized systems that are easily manipulated (Keddy 1989). Model systems can provide valuable insights into biological processes which may then be applied to a wide range of other systems (Rosenblueth & Wiener 1945). This study focuses on two small, benthic fish species, bullheads *Cottus gobio* and stone loach *Barbatula*

barbatula, in a southern English chalk stream to investigate the role of competition in structuring stream fish communities.

1.5.1 Species

1.5.1.1 Bullheads

The bullhead or Miller's thumb, *Cottus gobio* Linnaeus 1758 (Plate 1a), is a small benthic-dwelling sculpin widely distributed across Europe from Greenland and Arctic areas of Scandinavia in the north to northern Italy in the south and eastwards to the Black Sea and Russia (Mills & Mann 1983; Greenhalgh 1999). Bullheads are widespread and common across England and Wales, but rare in Scotland, and absent from Ireland (Maitland 1972). They prefer swift-flowing, well-oxygenated water and can attain high densities in shallow riffles (Mills & Mann 1983; Roussel & Bardonnnet 1997). The bullhead exhibits marked life history variation across its range, with reduced growth rates accompanied by increased longevity at higher latitudes. In the productive chalk streams of southern England, individuals grow rapidly (reaching 50 - 60 mm after one year), are short-lived (3 - 4 years), mature early and spawn several batches of eggs each year during a protracted spawning season February-June (Fox 1978a; Mills & Mann 1983). Bullheads are solitary, displaying aggressive behaviour towards conspecifics (Smyly 1957; Ladich 1989) and nocturnal, seeking the shelter of stones during the day and emerging to feed at night (Smyly 1957; Andreasson 1969a). Bullheads are visual, ambush predators and show a preference for large, active benthic macroinvertebrates such as *Gammarus pulex* (Smyly 1957; Welton *et al.* 1983). Studies have revealed high spatial and temporal variation in diet (Hartley 1948; Morris 1965; Mann & Orr 1969; Andreasson 1971; Abel 1973; Hyslop 1982; Welton *et al.* 1983; Copp *et al.* 1994), suggesting that the bullhead is a generalist predator that adopts a flexible, opportunistic foraging strategy in response to fluxes of key invertebrate groups.

1.5.1.2 Stone loach

The stone loach, *Barbatula barbatula* (Linnaeus 1758) (formerly *Noemacheilus barbatula*, Wheeler 1992) is a slender, bottom-dwelling fish, that inhabits a range of freshwater environments (Smyly 1955; Plate 1b). Stone loach occur sympatrically with bullheads across much of Europe from the Pyrenees to the Balkans and Russia, although they appear to be absent from northern areas, including much of Scandinavia and northern Scotland

Plate 1 Study organisms

(a) The bullhead *Cottus gobio*



Photo: J. Peat

(b) The stone loach *Barbatula barbatula*



Photo: Pisces Conservation

(Maitland 1972; Greenhalgh 1999). In streams, loach seek cover that provides visual isolation from predators (MacKenzie & Greenberg 1998), sheltering beneath stones, amongst vegetation, or even burying themselves in silt (Hyslop 1982). Stone loach generally inhabit deeper, depositional habitats (Prenda *et al.* 1997; MacKenzie & Greenberg 1998), and often show a preference for macrophytes where available (Hyslop 1982; Welton *et al.* 1983; Roussel *et al.* 1998). In the chalk streams of southern England, the loach is a fractional spawning species, laying several batches of eggs between late April and early August (Mills *et al.* 1983). Fish mature after one year and reach a maximum length of 120-150 mm after 4 years (Smyly 1955). Growth is concentrated in the period May-October (Mills *et al.* 1983). Stone loach are nocturnal or crepuscular (Welton *et al.* 1983; MacKenzie & Greenberg 1998; Fischer 2000) and are not territorial (Smyly 1955). In contrast to the bullhead, stone loach are active, tactile foragers that seek out prey using their barbels and are restricted to taking small prey species with low mobility (Smyly 1955; Welton *et al.* 1983). The diet is typically dominated by dipteran larvae such as chironomids (Hartley 1948; Smyly 1955; Maitland 1965; Welton *et al.* 1983; Rundle & Hildrew 1992), with caddisfly larvae and mayfly nymphs also common in spring and summer and crustaceans and amphipods becoming increasingly important during autumn and winter (Copp *et al.* 1994; Michel & Oberdorff 1995).

1.5.2 Chalk streams

Chalk streams are so-named because approximately 80 % of total annual discharge is derived from groundwater from Cretaceous chalk aquifers (Mann *et al.* 1989). The low contribution from runoff means that chalk streams have a stable hydrological regime relative to other river types and are rarely subject to floods or droughts that are common in many upland streams (Berrie 1992). Groundwater rises at a constant temperature of around 10°C throughout the year which confers high thermal stability, especially in the headwaters. Due to the underlying geology, chalk streams have low gradients and do not show the marked longitudinal gradient in physical conditions typical of most European rivers (Westlake *et al.* 1972). This combination of limited physiographic relief and hydrological stability produces a low energy environment and consequently pool-riffle development is limited. The stream bed is composed of flint gravels and cobbles, with areas of silt in the margins and where macrophytes promote sedimentation. Water quality

and clarity are generally good and concentrations of nitrates and phosphates are high (Westlake *et al.* 1972; Berrie 1992).

High concentrations of dissolved inorganic nutrients and good light penetration, allied to the stable flows and warm temperatures, result in high autochthonous (indigenous) primary production, up to 500 g/m² dry wt. (Westlake *et al.* 1972). This organic production is characterised by a summer bloom of emergent vegetation, in particular water crowfoot (*Ranunculus penicillatus*). In addition, chalk streams receive a high input of allochthonous (acquired) organic material from bankside trees, chiefly alder (*Alnus glutinosa*) and willow (*Salix* spp.) (Dawson 1976). The abundance of plants and detritus supports high secondary production of benthic macroinvertebrates (Westlake *et al.* 1972). Consequently, density, biomass and production of fish are also high (Mann 1971; Mann *et al.* 1989). Chalk streams support a relatively diverse fish fauna, including populations of brown trout and Atlantic salmon that are of great sporting value to anglers. Relative abundance varies spatially and temporally but in smaller chalk streams, the fish community is commonly dominated by bullheads and stone loach (Mann 1971).

In the UK, chalk streams are restricted to areas of southern and eastern England. The principle systems are found in Hampshire and Dorset and include the Rivers Itchen, Test, Meon, Frome and Avon (Mann *et al.* 1989). This project was conducted on the Brandy Stream, a side channel of the River Itchen in southern England (51°03'N; 1°19'W; altitude 30 m). The Itchen is fed by groundwater from the South Downs east of Winchester and flows 17 km before discharging into Southampton Water. At the study site, the stream flows across a wide floodplain of rough pasture and is bordered on one side by a mature hedgerow of bramble (*Rubus allegheniensis*), hawthorn (*Crataegus monogyna*), laurel (*Laurus nobilis*), sycamore (*Acer pseudoplatanus*) and ash (*Fraxinus excelsior*). The stream averages approximately 5 m in width and is generally shallow (< 0.40 m) and swift-flowing (> 0.15 m/s). Bullheads and stone loach are the numerically dominant fish species, with brown trout, Atlantic salmon, minnows (*Phoxinus phoxinus*) eels (*Anguilla anguilla*), brook lamprey (*Lampetra planeri*), three-spined stickleback (*Gasterosteus aculeatus*), grayling (*Thymallus thymallus*) and pike (*Esox lucius*) also present at low densities (A. Davey, *personal observation*; CEFAS, *unpublished data*).

1.5.3 Advantages of this model system

This model system is well suited to studies of competitive interactions in stream fish. Firstly, fish communities of small chalk streams are numerically dominated by just two benthic fish species, thus representing a comparatively simple system within which to explore competitive interactions. Bullheads and stone loach show a high degree of ecological similarity (both are small, benthic nocturnal predators of macroinvertebrates), and have long been considered as potential competitors (Welton *et al.* 1983). Secondly, both bullheads and stone loach attain high densities, providing an abundant source of experimental animals. Thirdly, the system is experimentally tractable. Both species are small-bodied, are thought to show high site fidelity and prey almost exclusively on benthic macroinvertebrates (Welton *et al.* 1983), which means that they are unlikely to be affected by confinement in enclosures. *In situ* experimental manipulations are further aided by the high hydrological stability and water clarity of chalk streams. Fourthly, chalk streams are characterised by low hydraulic disturbance and high productivity compared to other temperate river types. This suggests *a priori* that deterministic biotic factors such as competition should be relatively important in structuring these assemblages (Horwitz 1978; Schlosser 1982; Menge & Sutherland 1987).

1.6 AIMS AND OBJECTIVES

Intraspecific and interspecific competitive interactions can regulate population abundance, limit species diversity and modify trophic interactions. Understanding the importance of competition in contemporary fish assemblages has been constrained by a lack of robust empirical evidence concerning the underlying mechanisms. The aim of this thesis is to investigate the role of competition in structuring stream fish communities, using two small benthic fish species, bullheads *Cottus gobio* and stone loach *Barbatula barbatula*, in chalk streams as a model system.

Specifically, the objectives of this thesis are:

- (1) To investigate the mechanisms and consequences of intraspecific competition among bullheads. Adult fish density was experimentally manipulated in the field to test for intraspecific competition and assess its potential to regulate bullhead populations (Chapter 2). Subsequent experiments were performed to determine whether competition occurs for food or shelter and to partition the effects of exploitation and interference competition (Chapters 2 and 3). The influence of intraspecific competition on the spatial distribution of fish was also examined by combining a field survey of microhabitat use with laboratory experiments (Chapter 4).
- (2) To investigate the mechanisms and consequences of interspecific competition between adult bullheads and stone loach. Microhabitat use of both species was compared in the field to assess the potential for habitat partitioning to moderate competitive interactions (Chapter 4). Presence and absence of bullheads and stone loach were then manipulated under field conditions to test for interspecific competition, determine the influence of flexible niche partitioning on individual performance (Chapter 5) and to examine the independent and interactive effects of multiple predators on lower trophic levels (Chapter 6).

- 2 -

MECHANISMS OF DENSITY DEPENDENCE IN BULLHEADS

2.1 ABSTRACT

The long-term persistence of populations without extinction suggests that population regulation should be ubiquitous in nature. Yet determining the underlying biological mechanisms, particularly the processes that produce density dependence in demographic rates and the stage in the life cycle at which they occur, has proved difficult in many systems. Density dependent mortality of larvae and juveniles is considered to be the main regulating factor in fish populations. Regulation could also occur at the adult stage via density dependent growth and fecundity, yet few studies have explicitly tested this hypothesis. In this study, bullheads *Cottus gobio* were used as a model species to examine density dependence in adult stream fish. Fish density, food availability and spatial connectivity were experimentally manipulated under semi-natural field conditions using cage enclosures to test for density dependent growth and to distinguish between exploitation and interference competition as the causative mechanism. Growth of adult bullheads declined with increasing fish density. Individuals grew faster when densities of invertebrate prey were experimentally elevated above ambient levels, indicating that bullheads were food limited. Parallel dietary shifts were observed in response to manipulation of both bullhead density and resource availability, suggesting that exploitation competition for *Gammarus pulex* was the primary mechanism responsible for density dependent growth. Evidence was sought, but not found, for interference competition. Thus, density dependent growth at the adult stage may potentially regulate bullhead populations via effects on fecundity and survival. The exact consequences for population dynamics will depend upon the action of stochastic events and deterministic processes at other stages of the life cycle. However, the high density of bullheads in chalk streams suggests that population regulation at the adult stage is an important and widespread process in this species.

2.2 INTRODUCTION

Determining the extent to which animal populations are regulated has long been a core theme in ecology (Nicholson 1933; Andrewartha & Birch 1954; Turchin 1999; Hixon *et al.* 2002). Regulation occurs when stabilizing density dependent processes act to bound fluctuations in population size by altering key demographic rates of individuals (Murdoch 1994). The long-term persistence of populations without extinction suggests that population regulation should be ubiquitous in nature, yet robust empirical evidence for density dependence is limited (Murdoch 1994). Searching for density dependence in time series of estimated population densities has proved to be unreliable, both failing to detect density dependence when it is present and finding spurious density dependence when it is not (Gaston & Lawton 1987; Pollard *et al.* 1987; Wolda & Dennis 1993; but see Lande *et al.* 2002). Field manipulations of population density represent a more direct approach to examining density dependence in demographic rates, but often pose substantial practical difficulties and consequently are seldom performed in many systems (Harrison & Cappuccino 1995).

Attempts to draw generalizations about regulation have been constrained by a lack of knowledge concerning the underlying biological mechanisms, in particular the processes that produce density dependence and the stage in the life cycle at which they occur (Sinclair 1989; Murdoch 1994; Forrester & Steele 2000). Mechanistic understanding is critical as it provides the basis for predicting spatio-temporal variation in population regulation by linking individual behaviour to population dynamics (Wiens *et al.* 1993; Murdoch 1994; Sutherland 1996). Whilst a general process has been identified in some studies, the exact way in which it operates to produce density dependence has often not been determined. For example, intraspecific competition is commonly described as an important potential regulating factor (Hixon *et al.* 2002) but the mode of competition and the limiting resource are often not known. Whilst the latter may be identified by direct observation, distinguishing between exploitation and interference has proved less tractable, relying on detailed study of behaviour or resource availability (Griffith & Poulson 1993; Goss-Custard *et al.* 2001) or fitting models of resource use incorporating competition parameters (Doncaster & Gustafsson 1999). Manipulation of resource availability (Boss & Richardson 2002) and direct interaction with conspecifics (Imre *et al.*

2002) holds much potential to distinguish alternative competitive mechanisms, but to date such experiments have not been performed simultaneously.

Compared to other animal groups, relatively little is known about the mechanisms that regulate freshwater fish populations (see Sinclair 1989; Shepherd & Cushing 1990 for reviews). Theoretical and empirical studies suggest that fish populations are regulated primarily by density dependent mortality during early life. Individual-based modelling of fish growth predicts that exploitation competition for prey resources will cause density dependent growth and mortality at a critical body-mass corresponding to the juvenile life stage (Cowan *et al.* 2000). Although evidence is sparse, the majority of field studies confirm that density dependent mortality occurs almost exclusively at the larval or early juvenile stage (Elliott 1985; Charnov 1986; Shepherd & Cushing 1990; Jonsson *et al.* 1998). It has been suggested, however, that populations could also be regulated at the adult stage via density dependence in individual growth rate (Shepherd & Cushing 1990). This mechanism is potentially very powerful because fecundity and survival are strongly correlated with body size in fish (Mann 1971; Sogard 1997). Nevertheless, empirical evidence for density dependence among adult fish is extremely limited (Le Cren 1987; Elliott & Hurley 1998).

Food, foraging space and shelter are commonly cited as potential limiting factors for freshwater fish, yet knowledge of how intraspecific competition generates density dependence in per capita demographic rates remains cursory. Density dependent mortality in juvenile fish is thought to involve an interaction between food supply and predation, whereby exploitation for food at high densities results in slower growth and prolongs the critical period during which fish are vulnerable to gape-limited predators (Sinclair 1989; Shepherd & Cushing 1990). In salmonids, interference competition for territories among juveniles has been shown to regulate populations via density dependent mortality and emigration (Elliott 1985, 1990; Grant & Kramer 1990) but strong compensatory growth responses at low population densities suggest that exploitation competition may also be important (Jenkins *et al.* 1999), possibly due to shadow competition (Elliott 2002).

The aim of this study was to examine the occurrence and mechanisms of density dependence in adult stream fish using bullheads *Cottus gobio* as a model system. *Cottus*

species are small, benthic fish that have small home ranges (Brown & Downhower 1982; Hill & Grossman 1987) and can attain high densities in shallow stony streams. These characteristics make them ideal for investigating population-level processes by experimental manipulation. Bullheads are abundant in the chalk streams of southern England (Mann 1971). Early life-stages (eggs and fry) suffer high mortality due to invertebrate predation and fungal infection (Green 1975; Fox 1978b), but less attention has focused on later life-stages. Adult bullheads are solitary and behave aggressively towards conspecifics (Smyly 1957; Ladich 1989). They are also visual, ambush predators that show a preference for large, active benthic macroinvertebrates such as *Gammarus pulex* L. (Smyly 1957; Welton *et al.* 1983). Predation by bullheads has been shown to significantly reduce benthic prey densities (Englund & Olsson 1996; Dahl 1998a), suggesting that food may be a limiting resource. Both exploitation and interference competition could therefore potentially regulate populations at the adult stage via density dependent individual growth. This hypothesis was tested by conducting two field experiments. The first tested for density dependence by examining the effect of fish density on individual growth in body size. The second experiment partitioned the effects of exploitation and interference competition by testing the following predictions: (i) growth of bullheads will be enhanced by increased food availability if there is exploitation competition, and (ii) growth of bullheads will be enhanced by reduced spatial connectivity (and hence reduced encounters with conspecifics) if there is interference competition. Fish density, food availability and spatial connectivity were manipulated *in situ* using cage enclosures. Prey consumption of bullheads was measured to provide further insight into the underlying mechanisms.

2.3 METHODS

2.3.1 Study site

The study was conducted on the Brandy Stream (see section 1.5.2 for description). An electrofishing survey during August 2002 estimated the density of adult (>50 mm) bullheads at 3.4 fish/m² in the stream as a whole, and up to 7.6 fish/m² in preferred riffle habitats (see Chapter 4). Mean water temperature during experiments 1 and 2 was 15.5°C (minimum 13.7°C; maximum 17.6°C) and 12.2°C (minimum 10.8°C; maximum 14.1°C) respectively (Seamon mini temperature recorder, Húgrún, Reykjavik, Iceland).

2.3.2 Experimental enclosures

The experimental manipulations were performed using cage enclosures, each 1.4 m long, 0.8 m wide (enclosed area = 1.12 m²) and 0.3 m high. Enclosures had solid metal sides and base and 6 mm wire-mesh on the up- and down-stream ends to permit water to flow through the structure (Plate 2a). Enclosures were established in water 0.17-0.27 m deep with velocities ranging from 0.17 to 0.39 m/s. The base of each enclosure was covered with 10-20 mm gravel, creating a substrate 25 mm deep, and bricks and cobbles were then introduced to provide shelter. Plastic netting was placed over the open top of each enclosure to deter avian predators. Although this has the potential to affect their behaviour, it was necessary to ensure that the treatments were maintained. Enclosures were positioned approximately 4 m apart and staggered to reduce the effects of upstream enclosures (Plate 2b). The up- and down-stream wire meshes were removed for several weeks prior to the start of each experiment to allow invertebrate prey to colonize the enclosures. Once replaced to enclose fish, the wire meshes were cleaned every 12 hours to remove accumulated plant debris and maintain water flow through the enclosures.

2.3.3 Experimental design and protocol

2.3.3.1 Experiment 1: Testing for density dependence

Twelve replicate enclosures were established on 7 June 2000 as described above. All fish used in the experiment were collected locally from the Brandy Stream by electrofishing between 20-22 July and held in stock enclosures. On 23 July, 56 adult bullheads were weighed to 0.01 g, measured to 0.1 mm (total length, TL) and randomly allocated to three density treatments: two, four and eight fish per enclosure. These densities of 1.8, 3.6 and 7.1 fish/m² corresponded to approximately half, ambient and double the mean density of adult bullheads in the Brandy Stream. The experimental animals ranged in initial mass from 2.05 g to 7.38 g (mean 3.56 g) and in initial TL from 55.7 mm to 82.3 mm (mean 65.5 mm). Treatments were replicated four times and randomly assigned to enclosures.

Plate 2 Cage enclosures on the Brandy Stream

(a)



(b)



Photos: A. Davey

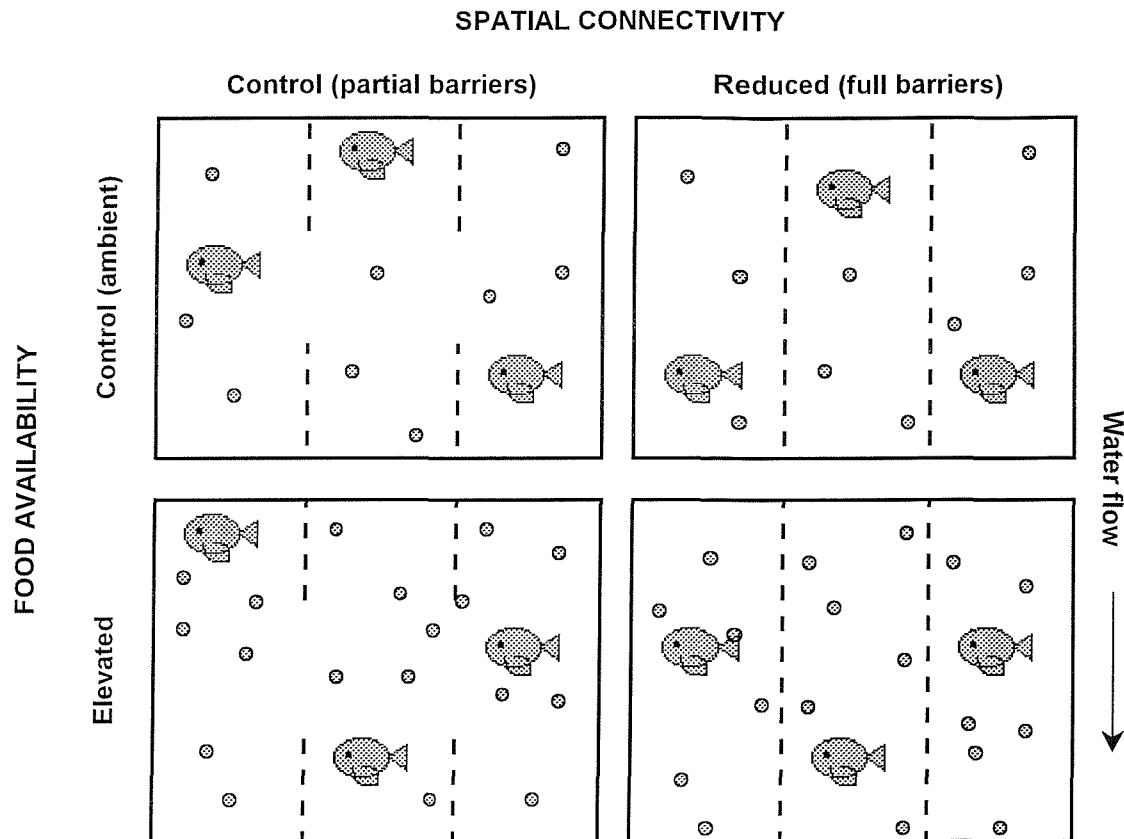


Figure 2.1 Experimental design to separate the effects of exploitation and interference competition. Bullheads were held in replicate stream enclosures under two levels of prey density (ambient and elevated, indicated by dots) crossed with two levels of spatial connectivity (normal and reduced). Longitudinal barriers (dotted lines) were used to manipulate spatial connectivity and, hence, the amount of direct interaction between conspecifics. Three bullheads were stocked into each enclosure.

The fish were held in the enclosures for 14 days. Three bullheads that died during the experiment were replaced with fish of similar size to maintain the treatments.

2.3.3.2 Experiment 2: Distinguishing between exploitation and interference competition

The second experiment used an array of 20 enclosures, each half the length of those used in experiment 1, which were established on 14 August 2002. A factorial experimental design was used, crossing two levels of food availability with two levels of spatial connectivity (Figure 2.1). By simultaneously manipulating both resource availability and the amount of direct interaction between conspecifics, it was possible to determine whether density dependent rates of prey consumption by bullheads, and hence individual

growth, were a function of prey density alone (exploitation competition) and/or bullhead density *per se* (interference competition).

Food availability was supplemented in half the enclosures by periodically adding benthic macroinvertebrates during the experiment to elevate prey densities (see below). Prey densities in the control treatment were left at ambient levels. The degree of spatial connectivity was manipulated by erecting two barriers in each enclosure parallel to the water flow, so partitioning the space into three sections of equal area. The barriers were constructed from 6 mm wire mesh that was permeable to invertebrate prey. To restrict interaction between bullheads, half the enclosures were fitted with complete barriers that prevented fish moving between sections, and fish stocked individually into each section. Using barriers to hold fish separately provided a measure of the performance of bullheads in the absence of direct interactions between conspecifics and therefore allowed the effect of interference competition to be evaluated. Control enclosures were fitted with partial barriers containing a 0.3 m gap that allowed fish to move between sections and interact normally. Each of the four treatments was replicated five times and treatments were randomly assigned to enclosures.

All experimental fish were sourced from the Brandy Stream by electrofishing on 27 September 2002 and held in stock enclosures. On 29 September, 60 adult bullheads were weighed to 0.01 g, measured to 0.1 mm (TL) and randomly assigned to treatments. Fish ranged in initial mass from 1.47 g to 4.52 g (mean 2.56 g) and in initial TL from 52.0 mm to 72.1 mm (mean 60.0 mm). Bullheads were marked with subcutaneous elastomer tags (Northwest Marine Technology Inc., WA, USA) to allow individual recognition. Three fish were released into each enclosure, one in the center of each section, representing a density of 5.4 fish/m². The experiment was run for 12 days.

Macroinvertebrates were added to food addition treatments on 2, 6 and 9 October. All animals were collected locally by carefully disturbing the stream bed and catching downstream-drifting individuals in a pond net (500 µm mesh). To control the number of animals added, replicate 30 ml samples of macroinvertebrates were measured out using a measuring cylinder. On each date, a total of 90 ml of macroinvertebrates were released into each food addition enclosure (30 ml per section). Analysis of samples ($n = 5$) showed

that *Gammarus pulex* accounted for 90 % of all animals, with a mean of 1645 (\pm 298 S.D.) individuals per 90 ml. This was equivalent to elevating benthic densities of *Gammarus pulex* by 8812 (\pm 1598) individuals/m² during the course of the experiment, approximately doubling ambient density. To reduce the immediate downstream drift of animals, a board was temporarily positioned across the upstream mouth of recipient enclosures to stop water flow, and macroinvertebrates then released as close to the substrate as possible. As a procedural control, the remaining 10 cages were also temporarily screened off and 90 ml of gravel added to each to simulate the disturbance caused by adding invertebrates.

2.3.4 Data collection

At the end of each experiment, enclosures were searched and bullheads removed with a dip net. Fish were then killed by an overdose of anesthetic, identified, re-weighed, re-measured and preserved in 70 % ethanol solution. This work was conducted between 0700 and 1000 h to minimize digestion of consumed prey. In the laboratory, stomachs of experimental fish were dissected out and their contents examined under x40 magnification using a dissecting microscope. Prey items were identified to the lowest possible taxonomic level, counted, and measured to 0.01 mm using a graticule. Dimensions of prey items were converted to dry weight biomass using published mass-length relationships (Ladle *et al.* 1972; Bass 1976; Mackey 1977; Mason 1977; Welton 1979; Meyer 1989). Stomach contents were observed in various degrees of digestion. Incomplete prey items were assumed to be whole for the purpose of biomass determination. Where no body dimension could be recorded, a biomass was attributed based upon the average of other specimens within the sample. Occasionally prey could not be identified and these were excluded from analysis. Several authors warn of the effect of different methodologies and against transferring mass-length relationships between stream types (Meyer 1989; Johnston & Cunjak 1999). Therefore attempts were made to match the preservation method and stream type in published equations to those of this study.

2.3.5 Statistical analysis

The performance of bullheads was assessed by prey consumption and growth in body size. Prey consumption was calculated as the number of individuals of each invertebrate taxon per fish stomach. Total food consumption was also measured as the total dry weight

biomass of all prey consumed, divided by fish mass to the power of 0.75 to take account of allometric relationship between body size and food consumption (Steingrimsson & Grant 1999). Growth was expressed as the change over time in body mass and TL. Calculations were performed for all surviving fish, with the exception of four fish that moved across the barriers in experiment 2, and the four neighbours that they invaded, which were omitted from the analysis.

Analyses were performed on the means for each enclosure ($n = 12$ data points for experiment 1 and $n = 20$ for experiment 2). Response variables were tested with Cochran's C-test for homogeneity of variances and log-transformed where necessary to normalise distributions and stabilise variances. To test for density dependence, response variables from experiment 1 were regressed against initial fish density. Spearman's rank correlation was used when transformation failed to correct heterogeneous variances. To distinguish between exploitation and interference competition, response variables from experiment 2 were tested by two-way ANOVA with food availability, spatial connectivity and their interaction as fixed factors. Post-hoc power analysis was performed for non-significant results where necessary (Zar 1999). SPSS v.10.0 (SPSS Inc., Chicago) was used for all statistical procedures and significance evaluated using $\alpha = 0.05$.

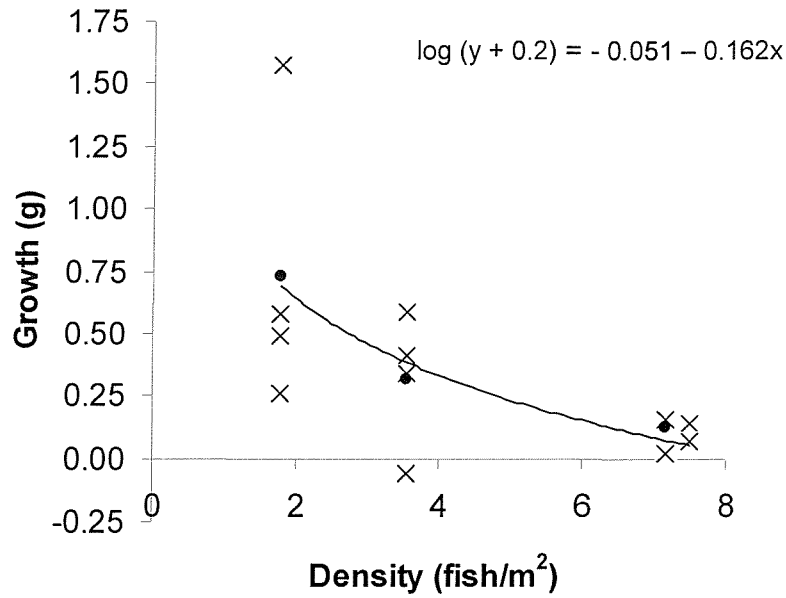
2.4 RESULTS

2.4.1 Experiment 1: Testing for density dependence

Fish density strongly affected bullhead performance. Both growth in mass (regression: $F_{1,10} = 5.108$, $P = 0.047$) and growth in TL (regression: $F_{1,10} = 8.733$, $P = 0.014$) were negatively density dependent (Figure 2.2). Mean growth in the highest-density treatment (0.12 g and 0.5 mm) was 83 % lower than in the low-density control (0.73 g and 2.8 mm). As a result of strong density dependent growth, total biomass production per enclosure was unrelated to stocking density (regression: $F_{1,10} = 0.582$, $P = 0.463$) indicating exact density compensation in production.

The diet of bullheads was dominated numerically by *Gammarus pulex* (67 %), followed by *Baetis* nymphs (14 %), Simuliidae larvae (11 %) and chironomid larvae (4 %) (Table 2.1).

(a) Growth in mass



(b) Growth in TL

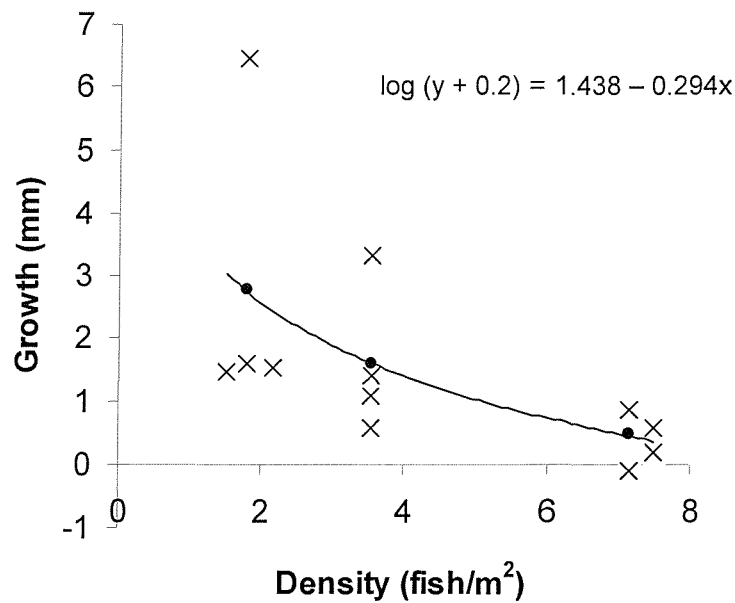


Figure 2.2 The relationship between stocking density of bullheads and their subsequent performance during experiment 1, as measured by growth in (a) mass and (b) TL. Crosses indicate enclosure means based on 2, 4 or 8 fish per enclosure; dots indicate treatment means based on four replicate enclosures per treatment. Some points are offset horizontally for clarity. Regression lines show significant relationships ($P < 0.05$).

Consumption of chironomid larvae (Spearman's $r_s = 0.701$, $n = 12$, $P = 0.011$) and *Baetis* nymphs (regression: $F_{1,10} = 5.535$, $P = 0.040$) increased with bullhead density. In contrast, consumption of *Gammarus pulex* and Simuliidae larvae was unrelated to stocking density (regression: $F_{1,10} = 1.760$, $P = 0.214$ and $F_{1,10} = 1.274$, $P = 0.285$ respectively). Other prey

Table 2.1 Prey consumption of bullheads in experiment 1, expressed as mean number and dry weight biomass of prey consumed per fish. Fish were held in enclosures at three densities (2, 4 or 8 fish per enclosure). Prey consumption was recorded at the end of the experiment by examining stomach contents.

Fish per enclosure	Number			Biomass (mg)		
	2	4	8	2	4	8
<i>Gammarus pulex</i>	5.50	5.50	4.17	30.45	25.63	21.31
<i>Baetis</i> spp.	0.38	0.71	1.27	0.06	0.28	0.36
Chironomidae	0.00	0.00	0.43	0.00	0.00	0.02
Simuliidae	2.38	0.36	0.53	0.60	0.11	0.14
Other prey	0.25	0.43	0.40	0.20	1.19	0.29
TOTAL	8.51	7.00	6.80	31.31	27.21	22.12

Table 2.2 Prey consumption of bullheads in experiment 2, expressed as mean number and dry weight biomass of prey consumed per fish. Fish were held in enclosures at two levels of food availability (ambient, elevated) crossed with two levels spatial connectivity (with and without a complete barrier). Three fish were stocked into each enclosure and prey consumption recorded at the end of the experiment by examining stomach contents.

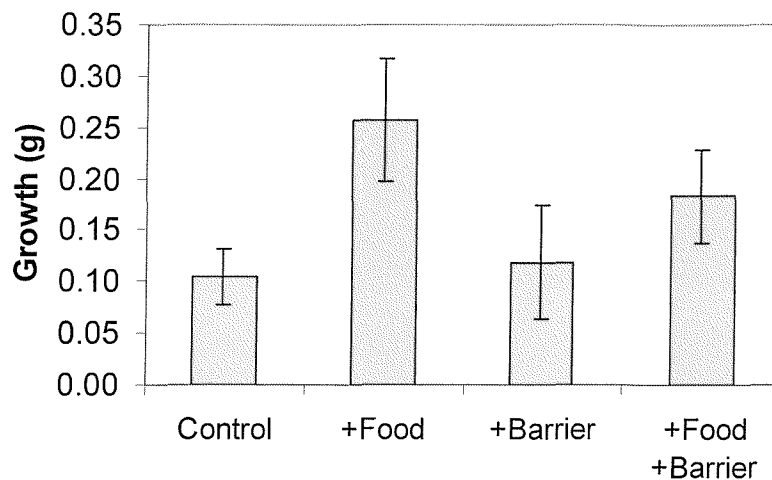
Treatment	Number				Biomass (mg)			
	Control	+ Food	+ Barrier	+ Food + Barrier	Control	+ Food	+ Barrier	+ Food + Barrier
<i>Gammarus pulex</i>	0.47	1.33	0.60	1.40	1.55	4.26	2.75	3.93
<i>Baetis</i> spp.	1.13	0.63	0.93	0.20	0.97	0.40	0.74	0.06
Chironomidae	5.80	3.40	3.47	0.60	0.56	0.33	0.25	0.03
Simuliidae	1.07	0.73	0.93	0.00	0.23	0.24	0.24	0.00
Other prey	0.34	0.21	0.74	0.48	0.49	0.38	1.18	0.57
TOTAL	8.81	6.30	6.67	2.68	3.80	5.61	5.16	4.59

taxa were consumed too infrequently for analysis. *Gammarus pulex* was the most important prey species, accounting for over 94% of total prey biomass in all three treatments (Table 2.1). Mean prey biomass per fish was 24.90 mg (dry weight). There was no relationship between fish density and total prey biomass consumed per fish (regression: $F_{1,10} = 0.660$, $P = 0.436$).

2.4.2 Experiment 2: Distinguishing between exploitation and interference competition

Mean growth in mass of bullheads was 97 % higher in food addition treatments than in the controls (ANOVA: $F_{1,16} = 4.959$, $P = 0.041$; Figure 2.3a) and a similar pattern was

(a) Growth in mass



(b) Growth in TL

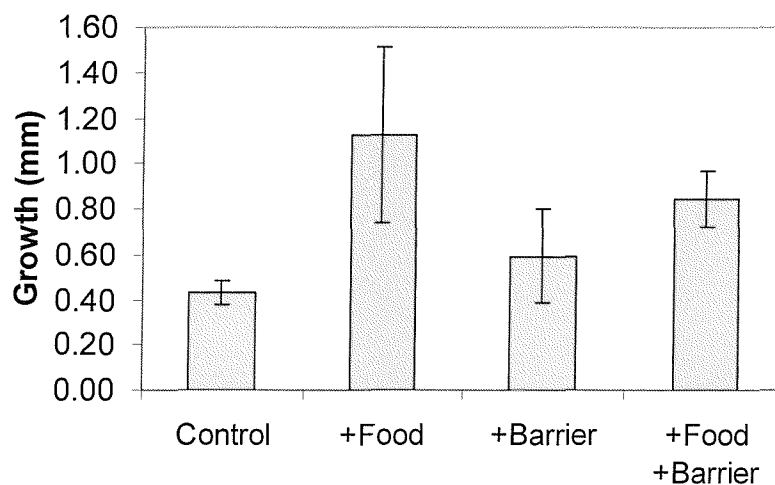
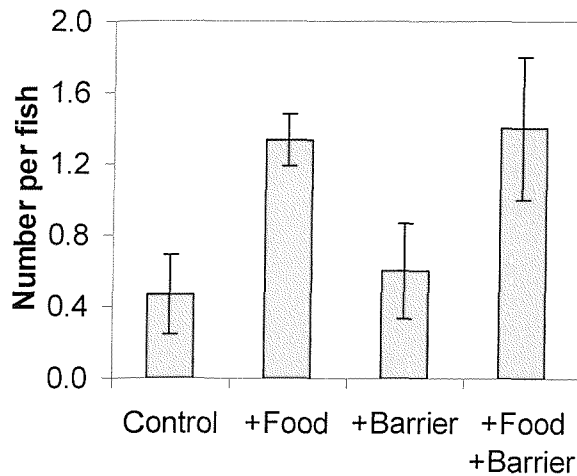


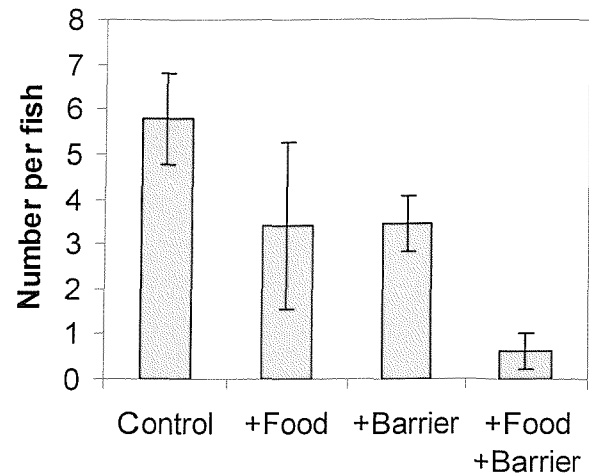
Figure 2.3 Mean (± 1 S.E.) growth in (a) mass and (b) TL of bullheads during experiment 2. Fish were held in enclosures at two levels of food availability (ambient, elevated) crossed with two levels of spatial connectivity (a barrier effect). Three fish were stocked into each enclosure. Means are based on five replicate enclosures per treatment.

observed for growth in TL, although the effect was marginally non-significant (ANOVA: $F_{1,16} = 4.203$, $P = 0.057$; Figure 2.3b). In contrast, spatial connectivity had no effect on growth in mass (ANOVA: $F_{1,16} = 0.333$, $P = 0.572$) or growth in TL (ANOVA: $F_{1,16} = 0.061$, $P = 0.808$). Although the power of tests for a barrier effect were low (< 0.20), food availability explained over 10 times more variation in growth than spatial connectivity, indicating that even if there was interference competition, its effect was minor relative to that of exploitation competition. The effect of food addition on growth did not depend upon the level of spatial connectivity (ANOVA interaction: mass: $F_{1,16} = 0.823$, $P = 0.378$; TL: $F_{1,16} = 0.885$, $P = 0.361$).

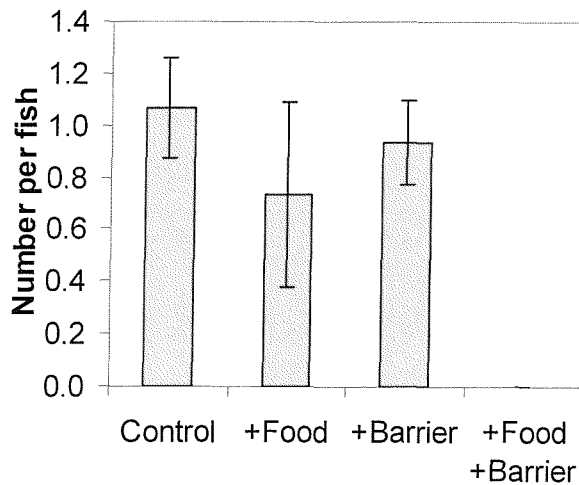
(a) *Gammarus pulex*



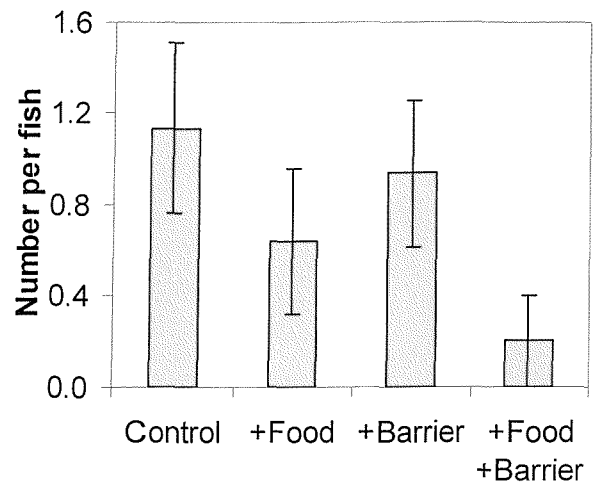
(b) Chironomidae



(c) Simuliidae



(d) *Baetis* spp.



(e) Total prey biomass

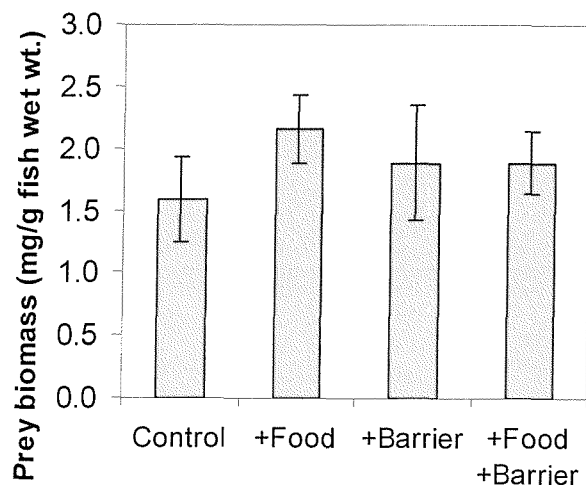


Figure 2.4 Prey consumption of bullheads in experiment 2, expressed as numbers of (a) *Gammarus pulex*, (b) Chironomidae, (c) Simuliidae and (d) *Baetis* nymphs per fish, and (e) total dry weight biomass of prey. Bullheads were held in enclosures at two levels of food availability (ambient, elevated) crossed with two levels of spatial connectivity (a barrier effect). Three fish were stocked into each enclosure and their prey consumption estimated by examining stomach contents at the end of the experiment. Means (± 1 S.E.) are based on five replicate enclosures per treatment.

As in experiment 1, the diet of bullheads was dominated by *Gammarus pulex*, chironomid larvae, *Baetis* nymphs and Simuliidae larvae (Table 2.2). Bullheads displayed a strong dietary shift in response to prey density, consuming more *Gammarus pulex* (ANOVA: $F_{1,16} = 9.532$, $P = 0.007$; Figure 2.4a), fewer chironomid larvae (ANOVA: $F_{1,16} = 5.570$, $P = 0.031$; Figure 2.4b) and fewer Simuliidae larvae (ANOVA: $F_{1,16} = 8.480$, $P = 0.010$; Figure 2.4c) at elevated prey densities. There was also a suggestion that consumption of *Baetis* nymphs was lower in food addition treatments (ANOVA: $F_{1,16} = 3.782$, $P = 0.070$; Figure 2.4d). Predation upon chironomid larvae was further reduced when fish were isolated by barriers (ANOVA: $F_{1,16} = 5.320$, $P = 0.035$; Figure 2.4b), and there was a suggestion that the same was occurring for Simuliidae larvae (ANOVA: $F_{1,16} = 4.008$, $P = 0.063$; Figure 2.4c). Consumption of *Gammarus pulex* and *Baetis* nymphs was unaffected by the degree of spatial connectivity (ANOVA: $F_{1,16} = 0.160$, $p = 0.695$ and $F_{1,16} = 0.977$, $P = 0.338$ respectively; Figures 2.4a and 2.4d). Interaction between food availability and spatial connectivity had no significant effect on consumption of any prey taxa (ANOVA interaction: all $P > 0.20$). Bullheads contained a mean of 4.70 mg (dry weight) of invertebrate prey, or 1.9 mg/g of fish wet weight, with *Gammarus pulex* accounting for 64 % of total prey biomass (Table 2.2). Total prey consumption was unaffected by food availability (ANOVA: $F_{1,16} = 0.732$, $P = 0.405$), spatial connectivity (ANOVA: $F_{1,16} = 0.009$, $P = 0.925$) or their interaction (ANOVA interaction: $F_{1,16} = 1.025$, $P = 0.326$) (Figure 2.4e).

2.5 DISCUSSION

The aim of this study was to test for density dependent growth among adult bullheads and to elucidate the mechanisms responsible. To overcome the problems of detection inherent in statistical analyses of census data, an experimental approach was adopted to infer density dependence in demographic rates from direct measurements of individual growth (Murdoch 1994; Harrison & Cappuccino 1995). Using field enclosures to manipulate animal densities *in situ* risks affecting the behaviour of the focal species or modifying its habitat. However, bullheads were not thought to be stressed by confinement within enclosures because *Cottus* species are known to have small home ranges and low movement rates (Brown & Downhower 1982; Hill & Grossman 1987) and the growth

rates and dietary composition of bullheads during the experiments were comparable to those recorded for wild fish (Mann & Orr 1969; Mann 1971; Green 1975). Furthermore, the enclosures closely approximated natural conditions and supported an assemblage of invertebrate species similar to that in the surrounding stream (A. Davey, *personal observation*). It seems unlikely, therefore, that the observed responses of bullheads were artefacts caused by the use of field enclosures. Instead, this study provides new insight into the timing and processes of density dependence in fish populations.

2.5.1 Timing of density dependence in the life cycle

Individual growth rate of adult bullheads showed strong negative density dependence. This result contrasts with the prevailing view that density dependence in fish occurs almost exclusively at the larval or early juvenile stage (Charnov 1986; Sinclair 1989; Shepherd & Cushing 1990). This discrepancy may be accounted for by the bias in the literature towards commercially important salmonid species, which frequently display strong territorial competition amongst juveniles (Elliott 1985; Grant & Kramer 1990; Jenkins *et al.* 1999; Keeley 2001), and the emphasis of fisheries biologists towards the study of mortality rates rather than sub-lethal density dependent responses. This study adds to a small but growing body of evidence that fish populations can potentially be regulated at the adult stage via density dependent growth and fecundity. For example, Le Cren (1987) observed density dependent fecundity in perch, *Perca fluviatilis* L., in Lake Windermere, and key-factor analysis of resident brown trout in a Lake District stream has revealed population regulation at the adult stage, although the exact mechanism remains uncertain (Elliott & Hurley 1998). Density dependence in adult freshwater fish is likely to be more prevalent than currently believed for two reasons. Firstly, the marked quantitative and qualitative changes in resource requirements that characterize the ontogeny of many fish species provide the necessary conditions for the development of demographic bottlenecks after sexual maturity (Werner 1986; Beck 1995). Secondly, in temperate environments, seasonal variation in prey abundance and water temperature can lead to annual bouts of intraspecific competition when food abundance is low relative to the metabolic demands of the population (Persson & Johansson 1992).

2.5.2 Mechanisms of density dependence

Attempts to assess the prevalence of population regulation in natural systems have been constrained by a lack of knowledge concerning the mechanisms giving rise to density dependence in demographic rates (Sinclair 1989; Murdoch 1994; Forrester & Steele 2000). Competition has been implicated as the underlying process for density dependence in most studies of freshwater fish (for example Elliott 1990; Tonn *et al.* 1994; Jenkins *et al.* 1999), but separating the effects of exploitation and interference competition has proved challenging. In this study, bullheads grew faster at reduced density and displayed a dietary shift, switching from alternative prey such as *Baetis* nymphs and Chironomid larvae to preferred *Gammarus pulex*. Similar responses were observed when densities of invertebrate prey were elevated above ambient levels. These parallel responses to manipulation of both focal species density and resource availability indicate that bullheads were food limited and provide strong evidence that exploitation competition for *Gammarus pulex* was the primary mechanism responsible for density dependent growth. In contrast, no evidence was found for interference competition.

Although this study could not directly attribute resource limitation to predator impacts on prey, bullheads have previously been shown to reduce local prey availability both directly through consumption (Englund & Olsson 1996; Dahl 1998a) and indirectly by eliciting anti-predator responses in prey (Andersson *et al.* 1986). Strong effects of freshwater fish on prey are well documented (Wooster 1994; Wooster & Sih 1995; Dahl & Greenberg 1996; Shurin *et al.* 2002), but further food addition experiments are required to determine the generality of food limitation (for example Boss & Richardson 2002). Prey availability is also reduced when heterogeneous substrates provide a refuge from predation (Holomuzki & Stevenson 1992; Power 1992). Indeed, if only a small fraction of the total prey population is accessible to predators, then resource limitation may occur without a significant reduction in total prey density. This may explain the occurrence of exploitation competition despite high ambient prey densities in the present study.

Bouts of strong exploitation competition are predicted to occur periodically in temperate freshwater fish populations (Persson & Johansson 1992). However, behavioural plasticity is a common trait of animals in temporally variable environments (Dill 1983) and flexible foraging behaviour may ameliorate competitive interactions (Nakano *et al.* 1999). In the

foraging behaviour may ameliorate competitive interactions (Nakano *et al.* 1999). In the present study, growth of bullheads was density dependent despite a dietary shift that maintained total prey biomass consumption, implying that the alternative foraging strategy was less efficient either because of higher energetic costs or lower nutritional quality of prey.

The absence of interference competition in this study was surprising because bullheads are known to behave aggressively towards conspecifics when active at night (Smyly 1957; Ladich 1989). Since spatial connectivity was confounded with total area available for movement, it is possible that negative effects of competition on growth were obscured by a positive response of fish to reduced confinement. However, this is unlikely given that the bullheads did not appear to be stressed by enclosure, as argued above. Instead, the complex substrate probably minimized any interference interactions by visually isolating conspecifics (Kalleberg 1958; Imre *et al.* 2002).

2.5.3 Implications for population dynamics

Density dependence in individual growth rate of adults is likely to have important consequences for population dynamics of bullheads via effects on demographic parameters such as fecundity and survival. Female fecundity is positively correlated with size (Mann 1971; Green 1975; Fox 1978a; Marconato & Bisazza 1988) and in chalk streams, where the bullhead is a fractional spawning species, larger individuals tend to commence spawning earlier in the year, laying more batches of eggs (Fox 1978a). Females prefer larger males (Marconato & Rasotto 1983) and consequently male reproductive success, as measured by the number of matings and number of eggs fertilized, increases with fish size (Marconato & Bisazza 1988). Density dependent adult growth is also likely to translate into density dependent survival since larger fish are generally less vulnerable to predators, have higher tolerance to environmental extremes and are more resistant to starvation during stressful periods such as winter than smaller individuals (Cushing 1981; Sogard 1997). Therefore density dependent adult growth is expected to influence both current population size and subsequent reproductive output.

Detecting density dependence only identifies exploitation competition among adults as a potential regulating factor. Its importance for population regulation will depend upon the

action of other density independent and density dependent processes. Firstly, heavy density independent mortality during early life-stages may hold populations below carrying capacity and preclude the occurrence of intraspecific competition amongst adults. Bullhead eggs are susceptible to fungal infection (Fox 1978a) and predation by invertebrate predators (Fox 1978b). Larvae also suffer predation from other small fish species such as three-spined stickleback *Gasterosteus aculeatus* (Fox 1978a). Despite this, local densities of adult bullheads in chalk streams often exceed 2 fish/m² (Mann 1971; Green 1975; Fox 1978a), suggesting that exploitation competition among adult fish is a widespread phenomenon. Secondly, density dependence may occur at more than one life-stage as a consequence of ontogenetic changes in limiting resources (Werner & Gilliam 1984; Werner 1986). Previous studies have suggested that mortality of bullhead fry is density dependent (Green 1975; Fox 1978a) and that nest sites may be limiting for *Cottus* species (Natsumeda 2001). Sequential density dependencies may act in an additive or compensatory manner to produce complex and unpredictable population dynamics (Astrom *et al.* 1996; Hellriegel 2000). Consequently, further data on the prevalence, strength and consequences of competition for resources at each stage of the life cycle will be required to evaluate the relative importance of these alternative regulating mechanisms in stabilizing population fluctuations.

2.5.4 Conclusions

Revealing the mechanisms that translate variation in density into variation in per capita demographic rates is vital to understanding how animal populations are regulated. Whilst heavy mortality of young fish can be important in determining population size, this study has demonstrated a significant limiting effect of food for adult fish. Exploitation competition for preferred prey may therefore potentially regulate freshwater fish populations at the adult stage via density dependence in growth in body size and, ultimately, fecundity. However, further research is required to establish the generality of this mechanism and to assess its relevance for population regulation.

- 3 -

MODELLING DYNAMICS OF SHELTER USE IN BULLHEADS: THE EFFECT OF INTRASPECIFIC COMPETITION

3.1 ABSTRACT

Shelter is important for mobile animals living in hostile environments as a refuge from predation and harmful physical conditions. Shelter may influence both the spatial distribution of individuals and population abundance via effects on rates of growth, mortality and emigration. Understanding the functional significance of shelter requires knowledge of the behavioural mechanisms that govern dynamics of shelter use and the individual-level responses to shelter occupation. The aim of this study was to investigate the influence of intraspecific competition on shelter use and to examine the consequences of individual behaviour for population-level processes, using bullheads *Cottus gobio* as a model system. Fish density and shelter density were manipulated in a replicated field experiment using cage enclosures. Shelter use and movement of individually marked bullheads were recorded twice daily for ten days and growth in body size used as a measure of performance. The strength of exploitation and interference competition was estimated from the observed dynamics of shelter use by fitting a first order Markov chain model incorporating competition coefficients. Bullheads seldom shared shelters with conspecifics, indicating exploitation competition, and also engaged in interference competition, which limited the ability of unsheltered fish to colonise vacant shelters at high fish density. As a result, the proportion of fish in shelter was negatively density dependent. Large fish had a higher probability of shelter use than small fish, particularly when shelter availability was low, indicating asymmetrical intraspecific competition between size classes. Unsheltered fish attempted to emigrate from enclosures, suggesting that competition for shelter can determine local density and that shelter availability sets the carrying capacity. There was no evidence that survival and somatic growth of bullheads was affected by shelter use, although shelter availability may influence population size if unsheltered individuals displaced to sub-optimal habitats suffer reduced fitness.

3.2 INTRODUCTION

One of the primary goals in ecology is to understand the factors that determine the distribution and abundance of animals. Shelter, or cover, is an important resource for mobile animals (Elton 1939; Allouche 2002), providing refuge from a hostile physical environment (Smith & Griffith 1994; Williams & Morritt 1995; Winterbottom *et al.* 1997; Williams *et al.* 1999) and predation (Everett & Ruiz 1993; Valdimarsson & Metcalfe 1998). Availability of shelter can influence the spatial distribution of individuals and limit population abundance. Positive selection for shelter has been shown to influence patterns of habitat use in reef fish (Steele 1999), crayfish (Usio & Townsend 2000), snails (Crowl & Schnell 1990), and amphibians (Barr & Babbitt 2002). Furthermore, shelter bottlenecks have been demonstrated to limit survival and recruitment in a variety of taxa including stone crabs (Beck 1995), spiny lobsters (Butler & Herrnkind 1997), gobies (Steele 1999; Kroon *et al.* 2000) and damselfishes (Holbrook & Schmitt 2002).

In streams, shelter may take a variety of forms including interstitial spaces in the stream bed, undercut banks and coarse woody debris (MacKenzie & Greenberg 1998; Allouche 2002). Use of interstitial shelters is common amongst benthic fish (Brown 1991; MacKenzie & Greenberg 1998; Mullen & Burton 1998) and many salmonid species such also seek refuge in the stream bed during winter (Cunjak & Power 1986; Cunjak 1988; Fraser *et al.* 1995; Gries & Juanes 1998; Harwood *et al.* 2002). Concealment behaviour is used primarily to provide visual isolation from predators (Harvey & Stewart 1991; Gregory & Griffith 1996b; MacKenzie & Greenberg 1998; Allouche & Gaudin 2001) but may also provide refuge from high water velocity (Allouche 2002) or low water temperatures (Smith & Griffith 1994). Positive correlations between abundance of shelter and population abundance or biomass are well documented in stream fish (see Allouche 2002 for review). Moreover, experiments in which shelter is supplemented confirm that shelter density is an important determinant of fish density in the field and suggest that competition for shelter may limit population size (Boussu 1954; Saunders & Smith 1962; Eklöv & Greenberg 1998). It is often uncertain, however, whether addition of shelter affects demographic parameters such as survival or recruitment, or simply causes the redistribution of existing fish (the attraction vs. production debate, Bohnsack 1989; Riley & Fausch 1995).

The functional relationship between shelter availability and population abundance will depend upon the behavioural processes that control access to shelter and the consequences of shelter use for the individual (Sutherland 1996; Allouche 2002). But although shelter clearly influences population dynamics, little is known about the mechanisms that link individual behaviour to population level patterns (Allouche 2002). Competition for shelter may occur in two main ways. First, sheltered individuals may defend a shelter and prevent further colonisation by unsheltered individuals (Mullen & Burton 1998; Figler *et al.* 1999). Second, agonistic or avoidance behaviours may reduce the rate at which shelters are colonised, independently of shelter availability. Both forms of interaction may be considered as interference competition, but here I define occupation of shelter as exploitation (c.f. consumption of prey) and other interactions that reduce colonisation rate as interference. Measuring density dependence in exploitation rate has proved difficult for predators foraging on prey (Goss-Custard *et al.* 1995; Stillman *et al.* 1997; van der Meer & Ens 1997) and has rarely been attempted for resources that are exploited by occupation rather than consumption (Doncaster & Gustafsson 1999). Second, if asymmetries in colonisation efficiency or competitive ability exist then individuals may not have an equal probability of shelter use. For example, body size (Mullen & Burton 1998; Figler *et al.* 1999) and species identity (Baltz *et al.* 1982; Greenberg 1988; Soderback 1994; Dubs & Corkum 1996; Guan & Wiles 1997; Vorburger & Ribi 1999) can influence individual success in one-on-one contests for shelter. Size- or species-specific differences in shelter use may have important implications for population dynamics. Third, the exact consequences of lacking shelter will determine how shelter availability affects local and absolute population size. Individuals that are unable to obtain shelter may suffer increased mortality risk (Holbrook & Schmitt 2002), lower growth (Fischer 2000), or may emigrate from a patch to seek shelter (Mesick 1988).

The aim of this study was to investigate how intraspecific competition influences individual shelter use and to examine the consequences of individual behaviour for population-level shelter use dynamics, using a benthic stream fish, the bullhead *Cottus gobio*, as a model system. The bullhead is a small fish of swift-flowing, well-oxygenated, shallow streams (Mills & Mann 1983; Roussel & Bardonnnet 1997). Like other freshwater sculpins, bullheads hide from predators during the day, selecting coarse substrates that provide interstitial shelter (Smyly 1957; Welton *et al.* 1983; Brown 1991). Bullheads are

generally solitary animals and agonistic behaviour between non-breeding individuals is common, involving threat displays, chasing and occasionally fights (Smyly 1957; Ladich 1989). The objectives of this study were: (i) to determine the strength of exploitation and interference competition for shelter; (ii) to investigate correlates of individual success in obtaining shelter; and (iii) to examine the how individual responses to shelter use translate into effects at the population level. In this chapter, I first present a Markov chain model that describes dynamics of shelter use in a population of mobile animals by incorporating the effects of exploitation and interference competition. Secondly, I describe the results of a field experiment examining the effects of shelter density and fish density on shelter use, growth and movement of individually-marked bullheads, and fit the model to the empirical data to test for exploitation and interference competition.

3.3 METHODS

3.3.1 Markov chain model of shelter use dynamics

Consider a closed population of K fish competing for access to S shelters. The number of fish in each of i shelters is denoted by n_i and $\sum n_i = N$, the total number of fish in shelter. The dynamics of shelter use are defined by a set of rules describing the rates at which fish depart and colonise shelters:

- (1) Each of N sheltered fish leaves shelter and become unsheltered at unitary rate d .
- (2) At the same time, each of $K-N$ unsheltered fish encounters shelters in proportion to their abundance at unitary rate per shelter c . The encounter rate is reduced by avoidance behaviour and aggressive interactions between conspecifics that reduce search efficiency. Following Hassell and Varley (1969), interference is modelled as a power function of the total number of animals in the population (c/K^m). On attempting to enter a shelter, an unsheltered fish has probability a of being repulsed by each of n resident fish. Thus, parameter m represents the strength of interference competition ($m \geq 0$) whilst parameter a is a coefficient of exploitation competition ($0 \leq a \leq 1$).

If sheltered fish are distributed evenly across shelters, then rate of change in the number of fish in shelter (N) is given by:

$$\frac{dN}{dt} = \frac{cS}{K^m} (K - N)(1 - a)^{N/S} - dN \quad (3.1)$$

In reality, however, individuals cannot distribute themselves perfectly evenly, and so we require a model that takes into account the *distribution* of fish across shelters. It is natural to consider the movement of fish between shelters as a stochastic (random) process, which leads to the use of a continuous time Markov chain model.

A continuous time Markov chain describes a sequence of stochastic transitions between a countable set of alternative states known as the state space. A Markov chain is by definition a stochastic process that retains no memory of previous states, so that the future state of the system is dependent solely on its present state. The dynamics of the system are defined by a matrix of transition rates $Q = (q_{jk})$ that give the rate at which a system in state j moves into state k . That is, the probability of moving from state j at time t to state k at time $t + dt$, where dt is small, is approximately $q_{jk} dt$. Typically there will be a choice of states one can move to; the time spent in state j is exponentially distributed with parameter $q_j = \sum_k q_{jk}$ (mean time spent in state j is thus $1/q_j$), and when the system does change state it moves to state k with probability q_{jk}/q_j . Given the rate matrix Q , it is therefore possible to calculate the probability of moving from any state j to state k in time t , and the equilibrium probability of the system being in any given state.

To model shelter use as a Markov chain, each possible distribution of K fish across S shelters is considered as a separate state. To reduce the state space to a level that makes computation feasible, the identity of fish is disregarded and individuals are considered to be equivalent. For example, if $K = 2$ and $S = 4$ there are 15 unique states (Table 3.1). Since shelters were never observed to contain more than three fish in the field, states with $n_i > 3$ were omitted to further reduce the state space.

Table 3.1 State space for $K = 2$ and $S = 4$. Two fish can be distributed across four shelters in 15 unique ways.

Shelter status of fish	No. of fish in shelters 1 to 4	State No.
Both fish are unsheltered:	(0,0,0,0)	1
One fish is sheltered and the other not:	(1,0,0,0)	2
	(0,1,0,0)	3
	(0,0,1,0)	4
	(0,0,0,1)	5
Fish occupy different shelters:	(1,1,0,0)	6
	(1,0,1,0)	7
	(1,0,0,1)	8
	(0,1,1,0)	9
	(0,1,0,1)	10
	(0,0,1,1)	11
Both fish occupy the same shelter:	(2,0,0,0)	12
	(0,2,0,0)	13
	(0,0,2,0)	14
	(0,0,0,2)	15

A transition occurs when a single fish moves in or out of a shelter. The probability of transition between states can therefore be derived from the rates of departure and colonisation described above. Let the current state be $\omega = (n_1, \dots, n_i, \dots, n_S)$.

When $N < K$, unsheltered fish are available to colonise shelters, and so:

$$\omega \rightarrow (n_1 + 1, \dots, n_i, \dots, n_S) \quad \text{at rate} \quad (K - N) \cdot \frac{c}{K^m} \cdot (1 - a)^{n_i} \quad (3.2)$$

$$\omega \rightarrow (n_1, \dots, n_i + 1, \dots, n_S) \quad \text{at rate} \quad (K - N) \cdot \frac{c}{K^m} \cdot (1 - a)^{n_i} \quad (3.3)$$

$$\omega \rightarrow (n_1, \dots, n_i, \dots, n_S + 1) \quad \text{at rate} \quad (K - N) \cdot \frac{c}{K^m} \cdot (1 - a)^{n_s} \quad (3.4)$$

Similarly, when $N > 0$ sheltered fish may depart from shelters:

$$\omega \rightarrow (n_1 - 1, \dots, n_i, \dots, n_S) \quad \text{at rate} \quad n_i \cdot d \quad (3.5)$$

$$\omega \rightarrow (n_1, \dots, n_i - 1, \dots, n_S) \quad \text{at rate} \quad n_i \cdot d \quad (3.6)$$

$$\omega \rightarrow (n_1, \dots, n_i, \dots, n_S - 1) \quad \text{at rate} \quad n_S \cdot d \quad (3.7)$$

Thus, for a given system (K, S) , the dynamics of shelter use are fully described by the parameters a , m , d and c .

3.3.2 Field experiment

3.3.2.1 Study site

The field experiment was conducted on the Brandy Stream (see section 1.5.2), during June and July 2002. Water temperature ranged from 12.9 to 17.4 °C (mean 14.8 °C) during the experiment (Seamon mini temperature recorder, Hugrún, Reykjavik, Iceland).

3.3.2.2 Experimental enclosures

The experimental manipulations were performed *in situ* using 10 cage enclosures, each 2.8 m long, 0.8 m wide (enclosed area = 2.24 m²) and 0.3 m high. Enclosures had solid metal sides and base and 6 mm wire-mesh on the up- and down-stream ends to permit water to flow through. The enclosures were established on 5 June in a broad riffle (water depth 0.17 - 0.22 m; water velocity 0.13 - 0.24 m/s) and filled with gravel to a depth of 25 mm. To protect fish from avian predators, the open top of each enclosure was covered with plastic netting. The up- and down-stream wire meshes were removed for several weeks prior to the start of each experiment to allow invertebrates to colonise the enclosures. Once replaced to enclose fish, the wire meshes were cleaned every 12 hours to remove accumulated plant debris and maintain water flow through the enclosures.

3.3.2.3 Experimental design

A factorial experimental design was used, crossing two levels of shelter density (S) with five levels of fish density (K). Four or eight upturned house bricks were placed in each enclosure to provide shelter (internal dimensions: 90 x 75 x 30 mm). To avoid confounding availability of shelter with changes in flow heterogeneity or visual connectivity, four additional solid bricks were placed in the low shelter density treatments to hold habitat complexity constant (Figure 3.1). Enclosures were stocked with 2, 4, 6, 8 or

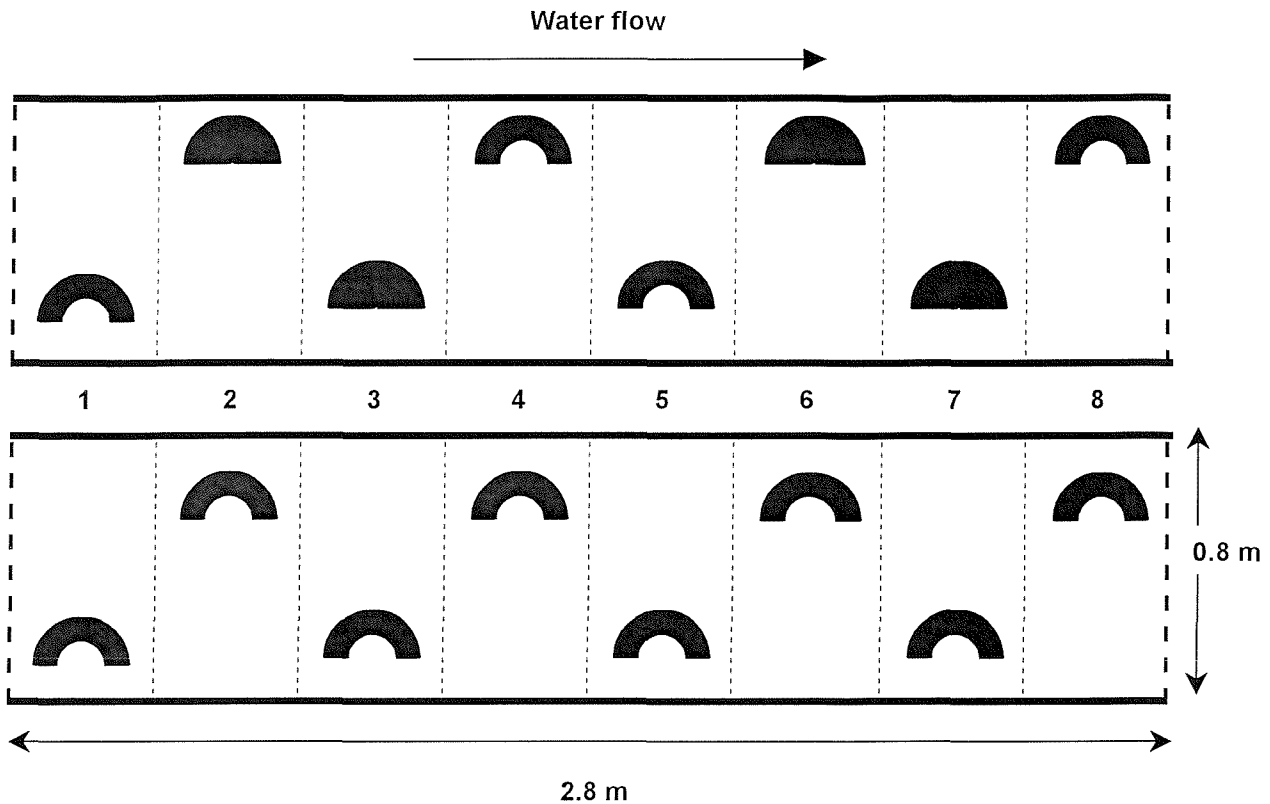


Figure 3.1 Flow-through stream enclosures were used to experimentally manipulate shelter density and fish density *in situ*. Enclosures contained either four or eight shelters (upturned house bricks), with four solid additional bricks in low shelter treatments to hold habitat complexity constant. Enclosures were then stocked with 2, 4, 6, 8 or 10 individually marked bullheads, and shelter use and longitudinal position (1-8) of each fish recorded twice daily for 10 days.

10 adult bullheads, corresponding to densities of 0.89 - 4.46 fish/m² that are within the natural range observed for bullheads in the Brandy stream (see Chapter 4). Two replicate trials were performed sequentially for each combination of treatments. Trials were conducted in two sets of ten (22 June - 3 July and 6 - 17 July).

3.3.2.4 Experimental protocol

All bullheads used in the study were collected from the Brandy Stream by electrofishing. For each set of trials, 60 fish were weighed to 0.01 g, measured to 0.1 mm (total length, TL) and individually marked using subcutaneous elastomer tags (Northwest Marine Technology Inc., WA, USA). Bullheads ranged in initial mass from 2.17 to 9.88 g (mean 3.50 g) and in TL from 56.8 to 89.2 mm (mean 64.5 mm). Fish were randomly assigned to treatments, and treatments randomly assigned to enclosures. New fish were used for each set of trials to ensure independence. For each trial, bullheads were allowed to acclimatise

for 48 h, after which use of shelter and longitudinal position (1 to 8 in Figure 3.1) of each individual were recorded by visual inspection twice daily (0730 - 0900 h and 1830 - 2100 h) for ten consecutive days. Enclosures were inspected in random order for each observation period. Diurnal observations provided an accurate measure of shelter use since bullheads were never observed to be active outside shelter during daylight hours. Two fish that died during the experiment were replaced with spare fish from a stock enclosure to maintain the treatments. At the termination of each trial, all surviving fish were reweighed and re-measured. Between trials, shelters were scrubbed and dried to remove any scent of previous occupants, and randomly reallocated to enclosures. The substrate in each enclosure was also redistributed.

3.3.3 Statistical analysis

3.3.3.1 Fitting the model

The Markov chain model was fitted to data from the field experiment using maximum likelihood to find the values of the parameters a , m , c and d that best reproduced the observed shelter use dynamics. To apply the model, shelter use of bullheads in each trial was represented as a sequence of states. The model assumes that a , m , c and d are constant, yet bullheads are known to be nocturnal (86 % of fish movements occurred at night), implying that these parameters are different from day to night. This complication was avoided by using only morning observations of fish shelter use (a total of 7 observations per trial at 24 hour intervals), and regarding the parameters as 24-hour averages. In this manner the transition rates can be considered constant for each time period.

For each trial, the likelihood of the observed sequence of states was determined for a given set of parameter values by calculating the conditional probability of observing each state given the preceding state and multiplying all conditional probabilities together to give a joint probability equal to the likelihood. The likelihoods from each trial were log-transformed and summed to give an overall log-likelihood (Hilborn & Mangel 1997). The maximum likelihood estimates (MLE) of a , m , c and d were then obtained using a constrained steepest-descent optimiser to maximise the log-likelihood.

The assumption that interference acts only on colonisation and not departure was validated by checking for density independence in the observed rate of departure of bullheads from shelter.

3.3.3.2 Individual-level responses

Responses of surviving bullheads were assessed by shelter use, growth in body size and movement rate ($n = 118$ data points). Shelter use was evaluated as the proportion of occasions an individual was observed in shelter. Growth was measured as the change in body mass and TL during the experiment, and used as an indicator of fitness. Movement rate was calculated as the mean distance between successive recaptures (units: sections per 12 h). Bullheads were successfully located on 93 % of occasions. When a fish was not located, it was considered to be out of shelter and distance moved was not recorded. Since the proportion of sheltered fish did not stabilise until five days into the experiment, only shelter use and movement data collected after this point were retained for analysis.

To investigate whether use of shelter by bullheads was dependent on body size, individual probability of shelter use was correlated with initial TL of fish. A correlation between body size and shelter use could be caused by intrinsic differences in shelter use efficiency or by asymmetrical competition between size classes. If intraspecific competition was the cause, however, any difference in shelter use between large and small fish is predicted to increase as shelter availability decreases. To test this prediction, the mean probability of shelter use was calculated separately for the largest 50 % and the smallest 50 % of the fish in each enclosure and expressed as a ratio. Values > 1 indicate that larger bullheads were more likely to occupy shelter than smaller fish, and vice versa. This was then regressed against shelter availability, expressed as shelters per fish (S/K).

To test the hypotheses that sheltered fish grow faster and move less than unsheltered fish, individual probability of shelter use was correlated with individual growth in mass, individual growth in TL and individual movement rate, with and without fish density and body size (initial TL) as partial correlates.

3.3.3.3 Population-level responses

Population-level responses of bullheads were assessed by calculating for each enclosure the mean growth and movement rate of surviving fish and the overall proportion of shelter use ($n = 20$ data points). Response variables were tested with Cochran's C-test for homogeneity of variances and analysed using a general linear model (GLM) with shelter density as a two-level fixed factor, fish density as a continuous fixed factor (covariate), and their interaction.

SPSS v 10.0 was used for all statistical tests, with response variables log-transformed where necessary. Statistical significance was evaluated at $\alpha = 0.05$.

3.4 RESULTS

3.4.1 Strength of exploitation and interference competition

The dynamics of shelter use of bullheads were well represented by the Markov chain model (Figure 3.2a). Maximum likelihood estimates (MLEs) of model parameters a , m , c and d were 0.93 ± 0.001 (95% C.I.), 1.40 ± 0.26 , 15.54 ± 302.4 and 0.51 ± 0.07 respectively. The MLE of a was close to 1, indicating strong exploitation competition and estimating that the probability of two fish sharing a shelter was less than 10 %. The MLE of m was significantly greater than 1, revealing strong interference competition that was an accelerating function of fish density. The high colonisation rate (c) relative to departure rate (d) showed that bullheads have high intrinsic shelter efficiency in the absence of conspecifics, although the high confidence interval for c indicates that the influence of colonisation rate is overridden by the other factors.

3.4.2 Individual-level responses

Bullheads displayed a high affinity for shelter, with 100 % shelter occupation in treatments where competition for shelter was lowest (Figure 3.2a). Sharing of shelters was uncommon, with shelters occupied by single fish on 84 % of occasions and two fish on 14 % of observation periods. Three fish were occasionally observed in a single shelter, but

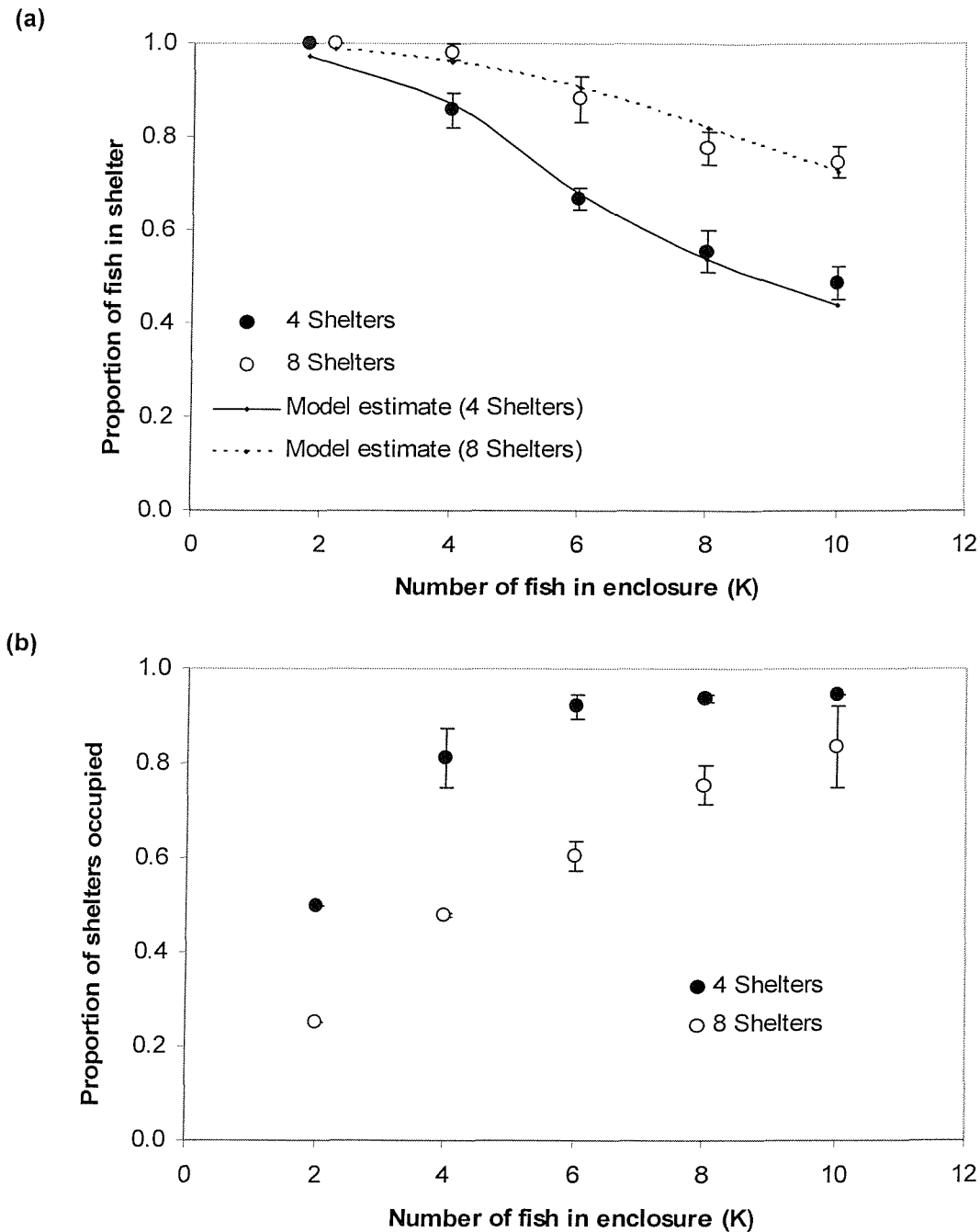


Figure 3.2 (a) Mean proportion of bullheads occupying shelter and (b) mean proportion of shelters occupied as a function of fish density (K) and shelter density (S) in cage enclosures. For each trial, shelter use was recorded twice daily for 10 days. Means (± 1 S.E.) are based on two replicate trials per treatment. Fitted lines in (a) show the mean proportion of bullheads in shelter estimated by the Markov chain model.

only at the highest fish density. Vacant shelters were observed in all treatments (Figure 3.2b). Use of shelters was very transient (Figure 3.3). The average duration of shelter occupancy was 1.5 days, and the probability of occupying a shelter for more than 3 days was just 5 %. The instantaneous probability of departure was independent of the duration of shelter occupancy (Figure 3.3).

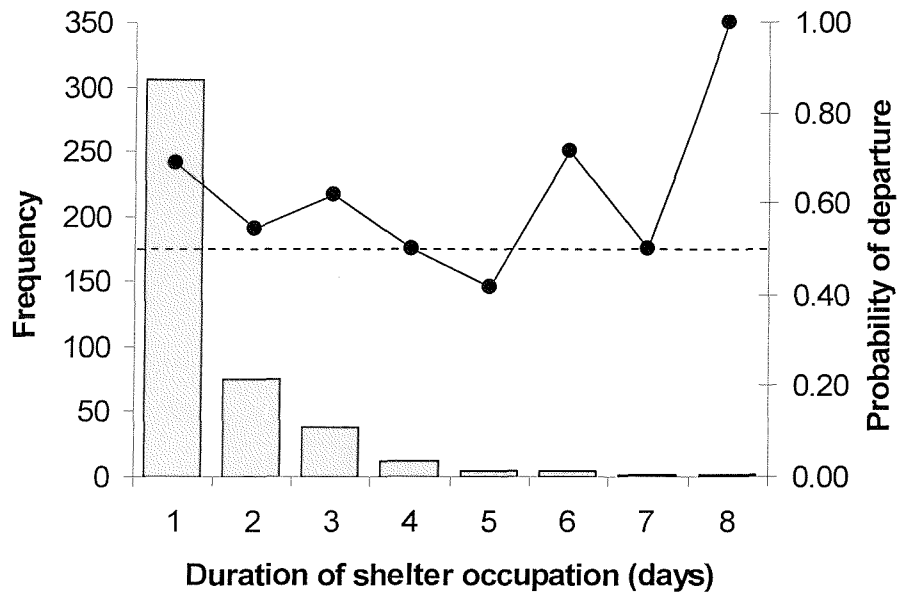


Figure 3.3 Duration of shelter occupation (bars) and instantaneous probability of departure from shelter (line) of individually marked bullheads in cage enclosures. $N = 444$ shelter occupation events. The horizontal dashed line indicates the Markov model estimate of departure probability ($d = 0.51$).

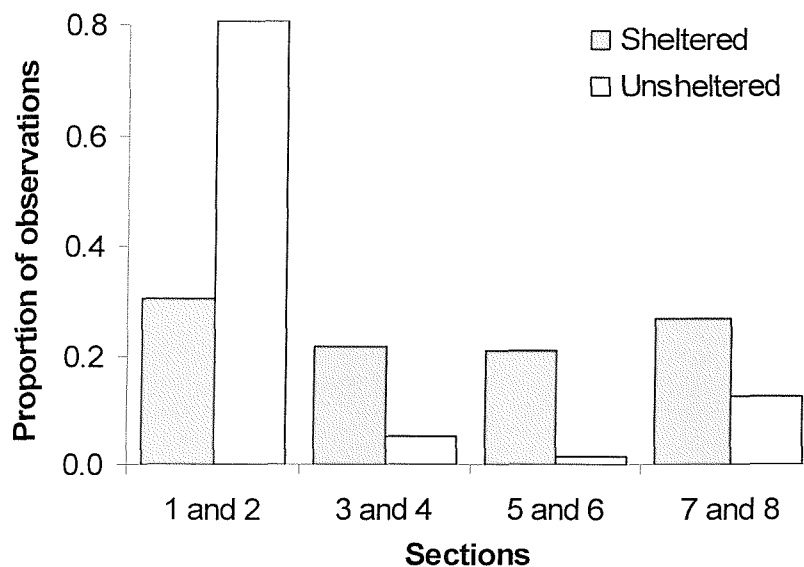


Figure 3.4 Longitudinal distribution of sheltered and unsheltered bullheads in cage enclosures (see Figure 3.1). Position of bullheads was recorded twice daily for 10 days.

Whilst sheltered fish were evenly distributed throughout the enclosures, unsheltered fish avoided central areas, with 80 % of recaptures made in sections 1 and 2 (Figure 3.4). This tendency to congregate at the upstream end of the enclosures suggested that unsheltered fish were attempting to emigrate.

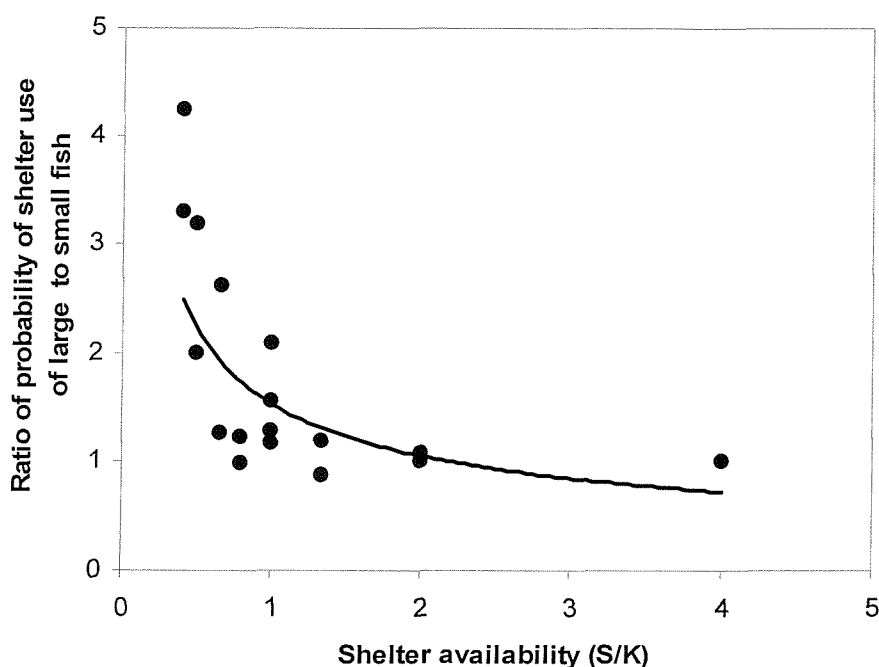


Figure 3.5 Probability of shelter use of large bullheads relative to that of smaller bullheads as a function of shelter availability (shelters per fish). A ratio of 1 indicates that the two size classes have an equal probability of shelter occupation. Two to ten bullheads were held in cage enclosures at two levels of shelter density and shelter use recorded twice daily for ten days. Regression line shows significant relationship ($P < 0.05$).

Probability of shelter use was positively correlated with body size (correlation: $r = 0.30$, $n = 118$, $P < 0.001$). Large fish consistently had a higher probability of shelter use than small fish across all treatments (Figure 3.5). Moreover, this advantage increased as shelter availability decreased (regression: $F_{1,10} = 5.210$, $P = 0.035$) with large fish nearly four times more likely be sheltered than small fish when shelter availability was most limited (Figure 3.5). There was no relationship between the proportion of time spent in shelter and growth in either body mass ($r = 0.16$, $n = 118$, $P = 0.086$) or TL (correlation: $r = 0.16$, $n = 118$, $P = 0.088$), even after statistically controlling for the effects of fish density and fish size.

The probability of a bullhead remaining faithful to a particular section over a 24 h period was 0.56 (Figure 3.6). Sheltered fish were more likely to move, and moved further, than unsheltered fish. Fish rarely moved more than four sections in a single day ($< 6\%$ of all

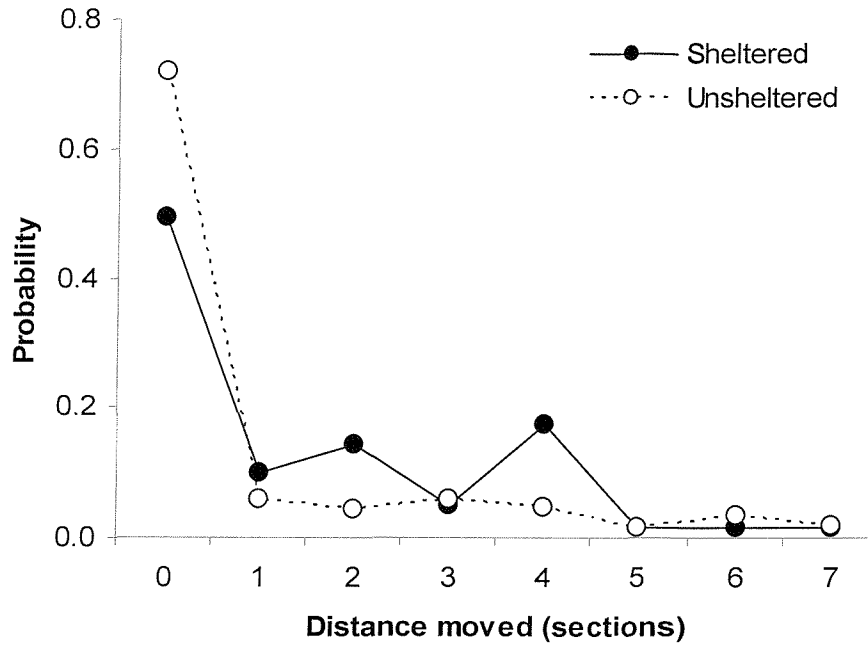


Figure 3.6 Probability of movement of sheltered and unsheltered bullheads. Fish were held in cage enclosures and net daily movement recorded for 10 consecutive days.

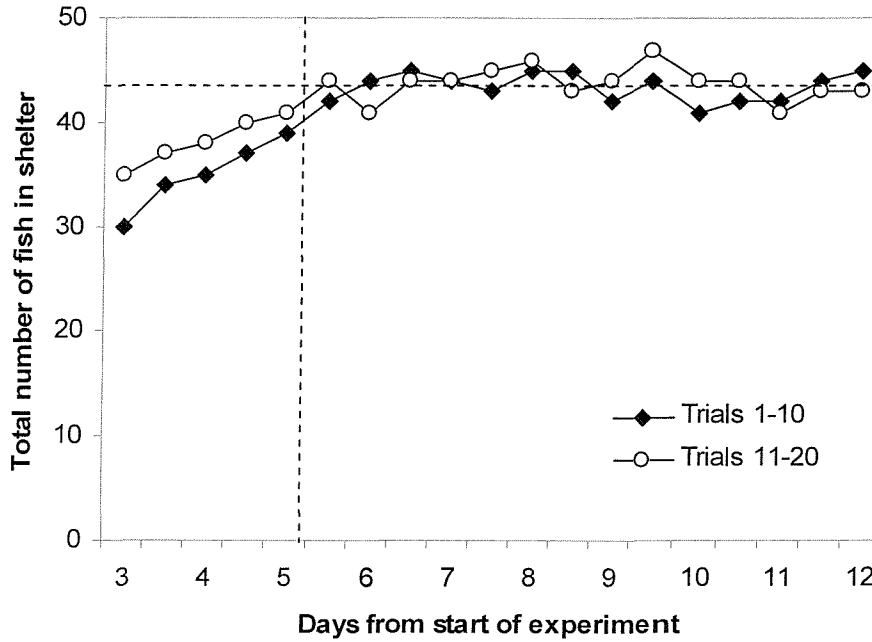


Figure 3.7 Change in number of bullheads occupying shelter over time. For each set of ten trials, the total number of fish in shelter across all enclosures (out of 60) is plotted at 12 h intervals. Shelter use stabilised five days after the start of the experiment as indicated by the dashed lines.

Table 3.2 Results of GLM for mean (a) probability of shelter use, (b) growth in mass, (c) growth in TL and (d) movement rate of bullheads stocked in enclosures at a range of densities under high and low shelter availability.

Source of variation	SS	df	MS	F	P
(a) Shelter use					
Density	0.418	1	0.418	188.088	< 0.001
Shelter	0.001	1	0.001	0.172	0.684
Density x Shelter	0.038	1	0.038	17.011	< 0.001
Error	0.036	16	0.002		
Total	0.626	19			
(b) Growth in mass					
Density	0.117	1	0.117	6.099	0.025
Shelter	0.005	1	0.005	0.267	0.612
Density x Shelter	0.003	1	0.003	0.160	0.694
Error	0.307	16	0.019		
Total	0.430	19			
(c) Growth in TL					
Density	1.496	1	1.496	6.174	0.024
Shelter	0.165	1	0.165	0.679	0.422
Density x Shelter	0.151	1	0.151	0.622	0.442
Error	3.877	16	0.242		
Total	5.540	19			
(d) Movement rate					
Density	0.001	1	0.001	0.001	0.997
Shelter	0.007	1	0.007	0.058	0.812
Density x Shelter	0.010	1	0.010	0.078	0.784
Error	2.037	16	0.127		
Total	2.047	19			

observations), but the use of enclosures may have caused movement rates of unsheltered fish to be underestimated. In contrast to the initial hypothesis, mean individual movement rate was positively correlated with probability of shelter use (correlation: $r = 0.25$, $n = 118$, $P = 0.010$). This relationship was still apparent after accounting for the potentially confounding effects of fish size and fish density (correlation: $r = 0.24$, $n = 118$, $P = 0.009$).

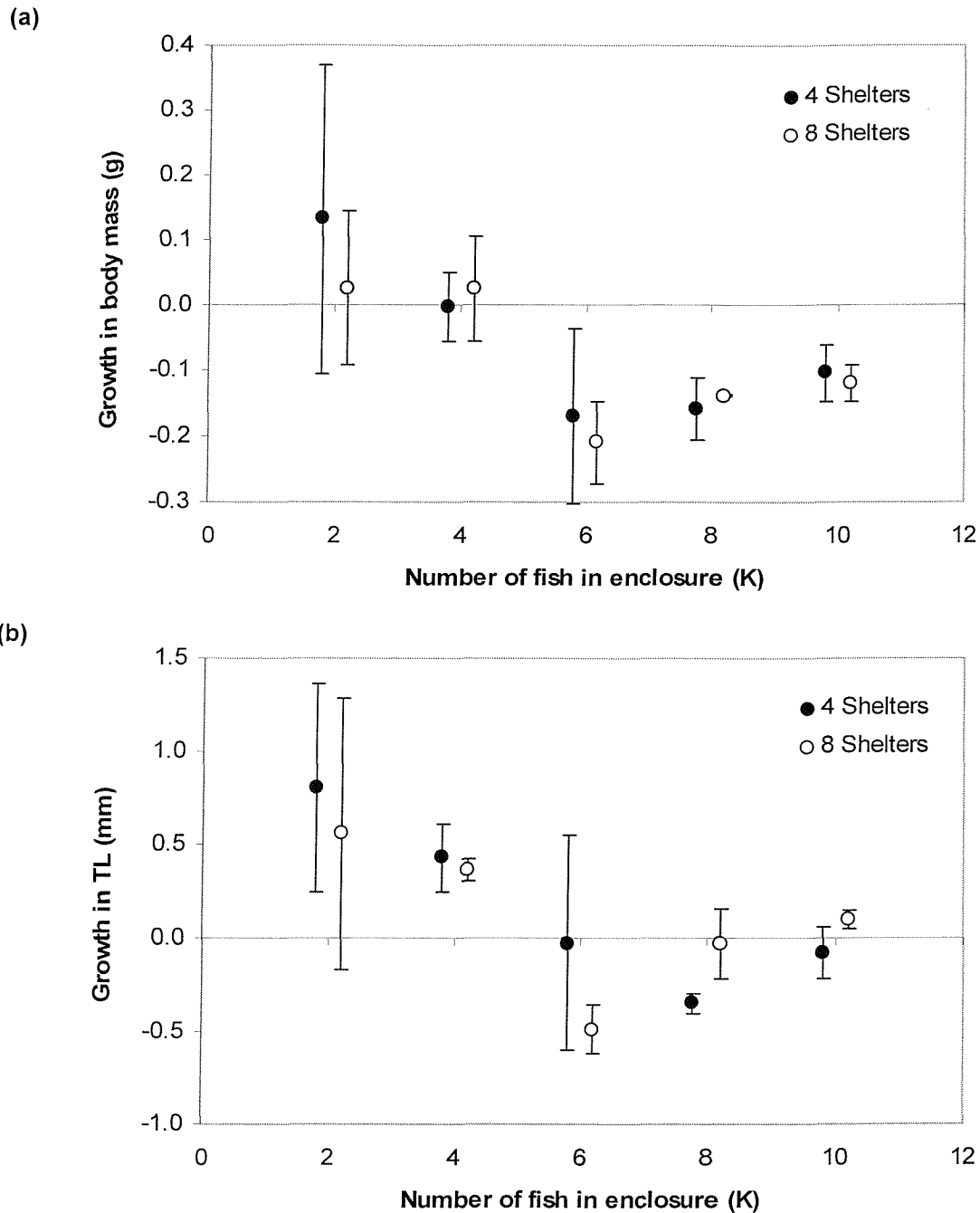


Figure 3.8 Mean growth in (a) mass and (b) TL of bullheads. Two to ten fish were stocked into enclosures under high and low shelter availability. Means (± 1 S.E.) are based on two replicate trials per treatment. Data points offset horizontally for clarity.

3.4.3 Population-level responses

Although bullheads rapidly colonised shelters, it took five days for the number of fish in shelter to stabilise (Figure 3.7), suggesting that equilibrium between colonisation and departure was reached only after an initial period of exploration. The proportion of fish in shelter was strongly density dependent (Table 3.2a), ranging from 100 % shelter use at the

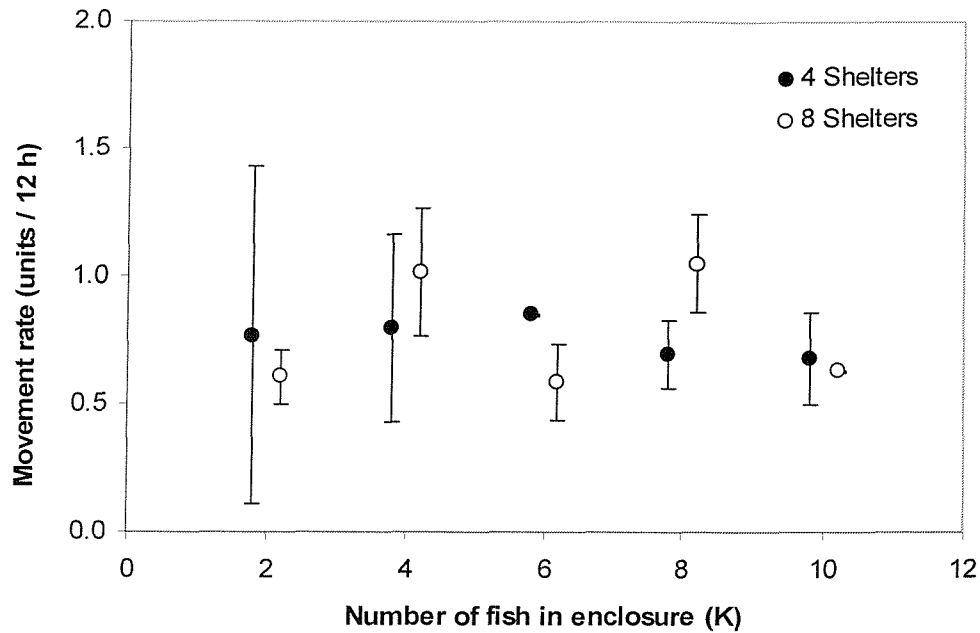


Figure 3.9 Mean movement rate of bullheads in cage enclosures as a function of fish density (K) and shelter density (S). Movement was calculated as the mean distance between successive recaptures. Means (± 1 S.E.) are based on two replicate trials per treatment. Data points offset horizontally for clarity.

lowest stocking density to 62 % at ten fish per enclosure (Figure 3.2a). Shelter use increased with increasing shelter density, but only at high fish densities when shelter availability was limiting (Table 3.2a; Figure 3.2a).

Mean growth in body mass of bullheads was negatively density dependent, with growth positive only at densities below 5 fish per enclosure (2.2 fish/m^2) (Table 3.2b; Figure 3.8a). There was no evidence, however, that density dependent growth was caused by competition for shelter since shelter availability had no effect on mean growth rates, nor on the form of the density dependent relationship (Table 3.2b; Figure 3.8a). Similar patterns were observed for growth in TL (Table 3.2c; Figure 3.8b). Mean movement rate of bullheads was 0.77 sections per 12 h (Figure 3.9). Movement was unaffected by fish density and shelter density (Table 1d).

3.5 DISCUSSION

3.5.1 Behavioural mechanisms of shelter use

The central goal of this study was to determine the influence of intraspecific competition on shelter use of individual bullheads, and to assess the consequences of individual behaviour for spatial distribution of fish and population dynamics. The application of a Markov chain model with biologically relevant parameters indicated that density dependent shelter use by bullheads was caused by a combination of exploitation and interference competition. Although shelter is known to be an important resource for many mobile animal species this is the first study to distinguish between, and quantify the strength of, contrasting competitive processes driving patterns of shelter use.

The detection of strong exploitation competition confirms previous anecdotal evidence that bullheads are solitary animals that defend shelters against colonisation by conspecifics (Smyly 1957). The frequency of shelter sharing predicted by the MLE of a was comparable to that observed in the field. Exploitation competition for shelter appears to be a widespread phenomenon in aquatic animals. Monopolising behaviour has been reported in a variety taxa, with individuals displacing both conspecifics (Gregory & Griffith 1996a; Mullen & Burton 1998; Figler *et al.* 1999; Harwood *et al.* 2002) and heterospecifics (Baltz *et al.* 1982; Greenberg 1988; Soderback 1994; Dubs & Corkum 1996; Guan & Wiles 1997; Vorburger & Ribi 1999; Harwood *et al.* 2002) from shelter. This study advances current understanding, however, by testing the assumption that a shelter can be occupied by a maximum of one individual, and estimating the strength of exploitation competition as the probability that two individuals will share a shelter. Factors that affect the level of aggression and hence the strength of exploitation competition will therefore have a strong influence on the carrying capacity of the environment. For example, hatchery-reared Atlantic salmon (*Salmo salar*) share shelters with much greater frequency than wild-reared fish (Griffiths & Armstrong 2002). Residence times of fish sharing a shelter were similar to those for solitary sheltered fish, suggesting that sharing was a stable arrangement that occurred between individuals of equivalent dominance. Although shelter defence is a common phenomenon, the benefit of monopolising a shelter is unclear. The probability of prey in structurally complex refuges being detected by predators is predicted to be positively density dependent (Rangeley & Kramer 1998), and so solitary shelter use may

minimise the chance of being detected by predators that use olfactory cues (Armstrong & Griffiths 2001; Griffiths & Armstrong 2002) and employ area-restricted searching (Rangeley & Kramer 1998). Defensive behaviour is therefore thought to be a strategy to reduce predation risk, but further studies are needed to test this hypothesis.

Bullheads also exhibited strong interference competition for shelter. Shelters were widely spaced within enclosures, so providing a conservative test of the strength of interference competition. Aggressive interactions between bullheads outside of shelters are common and take the form of threat displays, chasing and occasionally fights (Ladich 1989; A. Davey, *personal observation*). Density dependence in the colonisation efficiency of benthic shelters by bullheads is therefore thought to be an indirect consequence of territorial competition for foraging space at night. Interference competition is often considered to be a non-linear function of competitor density, with no or negligible interference at low density and stronger interference at higher densities as conspecifics come into closer proximity (Goss-Custard *et al.* 1995; Stillman *et al.* 1997). Consequently, the apparent accelerating intensity of interference with fish density ($m > 1$), is thought to be the result of density-dependent changes in individual behaviour rather than a synergistic interference effect amongst bullheads. Since this is the first study to explicitly recognise and test for interference competition for shelter, the influence of this process on dynamics of shelter use is likely to have been overlooked to date.

Individual fish did not have an equal probability of shelter use. Large bullheads were more likely to occupy shelters than small bullheads. Furthermore, the advantage associated with large body size increased with declining shelter availability, indicating that differences in shelter use between size classes were the result of asymmetrical intraspecific competition rather than intrinsic differences in shelter use efficiency. This finding is in agreement with previous studies that show that body size is a good predictor of success in one-on-one contests for shelter (Mullen & Burton 1998; Figler *et al.* 1999) and space (Sloman & Armstrong 2002). Individual shelter use was also positively correlated with movement rate. Although it is not possible to attribute cause and effect, it seems counterintuitive that occupation of shelter would cause fish to be more mobile. Rather, it seems likely that more mobile fish have a greater probability of locating shelters and are therefore more efficient colonisers. Mobility is thought to enhance the acquisition of resources that are distributed

unpredictably in time or space (Martin-Smith & Armstrong 2002). Thus, although the spatial configuration of shelters is static, the distribution of vacant shelters is in a continuous state of flux and so high mobility is required to track shelter availability.

3.5.2 Consequences for population-level processes

Shelter can influence populations at two levels. First, shelter density will determine local carrying capacity if unsheltered fish emigrate out of a patch to seek shelter. Second, shelter availability will limit total population size if unsheltered fish suffer a reduction in some component of fitness (growth, reproductive success, survival). These processes may be linked if unsheltered individuals emigrate or are displaced to lower quality habitat. Experimental addition of shelter has clearly demonstrated that shelter density is an important determinant of local fish abundance in the field (Boussu 1954; Saunders & Smith 1962; Eklöv & Greenberg 1998) but a lack of mechanistic understanding means that it is often not possible to determine whether short term numerical gains are the result of inward migration or increased survival (Bohnsack 1989).

In the current study, the high affinity of fish for shelter, density dependent shelter use and emigration of unsheltered fish from enclosures together suggest that competition for shelter can limit local population density. This study adds to a small body of literature showing that shelter use may be density dependent as a result of intraspecific competition (Armstrong & Griffiths 2001) or density dependent anti-predator tactics (Rangeley & Kramer 1998). Density dependent emigration is a common response to competition (Chapman 1962; Mesick 1988; Keeley 2001) and emigration of subdominant individuals in response to territorial competition for space has been shown to be an important process regulating populations of drift-feeding stream fish (Elliott 1990). Competition for shelter therefore also has the potential to regulate populations of benthic stream fish.

Most previous experimental manipulations of shelter density have confounded shelter availability with habitat complexity. More complex habitat structure may also increase local carrying capacity in territorial species by visually isolating conspecifics and thereby reducing intraspecific competition (Kalleberg 1958; Imre *et al.* 2002). By holding habitat complexity constant, this study demonstrates that shelter availability *per se* can affect local

density of mobile animals, although structural complexity cannot be eliminated as a factor influencing the spatial distribution of bullheads.

Interference for shelter also has at least two important implications for the spatial distribution and local abundance of benthic organisms such as bullheads. Firstly, local abundance may be limited by behavioural interactions independently of shelter availability, as colonisation rate becomes negligible at high fish density. This effect may account in part for the failure of bullheads to colonise all available shelters at high fish densities. Secondly, probability of shelter use may be affected by the spatial configuration as well as the abundance of shelters. Agonistic interactions are predicted to be more intense when shelters are clumped than when they are evenly dispersed. Under these conditions, local carrying capacity will not be a simple linear function of shelter availability.

There was little evidence that fitness of bullheads was affected by shelter availability. In contrast to Fischer (2000), who found that lack of adequate shelter can substantially affect metabolic rate and somatic growth of burbot (*Lota lota*), sheltered bullheads did not grow significantly faster than unsheltered individuals. Although mean growth in body size of bullheads was density dependent, increasing shelter density did not enhance fish growth, indicating that density dependent growth was not caused by a physiological response to shelter availability. Thus, responses of benthic fish to shelter absence are species-specific and will depend on the physiological constraints and behavioural flexibility of the species concerned (Fischer 2000). Shelter use may also influence fitness via changes in mortality rate. This study was unable to test whether unsheltered bullheads suffered increased predation risk. However, competition for shelter has been shown to result in density dependent predation mortality in damselfishes (Holbrook & Schmitt 2002) and asymmetrical competition between size classes has the potential to regulate populations by limiting recruitment of juveniles to adult habitats (Freeman & Stouder 1989). Competition for shelter could therefore account for the winter bottleneck observed in some stream fish (Gregory & Griffith 1996a), but further experiments are required to investigate the fitness consequences of shelter use.

3.5.3 Conclusions

Availability of shelter can control the spatial distribution of mobile animal species and limit their abundance by providing protection from predation and abiotic factors. The functional relationship between shelter availability and population-level processes will depend upon the behavioural mechanisms of shelter use and the qualitative and quantitative effects of shelter occupation on individual fitness. This study shows that exploitation and interference competition for shelter can result in density dependent shelter use and unequal access to shelter favouring large individuals. Interference competition will decouple local carrying capacity from shelter density, although direct agonistic interactions may be moderated by habitat complexity. Competition for shelter may therefore strongly affect the habitat use of bullheads, but its influence on population dynamics will depend upon whether subordinate individuals that are displaced to sub-optimal habitats suffer reduced fitness.

- 4 -

PATTERNS AND PROCESSES OF MICROHABITAT SELECTION IN A CHALK STREAM FISH COMMUNITY

4.1 ABSTRACT

Interspecific differences and ontogenetic shifts in microhabitat selection are common in freshwater fish. The aim of this study was to investigate the patterns and processes of microhabitat selection in a benthic stream fish community. Summer microhabitat use of bullheads *Cottus gobio* and stone loach *Barbatula barbatula* was surveyed by point abundance electrofishing. Both species displayed strong patterns of microhabitat selection. Bullheads selected riffles and the margins of macrophytes, whilst stone loach selected areas with high vegetation cover. Significant interspecific differences in microhabitat use were evident, possibly as a consequence of contrasting foraging strategies, but high intraspecific variation in habitat use meant that spatial segregation between the species was limited. Bullheads displayed an ontogenetic change in microhabitat use, with adults occupying coarser substrata than juveniles, particularly in unshaded parts of the stream. The mechanism underlying this habitat shift was investigated by experimentally manipulating bullhead density, size-class composition and light intensity under controlled laboratory conditions. At low fish density, both juvenile and adult fish preferred cobbles providing interstitial shelter, but at high fish density a significant proportion of juveniles were displaced onto finer substrata. Density dependent habitat use indicates that ontogenetic shifts in microhabitat use of bullheads are caused, at least in part, by competitive interactions between size classes rather than size-specific habitat preferences. Light intensity had no significant effect upon habitat selection, but some marginally non-significant effects suggested that light intensity may modify the strength of intraspecific competition. Thus, habitat partitioning in stream fish is influenced by a combination of competitive interactions and size- and species-specific morphological and behavioural adaptations.

4.2 INTRODUCTION

Resource partitioning is commonplace in nature (Toft 1985; Ross 1986; Schoener 1986). Theoretical consideration of interspecific resource partitioning based upon optimal foraging models suggests that species should segregate preferentially by habitat and subsequently along the trophic and temporal axes (Schoener 1974, 1986). Spatial segregation of species as a result of differences in microhabitat selection is thought to moderate interspecific competitive interactions and has been identified as an important mechanism of co-existence in ecological communities (Schoener 1986; Arlettaz 1999; Young 2001). Changes in microhabitat use during ontogeny result in intraspecific habitat partitioning between size classes (Polis 1984; Werner & Gilliam 1984). Population dynamics are therefore affected by processes operating within stages and by factors influencing transitions between stages (Mittelbach & Osenberg 1993; Beck 1995; Dahlgren & Eggleston 2000). Understanding the processes that generate interspecific and intraspecific differences in microhabitat use is therefore crucial to elucidating the controls on local species diversity and population size.

The physical complexity of the lotic environment offers much scope for spatial segregation of species and size classes, and interspecific microhabitat partitioning (Ross 1986) and ontogenetic microhabitat shifts (Werner & Gilliam 1984) are both common phenomena in stream fish. Important axes of organisation include water depth (Schlosser 1987; Gorman 1988; Harvey & Stewart 1991), water velocity (Facey & Grossman 1992; Mullen & Barton 1995) and substrate size (Finger 1982; van Snik Gray & Stauffer 1999). Microhabitat selection by stream fish is determined by a suite of interacting factors, including predation (Schlosser 1987; Harvey & Stewart 1991), food availability (Hill & Grossman 1993; Petty & Grossman 1996), physical constraints (Facey & Grossman 1992), and competition (Baltz *et al.* 1982). Selective segregation occurs as a result of species-specific or size-specific differences in vulnerability to predators, foraging behaviour or swimming ability (Schlosser & Toth 1984; Matthews 1985; Facey & Grossman 1992). Under these circumstances, fish are responding independently to extrinsic factors due to their unique morphological and behavioural adaptations. Microhabitat partitioning may also be caused by interactive segregation, whereby species or size classes diverge in microhabitat use in

response to interspecific or intraspecific competition (Greenberg 1988; Freeman & Stouder 1989; Mullen & Burton 1998; Young 2001).

The degree to which observed differences in microhabitat use indicate competitive interactions in contemporary fish communities has been the subject of much debate (Ross 1986; Heins & Matthews 1987). Distinguishing between selective and interactive mechanisms of resource partitioning using observational field data has proved to be difficult for a number of reasons. Firstly, in natural experiments, changes in habitat use in response to potential competitors are often confounded by spatial or temporal variation in habitat availability (Underwood 1986). Secondly, competitive interactions may be context dependent, leading to complex patterns of spatial segregation. For example, water temperature can switch the outcome of interspecific competition (Baltz *et al.* 1982; Taniguchi & Nakano 2000) and alter the intensity of competitive interactions (Greenberg 1988; Vehanen *et al.* 1999), and light intensity may also affect competitive interactions among fish, both directly (Valdimarsson & Metcalfe 2001) and indirectly (Britz & Pienaar 1992). As a result, knowledge of the role of competition in determining microhabitat use of stream fish remains cursory.

The principle aim of this study was to investigate the patterns and processes of microhabitat selection by two benthic fish, bullheads *Cottus gobio* and stone loach *Barbatula barbatula*, in a southern English chalk stream. Firstly, patterns of daytime (sheltering) microhabitat selection were described by surveying habitat use and habitat availability in the field. The specific objectives of this part of the work were:

- (i) to identify patterns of microhabitat selection of bullheads and stone loach;
- (ii) to compare the microhabitat use of bullheads and stone loach; and
- (iii) to compare the microhabitat use of juvenile and adult bullheads.

Secondly, the mechanisms determining microhabitat selection in bullheads were investigated experimentally under controlled laboratory conditions. I hypothesised that observed ontogenetic microhabitat shifts by bullheads in the field are caused by asymmetrical intraspecific competition between size classes and that strength of intraspecific competition depends on light intensity. To test this hypothesis, use of contrasting pebble and cobble habitat patches by adult and juvenile bullheads was recorded whilst manipulating bullhead density, size-class composition and light intensity.

4.3 METHODS

4.3.1 Field survey

4.3.1.1 Study site

The field survey was carried out on the Brandy Stream, a side channel of the River Itchen in southern England (see section 1.5.2 for details). At the study site, the stream flows across a broad floodplain and is shaded in places by a mature hedgerow of bramble (*Rubus allegheniensis*), hawthorn (*Crataegus monogyna*), laurel (*Laurus nobilis*), sycamore (*Acer pseudoplatanus*) and ash (*Fraxinus excelsior*). The channel has limited pool-riffle development, and the substratum is composed of a heterogeneous mosaic of flint gravels and cobbles overlain by silt where macrophytes promote sedimentation. The fish community is numerically dominated by bullheads and stone loach, with minnows (*Phoxinus phoxinus*), brown trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*), grayling (*Thymallus thymallus*), three-spined stickleback (*Gasterosteus aculeatus*), eels (*Anguilla anguilla*), pike (*Esox lucius*) and brook lamprey (*Lampetra planeri*) also present at low densities.

4.3.1.2 Sampling protocol

Sampling was conducted between 28 - 30 August 2002 along a 400 m length of channel. Three reaches, each about 40 m long and representative of the stream as a whole, were selected for intensive study. At each reach, 16 - 21 transects were established perpendicular to the bank at 2 m intervals. Microhabitat use and availability were measured at 1 m intervals along each transect, with the position of the first sampling point determined at random. A total of 280 points were sampled, each covering an area of 0.3 x 0.3 m (0.09 m²). Flow conditions were stable during the sampling period and water temperature ranged from 14.5 to 16.0°C (Seamon mini temperature recorder, Húgrún, Reykjavík, Iceland).

The daytime (0830 - 1800 h) sheltering microhabitat use of bullheads and stone loach was investigated using point abundance sampling by electrofishing (Copp & Garner 1995). Sampling took place in an upstream direction to minimise disturbance to unsampled areas. At each sampling point, fish were immobilized using an electrofishing unit (Electracatch, Wolverhampton, UK) fitted with a 0.15 m diameter anode. The small active radius and

concentrated electrical current generated by a small anode gives high precision and catching efficiency and facilitates the capture of small fish (Bohlin 1989; Copp & Garner 1995). Each point was fished for 5 seconds whilst disturbing the substrate to maximise capture efficiency, and all fish collected using a pond net. Care was taken to collect only those fish that were immobilised in the sampling area, to avoid over-estimating densities and mis-characterising microhabitat use. Total length (TL) of each fish was measured to the nearest mm. Bullheads were classified as adults or juveniles on the basis of TL. In chalk streams, bullheads reach sexual maturity at about 50 mm TL (Fox 1978c) and this length was therefore used to distinguish between the two size classes.

The microhabitat at each sampling point was described by measuring nine environmental variables: channel width, distance to nearest bank, total depth of water column, water velocity, cover, shade, vegetation, substratum composition and substratum stability. Widths and distances were measured to the nearest 0.1 m, and water depth to the nearest 0.01 m. Water velocity was measured close to the stream bed using a flowmeter (Model 10.150, Ott, Kempten, Germany) fitted with a 48 mm diameter propeller. The percentage of cover, shade and vegetation at each point were estimated visually on a five-point scale (0 = 0 %; 1 = 1-25 %; 2 = 26-50 %; 3 = 51-75 %; 4 = 76-100 %). Instream cover was defined as submerged structures (other than vegetation or substratum) beneath which fish could be hidden from overhead view, such as logs, roots, branches and floating detritus. Overhead cover was defined as aerial structures less than 0.5 m above the water surface able to obscure a fish from overhead view, for example undercut banks and overhanging vegetation. Degree of shading was estimated by the percentage of sky obscured by the overhead tree canopy and bankside vegetation. Percentage coverage was also recorded for each species of submergent and emergent macrophyte, all macrophytes combined, and for filamentous algae. Turbulence can also provide visual isolation from predators and so the occurrence of a broken water surface was scored as present or absent. The dominant substratum at each point was classified according to a modified Wentworth scale (Heggenes & Saltveit 1990) (Table 4.1). The largest substrate size present was also recorded, where different. Finally, the stability of the substratum was scored on a three-point scale (0 = uncompacted; 1 = stable; 2 = armoured).

Table 4.1 Modified Wentworth scale for stream substratum classification. Substrate size is measured along the longest axis.

Substratum type	Size (mm)	Class
Silt	<0.06	1
Sand	0.06 - 2	2
Fine gravel	2 - 8	3
Gravel	8 - 16	4
Small pebble	16 - 32	5
Pebble	32 - 64	6
Small cobble	64 - 128	7
Cobble	128 - 256	8
Boulder	>256	9

4.3.1.3 Statistical analysis

Total variation in microhabitat availability was summarised by performing a principal components analysis on the habitat variables x sample points matrix. Principal component axes (PCA) that were ecologically interpretable and had eigenvalues greater than 1 were retained for analysis. Individual fish were assigned the values of the habitat variables recorded for the point where it was found. Each fish was then scored for each component by multiplying the component score coefficients by the microhabitat data for that specimen. Components were divided into score classes and frequency distributions plotted to estimate both microhabitat availability and microhabitat use along each PCA. Using the availability data as expected frequencies, a G-test for goodness of fit was conducted to test for non-random habitat use by each species. Score classes were pooled where necessary to ensure that all expected frequencies were greater than 5 (Sokal & Rohlf 1995). If a significant result was obtained, a partitioned G-test was conducted to determine which classes were significantly over- or under-utilised (Zar 1999).

The strength of habitat selection along component axes was quantified by calculating a preference index for each score class using the formula of Jacobs (1974):

$$D = \frac{r - p}{r + p - 2rp} \quad (4.1)$$

where r is the proportion of resource use by the fish, and p the proportion of resource available in the environment, for that class. This index gives values from 1 (strong selection) to -1 (strong avoidance).

Differences in microhabitat use between bullheads and stone loach, and between adult and juvenile bullheads, were tested by one-way ANOVA. PCA scores and habitat variables were tested with Cochran's C-test for homogeneity of variances and transformed where necessary to normalise distributions and stabilise variances. Following exploratory analysis, a general linear model (GLM) was constructed to investigate the interactive effects of shade and fish size on substrate use by bullheads. All analyses were performed using SPSS v.10.0 (SPSS Inc., Chicago) and evaluated for significance at $\alpha = 0.05$.

4.3.2 Laboratory experiment

4.3.2.1 Experimental system

Three glass tanks were set up in a temperature-controlled room at the University of Southampton. Tanks measured 0.9 m (L) x 0.3 m (W) x 0.3-0.4 m (H) and were filled with pea gravel to a depth of 25 mm. Patches of coarse and fine substrata were established at opposite ends of each tank by adding either 6 cobbles (mean length = 144 mm \pm 16 S.D.) or 85 pebbles (mean length = 40 mm \pm 11 S.D.) to provide shelter. These two substrate classes were chosen to correspond to those selected most strongly by adult and juvenile bullheads in the Brandy Stream. The position of the cobbles and pebbles in the two halves of each tank was determined at random and switched after every two or three trials. A central drop-gate in each tank allowed the habitat patches to be isolated without disturbing the fish. Tanks were filled with water to a depth of 0.15 m and the sides covered with black plastic to minimise disturbance to the fish. Two airstones were positioned in the back corners of each tank. Water temperature during the experiment was measured daily with a thermometer and varied from 15.5 °C to 17.0 °C (mean 16.2 °C).

Artificial lighting with a 14 h light: 10 h dark photoperiod was provided by a set of fluorescent tubes positioned 1 m above the tanks (day), and a single incandescent bulb at floor level (night). To manipulate light intensity, sheets of cardboard were positioned above tanks to provide shading. A one-way ANOVA showed no dependence of mean

water temperature on shade treatment in the previous 24 h ($F_{1,26} = 0.036$, $p = 0.593$) indicating that experimental manipulations of light intensity were not confounded by changes in water temperature.

To compare light levels in the laboratory with those on the Brandy Stream, light intensity was measured using a photometer (model LI-250 - Li-COR BioSciences, Nebraska, USA) fitted with a Quantum sensor. The Quantum sensor measures photosynthetically active radiation (PAR) intensity (units: $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$). All readings were therefore converted to photometric visible radiation (units: lux or lumens/m²) using published conversion factors (McCree 1972). Laboratory measurements were made during the day and night under both unshaded and shaded conditions. Equivalent readings were taken in the field at midday and midnight under both 0 and 100 % tree canopy cover. All measurements were 15 second averages of light intensity at the water surface.

4.3.2.2 Experimental design

To investigate microhabitat use of bullheads, five different stocking treatments (8 juveniles, 16 juveniles, 8 adults, 16 adults, and 8 juveniles plus 8 adults per tank) were crossed with two levels of light intensity, high (unshaded) and low (shaded) (Figure 4.1). This factorial design permitted examination of the effect on bullhead habitat use of (i) total fish density, (ii) size-class composition (i.e. the relative effect of adding juvenile and adult bullheads), (iii) light intensity, (iv) interaction of light intensity with fish density and (v) interaction of light intensity with size-class composition. Each combination of treatments was replicated 4 times, giving a total of 40 trials. Trials were conducted in sets of three between 11 September and 11 October 2002. Treatments were randomly allocated to trials, with the logistical constraint that light conditions were the same for trials conducted simultaneously.

4.3.2.3 Study animals

All bullheads used in the experiment were collected from the Brandy Stream on 11 September 2002. Individuals less than 50 mm TL were classified as juveniles. Body mass of juvenile fish ($n = 49$) ranged from 0.28 g to 1.56 g (mean 0.78 g), and TL from 33 to 48 mm (mean 40 mm). Adults ($n = 32$) ranged in mass from 2.23 g to 5.05 g (mean 3.30 g)

		STOCKING TREATMENT				
		8 Juveniles	16 Juveniles	8 Adults	16 Adults	8 Juveniles + 8 Adults
LIGHT INTENSITY	High (Unshaded)	A $n = 4$	B $n = 4$	C $n = 4$	D $n = 4$	E $n = 4$
	Low (Shaded)	F $n = 4$	G $n = 4$	H $n = 4$	I $n = 4$	J $n = 4$

Figure 4.1 Experimental design to investigate microhabitat use of juvenile and adult bullheads in relation to light intensity, fish density and size-class composition. Four replicate trials were conducted for each combination of treatments (A-J).

and in TL from 54 to 74 mm (mean 63 mm). These mean lengths corresponded closely to those observed for juvenile and adult fish in the field (38 and 60 mm respectively).

4.3.2.4 Experimental protocol

For each set of three trials, bullheads were randomly assigned to treatments, and fish distributed equally between cobbles and pebbles. Surplus fish were held in a large stock tank between trials. Because of limited availability of experimental fish, individual bullheads were reused in subsequent trials, with fish randomly reassigned to treatments each time. Using the same fish more than once is less than ideal and could be construed as pseudo-replication (Hurlbert 1984). However, randomly reassigning fish in each set of trials avoids biasing the outcome of the experiment. Furthermore, this approach does not inflate statistical power by increasing the degrees of freedom, since the trial is retained as the experimental unit. The only assumption is, therefore, that the fish used in this experiment are a representative sample of the wild population. Microhabitat use of bullheads was assessed by releasing the drop-gates, searching both sides of each tank by hand and counting the number of fish on each substrate type. Observations were made after approximately 24 and 48 h, with the exception of trials 1 to 6, which were surveyed after 48 h only. Following observations at 24 h, fish were allowed to settle for 10-15 minutes before the drop-gates were raised. All observations were conducted between 1200 and 1600 h. Fish were fed *ad libitum* with live *Gammarus pulex* between trials.

4.3.2.5 Statistical analysis

Habitat use was evaluated as the proportion of fish occupying the cobble substrate. Data collected after 24 and 48 h were averaged to give a single data point for each trial. Response variables were arcsine-transformed to normalise residuals, and tested for homogeneity of variance using Cochran's C-test. For each size class of bullhead, the effect of stocking treatment and light intensity on habitat use was first examined by one-way ANOVA. Specific hypotheses were then tested by five *a priori* contrasts. Contrast 1 tested the null hypothesis of no effect of light intensity by comparing treatments A+B+E with treatments F+G+J for juveniles, and treatments C+D+E with treatments H+I+J for adults (Figure 4.1). Contrast 2 tested for density dependent habitat use by contrasting low (8 fish per tank) and high (16 fish per tank) density treatments (A+F vs. B+G+E+J for juveniles and C+H vs. D+I+E+J for adults; Figure 4.1). Contrast 3 examined the effect of size-class composition by comparing the relative effect of adding juveniles and adults (B+G vs. E+J for juveniles and D+I vs. E+J for adults; Figure 4.1). Contrast 4 tested the null hypothesis of no interaction between light intensity and fish density, and contrast 5 tested the null hypothesis of no interaction between light intensity and size-class. These contrasts decompose the among treatment sums of squares and are orthogonal to one another, together accounting for all explained variation in habitat use. The error mean square was therefore used as the denominator for all *F*-ratios. SPSS v.10.0 (SPSS Inc., Chicago) was used for all statistical procedures except for contrasts, which were performed by hand (see protocol in Appendix A). $\alpha = 0.05$ was used to evaluate statistical significance.

4.4 RESULTS

4.4.1 Field survey

4.4.1.1 Habitat availability

In the study reach, channel width varied between 3.4 to 7.0 m (mean 5.2 m), water depth ranged from 0.03 to 0.50 m (mean 0.21 m) and water velocity varied from 0.00 to 0.50 m/s (mean 0.19 m/s). Fine substrata were more abundant than coarser substrate types, with silt covering 31 % of the stream bed and boulders accounting for only 1 %. Total plant cover was approximately 32 %, of which 18 % was lesser water parsnip (*Berula erecta*), 7 %

water crowfoot (*Ranunculus penicillatus*) and 5 % water cress (*Rorippa nasturtium-aquaticum*). Starwort (*Callitriche* spp.), yellow flag (*Iris pseudacorus*), Canadian pondweed (*Elodea canadensis*), willow moss (*Fontinalis antipyretica*), water mint (*Mentha aquatica*), water speedwell (*Veronica anagallis-aquatica*) and water forget-me-not (*Myosotis scorpioides*) were present at low levels (less than 1 % total coverage). In addition, filamentous *Cladophora* algae (blanket weed) covered approximately 10 % of the stream bed. The degree of shading was highly variable, with 31 % of sampling points unshaded and 29 % heavily shaded (> 75 % cover).

The principal components analysis extracted nine principal component axes (PCA) with eigenvalues greater than 1, but only the first three components were ecologically interpretable and retained for further analysis (Table 4.2). The first axis (PCA 1; 13.9 % of total variance) described a geomorphological gradient from riffles to pools. Water velocity, surface turbulence and substrate size loaded positively, whilst water depth and channel width loaded negatively. PCA 2 (10.7 %) distinguished marginal areas from mid stream sites; overhead cover, watercress and yellow flag had positive loadings and water parsnip and *Cladophora* algae had negative loadings. Finally, PCA 3 (9.5 %) was best explained as a vegetation axis, being positively correlated with water parsnip and total plant cover and negatively correlated with substrate size and *Cladophora* algae.

4.4.1.2 Habitat use

A total of 319 bullheads were surveyed, representing a mean density of 12.6 fish/m². Bullheads ranged in size from 21 to 87 mm (mean 43.7 mm), and 73 % of individuals were juveniles. A total of 61 stone loach were recorded, representing a mean density of 2.4 fish/m². Individuals ranged in TL from 33 to 103 mm (mean 61.3 mm). Bullheads used riffles more than pools (G-test: PCA 1, $\chi^2 = 60.17$, $df = 7$, $P < 0.001$; Figure 4.2b), positively selecting water shallower than 0.35 m (G-test: $\chi^2 = 40.77$, $df = 7$, $P < 0.001$), water velocity over 0.15 m/s (G-test: $\chi^2 = 36.93$, $df = 8$, $P < 0.001$) and coarse substrates (G-test: $\chi^2 = 47.62$, $df = 8$, $P < 0.001$). Unlike bullheads, stone loach exhibited no significant selection for riffles or pools (G-test: PCA 1, $\chi^2 = 8.11$, $df = 5$, $P > 0.05$; Figure 4.2c). Bullheads were frequently observed sheltering along the margins of macrophytes adjacent to areas of gravel. This manifested itself as a significant preference for marginal areas over mid stream habitats (G-test: PCA 2, $\chi^2 = 16.67$, $df = 8$, $P < 0.05$; Figure 4.3b)

Table 4.2 Results of principal components analysis of microhabitat availability in the Brandy Stream. Loadings on the first three principal component axes (PCA) are given by the standardised regression coefficients between the component and environmental variables. Coefficients greater than 0.5 are highlighted in bold.

Habitat variable	PCA 1		PCA 2		PCA 3	
Width	-0.368	***	-0.255	***	-0.142	*
Distance from bank	-0.107		-0.613	***	0.217	***
Depth	-0.412	***	-0.074		-0.224	***
Velocity	0.777	***	-0.127	*	0.116	
Instream cover	-0.058		0.051		-0.071	
Overhead cover	-0.022		0.819	***	0.039	
Turbulence	0.730	***	-0.070		0.149	*
Shade	0.034		0.149	*	0.055	
<i>Berula erecta</i>	-0.129	*	-0.247	***	0.875	***
<i>Ranunculus penicillatus</i>	0.199	**	0.007		0.119	*
<i>Rorippa nasturtium-aquaticum</i>	-0.023		0.671	***	0.036	
<i>Callitriche</i> spp.	-0.039		0.022		-0.013	
<i>Iris pseudacorus</i>	-0.251	***	0.644	***	-0.002	
<i>Elodea canadensis</i>	-0.147	*	-0.055		-0.049	
<i>Fontinalis antipyretica</i>	0.044		-0.036		0.029	
<i>Mentha aquatica</i>	-0.068		-0.015		-0.026	
<i>Veronica anagallis-aquatica</i>	-0.016		-0.046		0.000	
<i>Myosotis scorpioides</i>	-0.132	*	-0.059		-0.038	
Total plants	-0.103		0.193	**	0.850	***
<i>Cladophora</i> algae	-0.222	***	-0.263	***	-0.387	***
Dominant substrate	0.809	***	-0.008		-0.345	***
Maximum substrate	0.815	***	-0.056		-0.315	***
Substrate stability	0.203	**	-0.115		-0.191	**
Eigenvalue	3.206		2.461		2.190	
% variation	13.9		10.7		9.5	

Significance of regression coefficient: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

and microhabitats with intermediate vegetation cover (G-test: PCA 3, $\chi^2 = 21.17$, $df = 7$, $P < 0.01$; Figure 4.4b). In contrast, stone loach exhibited no significant preference for mid-stream or marginal habitats (G-test: PCA 2, $\chi^2 = 0.10$, $df = 3$, $P > 0.05$ Figure 4.3c) and were more abundant at sites with high PCA 3 scores than expected by chance (G-test: $\chi^2 = 12.32$, $df = 5$, $P < 0.05$; Figure 4.4c) as a result of positive selection for high vegetation cover (G-test: $\chi^2 = 18.51$, $df = 4$, $P < 0.01$).

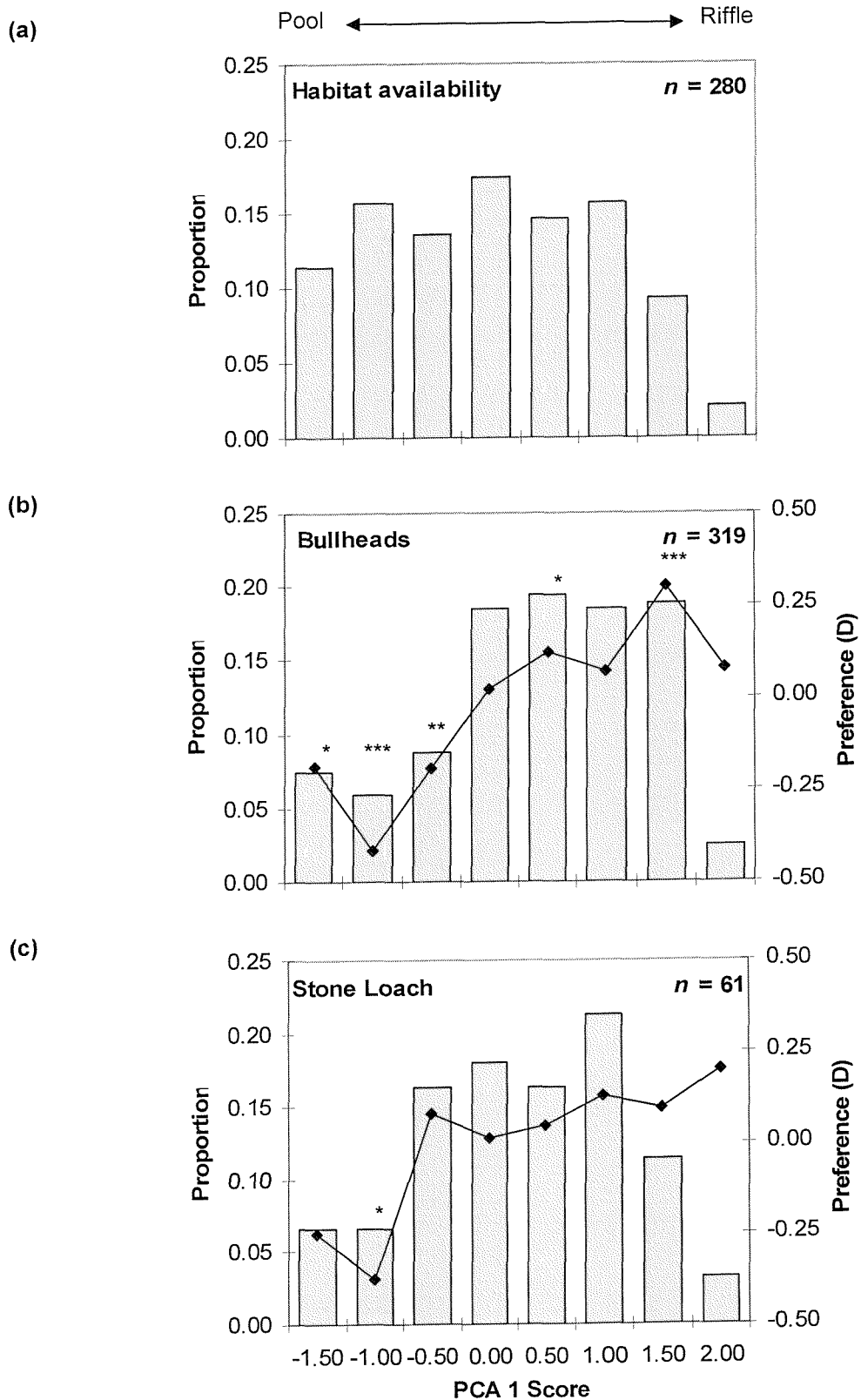


Figure 4.2 (a) Availability of habitat in the Brandy Stream, and habitat use (bars) and habitat selection (lines) of (b) bullheads and (c) stone loach. The principle components axis represents a geomorphological gradient from pools to riffles. Abscissa labels are midpoints of score classes. Asterisks indicate significant over or under-utilisation of a particular score class (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

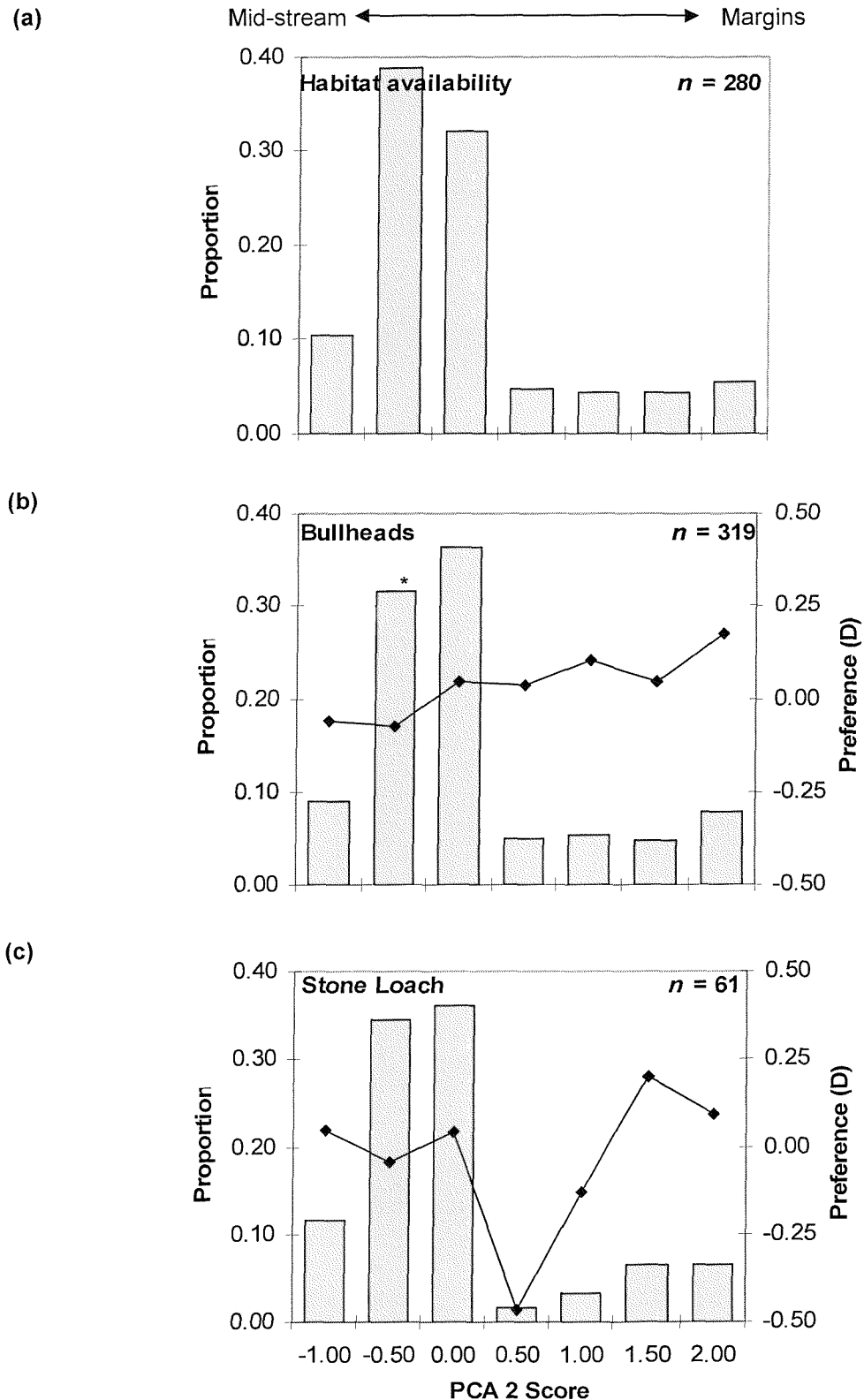


Figure 4.3 (a) Availability of habitat in the Brandy Stream, and habitat use (bars) and habitat selection (lines) of (b) bullheads and (c) stone loach. The principle components axis represents a lateral gradient from midstream to margins. Abscissa labels are midpoints of score classes. Asterisks indicate significant over or under-utilisation of a particular score class (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

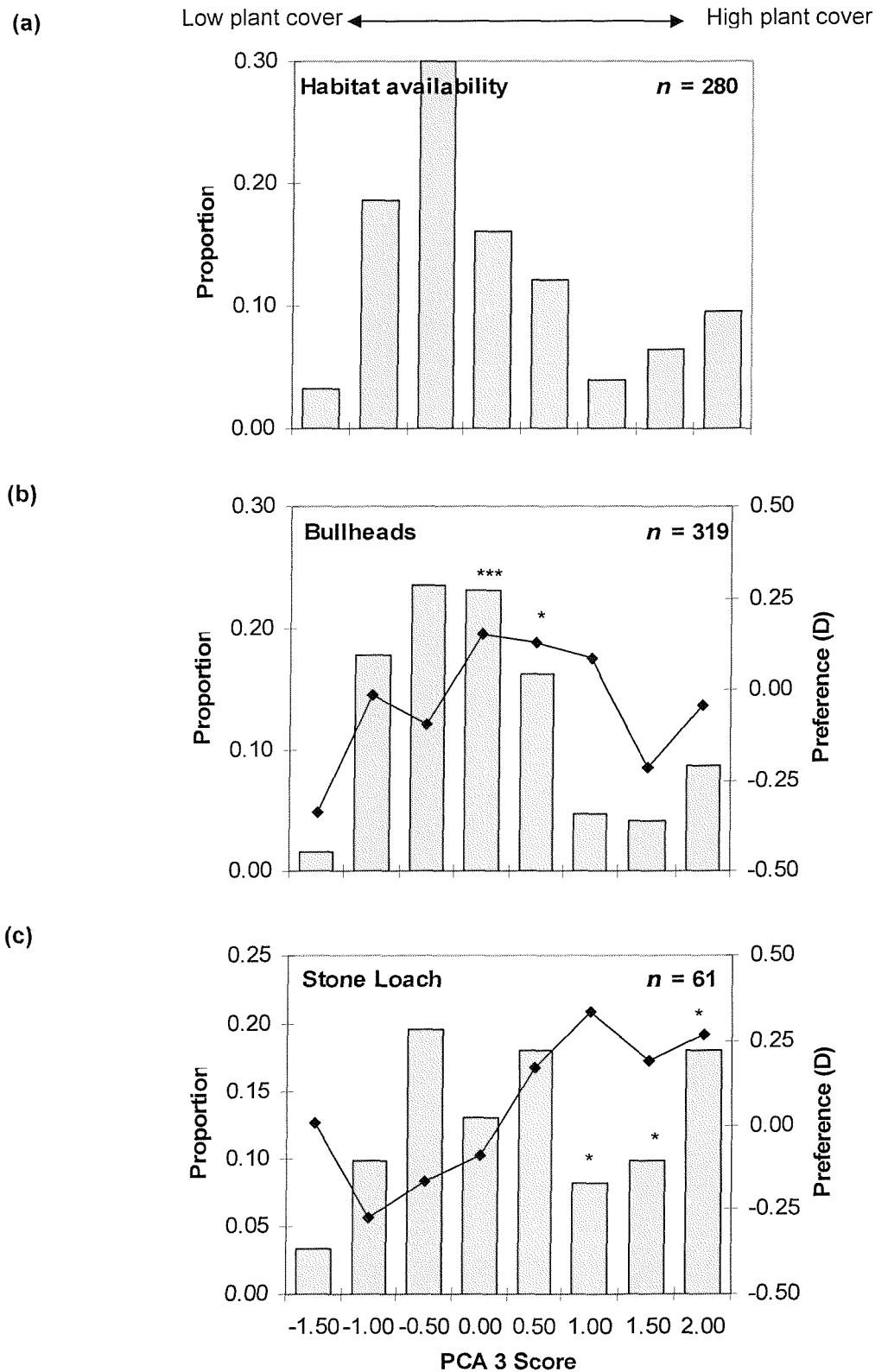


Figure 4.4 (a) Availability of habitat in the Brandy Stream, and habitat use (bars) and habitat selection (lines) of (b) bullheads and (c) stone loach. The principle components axis represents a gradient in vegetation cover. Abscissa labels are midpoints of score classes. Asterisks indicate significant over or under-utilisation of a particular score class (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

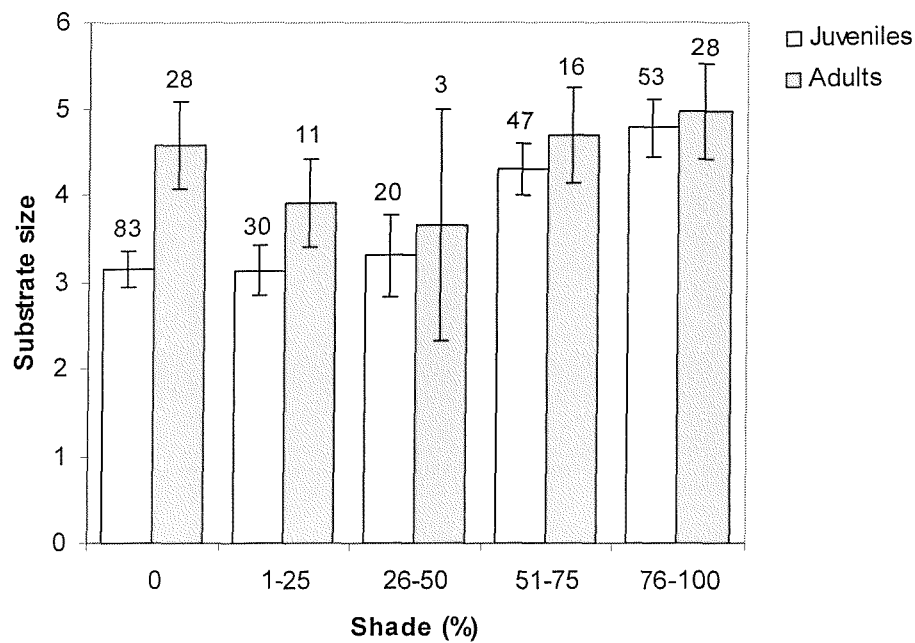


Figure 4.5 Mean (± 1 S.E.) size of substrate used by juvenile and adult bullheads along a shade gradient. Substrate size is measured on an ordinal scale as described in Table 4.1. Numbers above bars indicate sample sizes.

4.4.1.3 Interspecific differences

Bullheads and stone loach showed considerable overlap in microhabitat use (Figures 4.2 to 4.4), with no significant difference in distribution along PCA 1 (ANOVA: $F_{1,317} = 0.959$, $P = 0.328$) or PCA 2 (ANOVA: $F_{1,317} = 0.207$, $P = 0.649$). However, microhabitats occupied by stone loach had significantly more vegetation cover than those used by bullheads (ANOVA: PCA 3, $F_{1,317} = 8.398$, $P = 0.004$).

4.4.1.4 Intraspecific differences

Adult and juvenile bullheads showed significant differences in habitat use. Adults occupied riffles more than juveniles (ANOVA: PCA1, $F_{1,317} = 4.379$, $P = 0.037$), in particular selecting microhabitats with coarser substrates (ANOVA: $F_{1,317} = 8.760$, $P = 0.003$). Both size classes positively selected substrates >16 mm in diameter, but the preference for large substrates was much stronger in adults. The size of substrates used by bullheads was also dependent on the degree of tree canopy cover. Bullheads occupied coarser substrates with increasing shade (GLM: $F_{1,315} = 10.675$, $P = 0.001$; Figure 4.5) and there was a suggestion that juveniles responded more than adults to changing shade levels

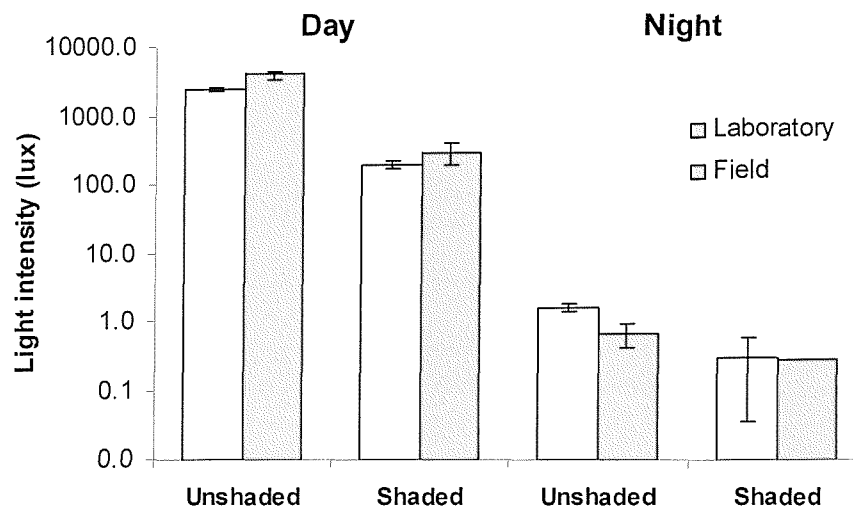


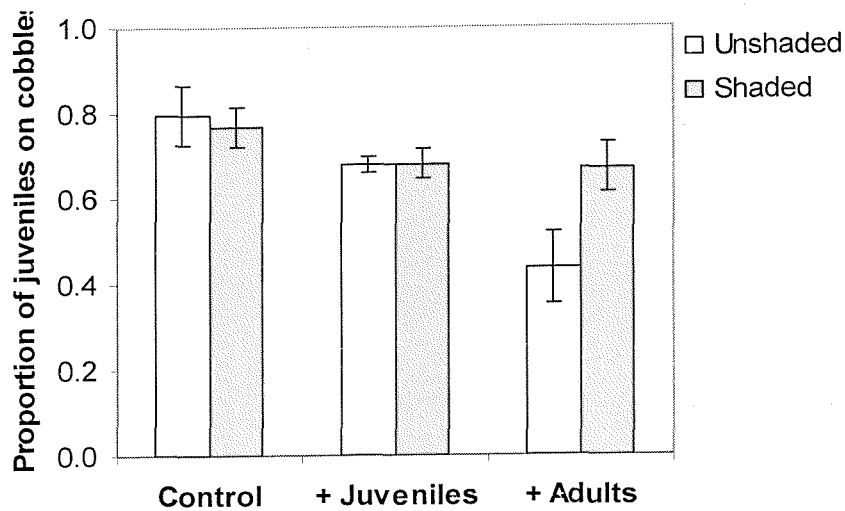
Figure 4.6 Mean (± 1 S.D.) light intensity in laboratory aquaria and on the Brandy Stream. Measurements were taken at the water surface under unshaded and shaded conditions during the day and night using a photometer fitted with a quantum sensor. Light intensity in shaded parts of the stream at night was below the detection limit of 0.56 lux and is therefore estimated.

(GLM: $F_{1,315} = 3.085$, $P = 0.080$). As a result, differences in substrate use between adult and juvenile fish were less pronounced in heavily shaded areas (Figure 4.5).

4.4.2 Laboratory experiment

Light levels in the laboratory closely approximated those in the field, with shading reducing light intensity by over 90 % during the day and 60 - 80 % at night (Figure 4.6). At low fish density, both juvenile and adult bullheads selected cobbles over pebbles, with over 80 % of fish occupying the coarser substrate (Figure 4.7). At high fish density, the proportion of juveniles on cobbles fell to 67 %, indicating density dependent habitat use (Contrast 2, Table 4.3; Figure 4.7a). There was a suggestion that addition of adults caused a bigger habitat shift than addition of juveniles, but the significance of this effect was marginal (Contrast 3, Table 4.3). Light intensity had no significant effect upon microhabitat use by juveniles (Contrast 1, Table 4.3), although there was a non-significant tendency for the impact of adults on juveniles to be reduced under shaded conditions (Contrast 5, Table 4.3; Figure 4.7a). Habitat use of adult bullheads was unaffected by light intensity (Contrast 1, Table 4.4) and fish density (Contrast 2, Table 4.4; Figure 4.7b). At high density, there was a suggestion that a greater proportion of adult fish used pebbles when only adult fish were present than in the mixed size-class treatment, but this

(a) Juveniles



(b) Adults

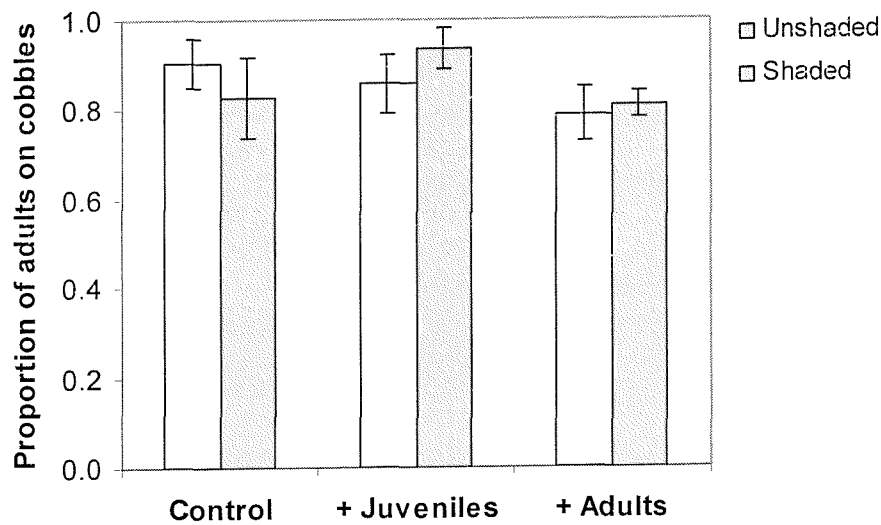


Figure 4.7 Mean (± 1 S.E.) habitat use of (a) juvenile and (b) adult bullheads held in laboratory tanks under three different stocking conditions (abscissa categories: low density control, high density with juveniles, high density with adults) crossed with two levels of light intensity (unshaded, shaded). $n = 4$ replicate trials for each combination of treatments.

difference was marginally non-significant (Contrast 3, Table 4.4). There were no significant interactions between light intensity and fish density (Contrast 4, Table 4.4) or between light intensity and size-class composition (Contrast 5, Table 4.4).

Table 4.3 ANOVA of arcsine-transformed proportion of juvenile bullheads occupying cobbles. Fish were held in tanks under three different stocking conditions crossed with two levels of light intensity, and habitat use recorded after 24 and 48 h. $n = 4$ replicates for each combination of treatments, giving a total of 24 trials.

Source of variation	SS	df	MS	F	P
Among treatments	1281.6	5	256.3	4.653	0.007
Contrast 1: Light	86.5	1	86.5	1.570	0.226
Contrast 2: Density	642.3	1	642.3	11.661	0.003
Contrast 3: Size class composition	220.9	1	220.9	4.011	0.061
Contrast 4: Light x Density	132.1	1	132.1	2.398	0.139
Contrast 5: Light x Composition	199.8	1	199.8	3.628	0.073
Error	991.4	18	55.1		
Total	2273.0	23			

Table 4.4 ANOVA of arcsine-transformed proportion of adult bullheads occupying cobbles. Fish were held in tanks under three different stocking conditions crossed with two levels of light intensity, and habitat use recorded after 24 and 48 h. $n = 4$ replicates for each combination of treatments, giving a total of 24 trials.

Source of variation	SS	df	MS	F	P
Among treatments	809.2	5	161.8	1.204	0.347
Contrast 1: Light	0.9	1	0.9	0.007	0.937
Contrast 2: Density	8.9	1	8.9	0.066	0.800
Contrast 3: Size class composition	523.2	1	523.2	3.891	0.064
Contrast 4: Light x Density	212.2	1	212.2	1.578	0.225
Contrast 5: Light x Composition	63.9	1	63.9	0.475	0.499
Error	2420.3	18	134.5		
Total	3229.5	23			

4.5 DISCUSSION

4.5.1 Interspecific microhabitat partitioning

This study has revealed strong patterns of microhabitat selection by two benthic fish species. The observed preference of bullheads for riffle habitats is in agreement with previous studies of cottid habitat use (Welton *et al.* 1983; Brown 1991; Roussel & Bardonnnet 1997). Freshwater *Cottus* species use coarse substrates as shelter (Brown 1991; Hesthagen & Heggenes 2003) and are morphologically adapted to maintain position in high velocities (Facey & Grossman 1992). Furthermore, foraging efficiency is maximised on gravel substrates where an ample stream of mobile invertebrate prey and good visibility favour a visual sit-and-wait predation strategy (Welton *et al.* 1983; Welton *et al.* 1991). In

the Brandy Stream, bullheads also positively selected microhabitats along the margins of macrophyte patches. The reason for this behaviour is unclear, but it may reflect a trade-off between availability of cover and proximity to suitable feeding areas (Dahlgren & Eggleston 2000). This result cautions against simple linear models of fish-habitat association and demonstrates the importance of spatial heterogeneity in generating valuable transitional or intermediate microhabitats.

Stone loach positively selected microhabitats with abundant vegetation. Previous studies have reported a strong preference of stone loach for cover that provides visual isolation from predators (Prenda *et al.* 1997; MacKenzie & Greenberg 1998). Stone loach will seek shelter by hiding beneath stones or burying themselves in silt (Maitland 1965; Hyslop 1982), but appear to prefer macrophytes when they are available (Hyslop 1982; Welton *et al.* 1983; Roussel *et al.* 1998). Stone loach are tactile, non-visual foragers that actively seek out prey using olfactory cues and are restricted to taking small prey species with low mobility such as chironomid larvae (Smyly 1955; Welton *et al.* 1983). Stone loach might, therefore, prefer macrophytes because vegetation provides both overhead cover and favourable conditions for a non-visual foraging strategy (Welton *et al.* 1983). Stone loach generally prefer pools to riffles (Maitland 1965; Prenda *et al.* 1997; MacKenzie & Greenberg 1998). However, the current study supports the findings of Roussel and Bardonnnet (1997) that stone loach do not select microhabitats on the basis of channel geomorphology. Thus, it appears that a strong preference for vegetation is of overriding importance in the microhabitat selection of this species.

Microhabitats used by stone loach had more vegetation cover than those selected by bullheads. Interspecific differences in habitat use are a common phenomenon in stream fish (Ross 1986), with fish segregating spatially vertically in the water column (Grossman *et al.* 1987; Gorman 1988; Welsh & Perry 1998), longitudinally along the pool-riffle sequence (Greenberg 1991; Greenberg *et al.* 1996; Roussel & Bardonnnet 1997) and laterally between marginal and mid-channel areas (Greenberg 1988). Benthic species may also be influenced by substrate characteristics (Finger 1982; Welton *et al.* 1983; Grossman & Freeman 1987; van Snik Gray & Stauffer 1999). Although this study did not explicitly examine the role of competition in generating the observed patterns of interspecific habitat partitioning, it seems likely that differences in microhabitat use of bullheads and stone

loach are caused by differences in their foraging strategies rather than interspecific competition (Welton *et al.* 1983; Welton *et al.* 1991). Some workers have proposed that significant differences in habitat use facilitate species co-existence by reducing interspecific competition (Schoener 1986). However, a reliance on average measures of habitat use may be misleading when, as in this study, high individual variation results in considerable spatial overlap between species despite a significant difference in mean habitat use. Thus, differences in microhabitat use of bullheads and stone loach will be of only limited importance in reducing any interspecific interactions.

4.5.2 Ontogenetic habitat shifts in bullheads

Microhabitat use of bullheads was size dependent, with adult fish using coarser substrates than juveniles in the field. Because size and age are strongly correlated in fishes, size-related differences in habitat use can be viewed as ontogenetic (Grossman & Freeman 1987). Ontogenetic habitat shifts are common in fish as a result of indeterminate growth and high individual size variation (Werner & Gilliam 1984; Werner 1986). Whilst water depth may be important in spatially segregating size classes of mid-water species, with individuals moving to deeper water with increasing age as their size renders them more susceptible to avian predators (Schlosser 1987; Harvey & Stewart 1991), substrate characteristics are thought to have more influence on benthic species. Benthic fish seek to minimise predation risk by occupying microhabitats that provide visual isolation from avian predators (MacKenzie & Greenberg 1998). Adult fish often utilise larger substrates (Mullen & Barton 1995) and make greater use of interstitial refuges (Schlosser & Toth 1984; van Snik Gray & Stauffer 1999) than juveniles. Consequently, microhabitat use becomes increasingly restricted with age and, in rivers such as the Brandy Stream where substrates become progressively less abundant with size, this behaviour could potentially lead to a demographic bottleneck at the adult stage (Beck 1995).

The laboratory experiment provided some support for the hypothesis that ontogenetic changes in microhabitat use of bullheads are caused by asymmetrical intraspecific competition between size classes. At low fish density, both juvenile and adult bullheads preferred coarse substrates, indicating that size-specific substrate use was not the result of different intrinsic preferences. At high fish density, a lower proportion of juveniles occupied the preferred cobble substrate, and there was a suggestion that habitat shifts of

juveniles were more pronounced in the presence of adult fish. In contrast, habitat use of adults was unaffected by fish density. Intraspecific competition is thought to be the primary mechanism responsible for density dependent habitat use since bullheads are known to be aggressive towards conspecifics (Smyly 1957; Ladich 1989). The alternative explanation, that juveniles were avoiding predation from adults, is unlikely since bullheads are rarely cannibalistic (Smyly 1957). Competitive interactions are frequently highly asymmetrical and body size has been shown to be a strong predictor of competitive ability in a variety of freshwater fish (Bohlin 1977; Freeman & Stouder 1989; Nakano 1995; Mullen & Burton 1998; Vehanen *et al.* 1999). Similar patterns of habitat use have been reported for the Siberian sculpin *Cottus poecilopus*, with competitively dominant adult fish displacing smaller juveniles onto finer substrates (Hesthagen & Heggenes 2003). Thus, ontogenetic shifts in substrate use in the field may result, at least in part, from intraspecific competition between size classes, although other factors such as size-specific changes in prey preference (Andreasson 1971) or predation risk (Schlosser 1987) cannot be discounted as contributory factors.

The effect of light intensity on microhabitat use of bullheads was unclear. Bullheads used coarser substrates under high tree canopy cover in the field but not under shaded conditions in the laboratory. Some marginal effects in the laboratory, however, suggest that light intensity may affect microhabitat use by modifying the strength or symmetry of competitive interactions between size-classes. Intraspecific competition could be condition dependent if the behaviour or competitive ability of fish varies with light intensity. Low light intensity has been shown to moderate competitive interactions among fish both directly by inhibiting the ability to visually detect conspecifics (Valdimarsson & Metcalfe 2001) and indirectly by reducing refuge-seeking behaviour (Britz & Pienaar 1992). Thus, co-existence of juvenile and adult bullheads on coarse substrata in heavily shaded areas may be due to weakened intraspecific competition. Alternatively, tree canopy cover might influence bullhead microhabitat selection by modifying risk of predation from avian predators, or by reducing the availability of invertebrate prey via bottom-up effects on primary production. Further experiments are required to test these hypotheses.

The consequences of intraspecific competition for bullheads are difficult to evaluate with the present data. Individuals that are displaced into sub-optimal habitat may suffer lower

foraging rates and reduced growth (Nakano 1995) or increased mortality (Holbrook & Schmitt 2002). At the population level, strong inter-cohort competition under a size-driven dominance hierarchy may limit recruitment of juveniles to adult habitats and lead to density dependent population regulation (Freeman & Stouder 1989; Nakano 1995).

4.5.3 Conclusions

This study demonstrates non-random microhabitat use of stream fish as a result of strong preferences for microhabitats that provide visual isolation from avian predators (MacKenzie & Greenberg 1998) and high densities of preferred prey (Petty & Grossman 1996) or physical conditions that promote foraging efficiency (Hill & Grossman 1993). The trade-off between these factors varies with species identity, producing interspecific differences in microhabitat use, but high individual variation in microhabitat use means that spatial segregation may still be limited. Ontogenetic shifts in microhabitat use can be caused, at least in part, by intraspecific competition between size classes rather than size-specific habitat preferences. However, condition dependent competitive interactions may produce complex patterns of habitat use and further studies are required to elucidate the exact mechanisms driving microhabitat selection.

- 5 -

INTERSPECIFIC INTERACTIONS BETWEEN STONE LOACH AND BULLHEADS

5.1 ABSTRACT

The concept of limiting similarity has driven the idea that the strength of competition between species is positively correlated with overlap in their resource use. Species can interact via a range of direct and indirect mechanisms, however, giving rise to a range of potential outcomes. Empirical assessment of the strength of interspecific interactions is therefore required to test the hypothesis that ecologically similar species are strong competitors. In this study, reciprocal interactions were examined between two small benthic fish species, stone loach *Barbatula barbatula* and bullheads *Cottus gobio*. Each species was held alone and with heterospecifics under semi-natural field conditions using cage enclosures. Survival, growth and prey consumption were used as indirect measures of fitness. Stone loach grew faster in the presence of bullheads indicating facilitation. The mechanism responsible was uncertain, but contrasting predator foraging strategies may have enhanced foraging efficiency by forcing prey to trade-off alternative defensive strategies. Survival and growth of bullheads was unaffected by the presence of stone loach despite a marked dietary shift from chironomid larvae and *Ancylus fluviatilis* to *Potamopyrgus jenkinsi*. A flexible, opportunistic foraging strategy appears to reduce the intensity of exploitation competition from stone loach, at least in the short term. The complex indirect trophic interactions observed in this benthic fish assemblage highlight the limitations of traditional measures of ecological similarity such as dietary overlap as indicators of the nature and strength of interspecific interactions and may account for the absence of a strong, overriding influence of interspecific competition at the population and community-scale.

5.2 INTRODUCTION

Interspecific competition is a fundamental process structuring ecological communities (Connell 1983; Schoener 1983). The theory of limiting similarity suggests that species can co-exist up to some critical level of similarity, beyond which competitive exclusion occurs as a result of intense interspecific competition (Abrams 1983). Allied to this concept is the idea that competitive interactions should be most intense between ecologically similar species and, hence, that the strength of interspecific competition may be predicted from observed similarity in resource use or morphology (MacArthur & Levins 1967). Attempts to assess the potential for competition from measures of niche overlap have been criticised, however, firstly because there is no definitive relationship between niche overlap and competitive strength (Colwell & Futuyma 1971; Sale 1974), and secondly because high niche overlap indicates no more than potential for competition without evidence for resource limitation (Prejs & Prejs 1987). Furthermore, it is increasingly being recognised that interspecific interactions are not always negative (Connell 1983; Bertness & Callaway 1994; Bruno *et al.* 2003). Species can also facilitate each other through a range of positive direct and indirect processes (Soluk & Collins 1988; Brönmark *et al.* 1991; Eklov & van Kooten 2001), giving rise to complex interspecific interactions (Soluk & Collins 1988; Arthur & Mitchell 1989; Resetarits 1997).

In stream fish communities, competition from non-game species is widely perceived to limit populations of salmonids and other sport fish on the basis that these species often show a superficial similarity in habitat use or dietary composition (Baltz *et al.* 1982), yet empirical evidence for interspecific competition is weak. Research on competition in stream fish has been largely based on descriptive studies of resource use. Species frequently partition resources along spatial, dietary and temporal axes (Moyle & Senanayaka 1984; Ross 1986; Gorman 1987; Greenberg 1991; Gray *et al.* 1997) but this does not unambiguously demonstrate that competition is active in contemporary communities. Manipulative experiments have clearly demonstrated effects of interspecific competition on individual fish (Le Cren 1965; Fausch & White 1981; Baltz *et al.* 1982) but evidence that interspecific competition influences population dynamics and community structure is more equivocal, with many studies failing to find evidence of competitive structuring at higher scales of ecological organisation (Degerman & Sers

1993; Hugueny & Paugy 1995; Oberdorff *et al.* 1998; Eklöv *et al.* 1999; Jorgensen *et al.* 1999).

The aim of this study was to test the hypothesis that species of high ecological similarity engage in interspecific competition by investigating interactions between two small, benthic fish species. Stone loach *Barbatula barbatula* and bullheads *Cottus gobio* occur sympatrically across much of Western Europe and dominate the fish fauna of shallow chalk streams in southern England (Mann 1971; Prenda *et al.* 1997). Both are active nocturnally and feed almost exclusively on benthic macroinvertebrates (Smyly 1955, 1957; Welton *et al.* 1983). As a result of considerable overlap in habitat use and dietary composition, stone loach and bullheads have long been considered as potential competitors (Welton *et al.* 1983), making them a good model system to investigate interspecific interactions in freshwater fish. This chapter presents the results of a manipulative field experiment examining the effects of interactions between stone loach and bullheads on individual performance. Each species was held alone and with heterospecifics under semi-natural field conditions using cage enclosures to test the prediction that survival, growth in body size and prey consumption of each species would be reduced in the presence of the other.

5.3 METHODS

5.3.1 Study site

The experiment was performed in the Brandy Stream (see section 1.5.2 for details) during August and September 2001. Water temperature ranged from 11.7 to 17.6 °C (mean 14.1 °C) during the experiment (Seamon mini temperature recorder, Hugarun, Reykjavik, Iceland).

5.3.2 Experimental enclosures

An array of 15 replicate enclosures each 1.4 m long, 0.8 m wide (1.12 m² in area) and 0.3 m high were used. Enclosures had solid metal sides and base and 6 mm wire-mesh on the up- and down-stream ends to permit water to flow through. To simulate a gravel riffle mesohabitat, enclosures were established in water 0.14-0.23 m deep with velocity 0.18-

0.37 m/s and the base of each covered with gravel and cobbles to create a substrate approximately 25 mm deep. Enclosures were placed approximately 4 m apart and staggered to reduce upstream enclosure effects. Plastic netting was placed over the open top of each enclosure to deter avian predators. Invertebrates were allowed to colonise the enclosures for 30 days prior to the start of the experiment by lowering the up- and down-stream wire meshes. The enclosures were rapidly colonised by benthic invertebrates and supported an assemblage of species similar to that found in the surrounding stream (A. Davey, *personal observation*). Once raised to enclose the fish, the wire meshes were scrubbed every 12 hours during the experiment to remove accumulated plant debris and maintain water flow through the enclosures.

5.3.3 Experimental design

Three treatments were established so that each species was held both alone and with heterospecifics: 5 stone loach, 5 bullheads, and 5 stone loach plus 5 bullheads. This additive design holds the density of the focal species constant to avoid confounding changes in heterospecific density with changes in conspecific density (Underwood 1986). The three treatments were each replicated five times and randomly assigned to enclosures. The stocking density of 4.5 fish/m² (5 fish per enclosure) was within the range of densities recorded for both bullheads and stone loach in chalk streams (Mann 1971; Prenda *et al.* 1997).

5.3.4 Experimental protocol

All experimental fish were caught from the Brandy Stream by electrofishing on 22 and 24 August. On 25 August, 50 adult fish of each species were weighed to 0.01 g, measured to 0.1 mm (total length, TL) and randomly assigned to treatments. Fish were marked with subcutaneous elastomer tags (Northwest Marine Technology Inc., WA, USA) to allow individual recognition. Stone loach ranged in initial mass from 2.02 g to 9.41 g (mean 4.40 g) and in length from 68.1 mm to 105.9 mm (mean 84.3 mm). Bullheads ranged in initial mass from 2.67 g to 10.15 g (mean 4.98 g) and in length from 62.1 mm to 92.5 mm (mean 72.9 mm). Fish were held in the enclosures for 21 days. Fish that died during the experiment were replaced with spare fish from a stock enclosure to maintain the treatments. At the end of the experiment on 15 September, the enclosures were searched

and fish removed with a dip net. Recovered fish were killed by an overdose of anaesthetic (2-phenoxyethanol), identified, re-weighed, re-measured and preserved in 70 % ethanol solution. This work was conducted between 0700 and 1000 h to minimize digestion of consumed prey.

In the laboratory, stomachs of experimental fish were dissected out and their contents examined under x40 magnification using a dissecting microscope. Prey items were identified to the lowest possible taxonomic level, counted, and one of five linear body dimensions measured to 0.01 mm using a graticule to estimate prey biomass. Body length (BL) was measured along the dorsal surface from the anterior edge of the head to the posterior tip of the last abdominal segment, with the exception of *Gammarus pulex*, which was measured from the anterior margin of the head to the posterior margin of the telson after straightening the body from its natural curved position. Head capsule width (HCW) was measured perpendicular to length at the widest point across the dorsal surface of the head. Shell height was measured for *Potamopyrgus jenkinsi*, shell length for *Ancylus fluviatilis* and shell width for *Valvata cristata*. Both BL and HCW were measured for well preserved specimens to derive empirical relationships between body dimensions and allow prediction of BL from HCW for poorly preserved or incomplete specimens. Stomach contents were observed in various degrees of digestion. Occasionally prey could not be identified and were excluded from analysis. Incomplete prey items were assumed to be whole for the purpose of biomass determination.

Dimensions of prey items were converted to soft-tissue dry weight biomass using published mass-length relationships (Ladle *et al.* 1972; Bass 1976; Mackey 1977; Mason 1977; Welton 1979; Meyer 1989; Benke *et al.* 1999). Body length was used in preference to head capsule width as this has been shown to be a more reliable predictor of biomass (Meyer 1989). Where necessary, HCW was converted to BL using published equations (Meyer 1989) or empirical relationships derived from the present study. Where no body dimension could be accurately measured, a biomass was attributed based upon the average of other specimens within the sample. Several authors warn of the effect of different methodologies and against transferring mass-length relationships between stream types (Meyer 1989; Johnston & Cunjak 1999). Attempts were therefore made to match the preservation method and stream type in published equations to those of this study.

5.3.5 Statistical analysis

The fitness of stone loach and bullheads was measured indirectly by survival, growth in body size and prey consumption. Survival was evaluated as the proportion of fish recovered from each enclosure at the end of the experiment. Growth was calculated as the change in body mass and TL of fish during the experiment. Consumption of each prey taxon was measured as the number of individuals and the total dry weight biomass per fish stomach, with the latter divided by fish mass to the power of 0.75 to take account of allometric relationship between body size and food consumption (Steingrímsson & Grant 1999). Calculations for growth and prey consumption were performed for all surviving fish, and then averaged for fish in each enclosure to form the units of analysis ($n = 5$ data points for each treatment). All three response variables were tested with Cochran's C-test for homogeneity of variances and log- or arcsine-transformed where necessary to normalise distributions and stabilise variances. Response variables were then analysed by one-way ANOVA with presence or absence of heterospecifics as a fixed factor. Where transformation failed to correct heterogeneous variances, a Mann-Whitney non-parametric one-way ANOVA was used instead. SPSS v.10.0 (SPSS Inc., Chicago) was used for all ANOVA tests and significance evaluated using $\alpha = 0.05$.

Interspecific dietary overlap was evaluated using Morisita's similarity index (Morisita 1959):

$$C_{jk} = \frac{2 \sum_{i=1}^m p_{ij} p_{ik}}{\sum_{i=1}^m p_{ij} \left(\frac{n_{ij} - 1}{N_j - 1} \right) + \sum_{i=1}^m p_{ik} \left(\frac{n_{ik} - 1}{N_k - 1} \right)} \quad (5.1)$$

where C_{jk} = overlap between species j and k ($0 \leq C_{jk} \leq 1$);

m = number of dietary categories;

p_{ij} = proportion of prey i in the diet of species j ;

p_{ik} = proportion of prey i in the diet of species k ;

n_{ij} = number of prey i consumed by species j ;

n_{ik} = number of prey i consumed by species k ;

N_j = total number of prey items consumed by species j ;

N_k = total number of prey items consumed by species k .

This index has been shown to estimate overlap in resource use with negligible bias over a range of conditions (Krebs 1999). Dietary overlap was calculated separately for control and mixed species treatments, using data pooled across replicate enclosures. Intraspecific differences in dietary composition of fish held with and without heterospecifics were also evaluated using Morisita's index by substituting experimental treatment for species as the grouping factor. This method provides a measure of the dietary niche shift in response to heterospecifics (C_S). The significance of these dietary shifts was assessed using a modified version of Sevenster and Bouton's randomisation test for interspecific dietary differences (Sevenster & Bouton 1998). For each species, enclosures were randomly reassigned to treatment groups and similarity in dietary composition between groups recalculated. This procedure was repeated 999 times to generate a distribution of C_S under the null hypothesis of no change in dietary composition in response to heterospecifics. A dietary shift was judged to be significant if $\leq 5\%$ of permuted values of C_S were less than or equal to that observed (Manly 1997).

5.4 RESULTS

5.4.1 Stone loach

Survival of stone loach was high. Only one fish died during the experiment and two additional fish were not recovered - it is not known whether they escaped, died or were simply not found. There was no effect of treatment on number of fish recovered (ANOVA: $F_{1,8} = 0.400$, $P = 0.545$). Average growth in body size of surviving stone loach was 0.39 g and 1.6 mm (Figure 5.1a). Contrary to the competition hypothesis, growth in mass was 60 % higher in the presence of bullheads than in the control (ANOVA: $F_{1,8} = 5.683$, $P = 0.044$), indicating facilitation. Growth in TL, in contrast, was unaffected by treatment (ANOVA: $F_{1,8} = 0.228$, $P = 0.646$).

The diet of stone loach was dominated by chironomid larvae, which accounted for 91 % of prey items and 66 % of prey biomass (Table 5.1). *Gammarus pulex* were consumed in much lower quantities, but still contributed 30 % to total prey biomass intake due to their large body size (Table 5.1b). In the presence of bullheads, stone loach consumed fewer chironomid larvae (ANOVA: $F_{1,8} = 6.740$, $P = 0.032$; Table 5.1a) and consequently total

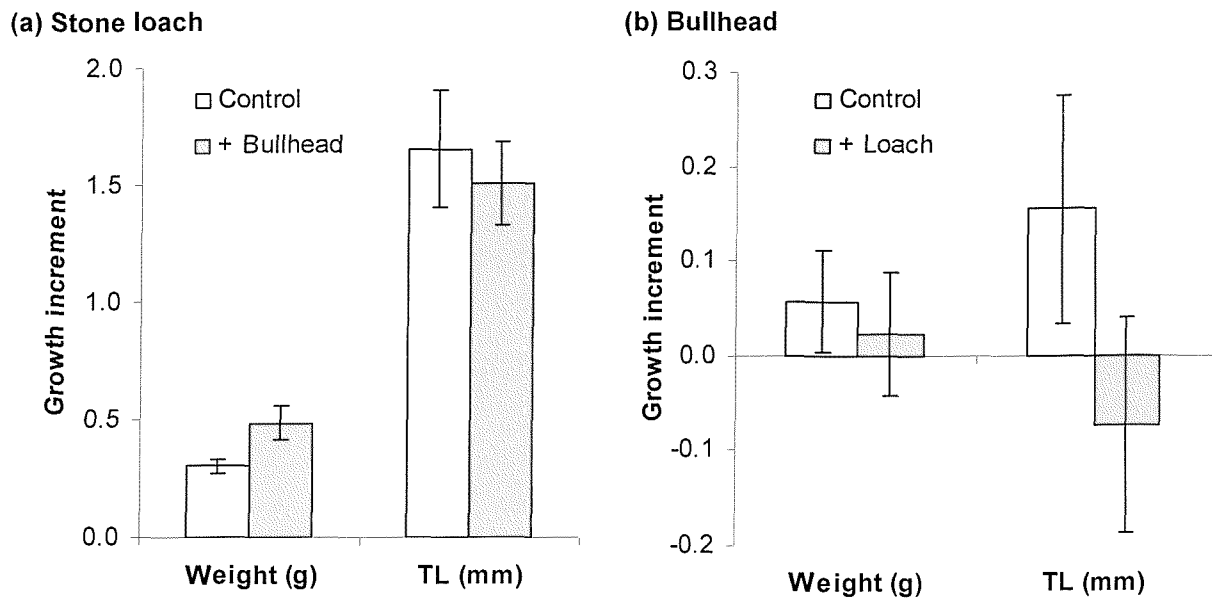


Figure 5.1 Growth in body size of (a) stone loach and (b) bullheads alone and with heterospecifics. Means (± 1 S.E.) are based on the growth of fish in five replicate enclosures per treatment.

prey biomass consumption was also lower (ANOVA: $F_{1,8} = 9.824$, $P = 0.014$; Table 5.1b). Despite a reduction in prey intake, stone loach displayed no significant shift in dietary composition when held with bullheads ($C_S = 0.99$, $P = 0.126$).

5.4.2 Bullheads

Survival of bullheads was also high (97 %) and unaffected by treatment (Mann Whitney U = 10, $P = 0.317$). Average growth in body size of surviving bullheads was 0.04 g and 0.1 mm (Figure 5.1b). Both growth in mass and growth in TL were unaffected by the presence of stone loach ($F_{1,8} = 0.164$, $P = 0.696$ and $F_{1,8} = 1.894$, $P = 0.206$ respectively), indicating no evidence of interspecific competition.

Bullheads had a much more varied diet than stone loach, with *Gammarus pulex* the most common prey (35 %) followed by chironomid larvae (19 %), *Ancylus fluviatilis* (16 %), ephemeropteran nymphs (13 %) and *Potamopyrgus jenkinsi* (9 %) (Table 5.1a).

Gammarus pulex (50 %) and *Ancylus fluviatilis* (40 %) accounted for the majority of prey biomass (Table 5.1b). In the presence of stone loach, bullheads consumed fewer

Table 5.1 Prey consumption of stone loach and bullheads held in enclosures with and without heterospecifics: (a) number of prey items per fish stomach and (b) dry weight biomass of prey per gram of fish mass. For each prey taxon, data given are mean (\pm 1 S.D.) prey consumption of individual fish, relative abundance in the diet (%) and significance of one-way ANOVA of mean prey consumption of fish in five replicate enclosures per treatment.

	Stone loach					Bullhead				
	Control		+ Bullheads		Sig.	Control		+ Loach		Sig.
	Mean ± SD	%	Mean ± SD	%		Mean ± SD	%	Mean ± SD	%	
(a) Number										
<i>Gammarus pulex</i>	1.9 ± 1.9	3	2.5 ± 2.4	6	NS	2.5 ± 2.5	30	2.8 ± 3.1	40	NS
<i>Baetis</i> spp.	0.3 ± 0.6	< 1	0.4 ± 1.1	< 1	NS	0.4 ± 0.8	5	0.5 ± 1.7	7	NS
Other Ephemeroptera	0.2 ± 0.5	< 1	0.4 ± 0.6	< 1	NS	0.4 ± 0.6	5	0.7 ± 1.3	10	NS
Chironomidae	57.8 ± 36.8	92	40.7 ± 33.1	89	*	2.3 ± 3.0	27	0.6 ± 0.8	9	*
Simuliidae	0.2 ± 0.5	< 1	0.1 ± 0.3	< 1	NS	0.1 ± 0.3	1	0.4 ± 0.8	6	NS
Trichoptera	0.6 ± 0.8	< 1	0.3 ± 0.6	< 1	NS	0.2 ± 0.4	2	0.2 ± 0.5	3	NS
<i>Potamopyrgus jenkinsi</i>	0.1 ± 0.2	< 1	0.0 ± 0.0	0	NS	0.2 ± 0.5	2	1.2 ± 2.5	17	**
<i>Ancylus fluviatilis</i>	0.0 ± 0.0	0	0.0 ± 0.0	0	NS	2.1 ± 3.2	25	0.4 ± 0.6	6	***
Other taxa	1.5 ± 1.4	3	1.4 ± 1.5	3	NS	0.2 ± 0.4	3	0.2 ± 0.4	2	NS
Total	62.6 ± 35.8	100	45.8 ± 33.7	100	*	8.4 ± 4.2	100	7.0 ± 5.2	100	NS
(b) Biomass (mg/g)										
<i>Gammarus pulex</i>	0.9 ± 1.5	25	0.8 ± 1.0	33	NS	2.1 ± 2.4	48	1.9 ± 2.2	65	NS
<i>Baetis</i> spp.	< 0.1 ± 0.0	< 1	0.1 ± 0.2	2	NS	0.1 ± 0.1	1	0.1 ± 0.2	2	NS
Other Ephemeroptera	< 0.1 ± 0.1	< 1	< 0.1 ± 0.1	< 1	NS	< 0.1 ± 0.1	< 1	< 0.1 ± 0.1	2	NS
Chironomidae	2.5 ± 1.8	71	1.5 ± 1.3	63	**	0.2 ± 0.3	4	< 0.1 ± 0.1	2	NS
Simuliidae	< 0.1 ± 0.0	< 1	< 0.1 ± 0.0	< 1	NS	< 0.1 ± 0.0	< 1	< 0.1 ± 0.1	< 1	NS
Trichoptera	0.1 ± 0.1	2	< 0.1 ± 0.0	< 1	NS	0.2 ± 0.7	4	0.1 ± 0.3	3	NS
<i>Potamopyrgus jenkinsi</i>	< 0.1 ± 0.0	< 1	0.0 ± 0.0	0	NS	< 0.1 ± 0.1	< 1	0.1 ± 0.3	4	*
<i>Ancylus fluviatilis</i>	0.0 ± 0.0	0	0.0 ± 0.0	0	NS	1.8 ± 3.0	42	0.6 ± 1.4	21	*
Other taxa	< 0.1 ± 0.0	< 1	< 0.1 ± 0.0	< 1	NS	< 0.1 ± 0.0	< 1	< 0.1 ± 0.0	< 1	NS
Total	3.5 ± 2.1	100	2.4 ± 1.6	100	**	4.4 ± 3.8	100	2.9 ± 2.5	100	NS

Significance of ANOVA: NS = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

chironomid larvae (ANOVA: $F_{1,8} = 7.106$, $P = 0.029$; Table 5.1a) and *Ancylus fluviatilis* (ANOVA: $F_{1,8} = 27.563$, $P = 0.001$; Table 5.1a) but more *Potamopyrgus jenkinsi* (ANOVA: $F_{1,8} = 16.738$, $P = 0.003$; Table 5.1a). This dietary shift was highly significant ($C_S = 0.77$, $P = 0.008$) and resulted in niche divergence, with interspecific dietary overlap falling from 0.46 when species were separate to 0.24 when held together. As a result of this resource partitioning, total prey biomass consumption of bullheads was not significantly different between control and loach addition treatments (ANOVA: $F_{1,8} = 3.458$, $P = 0.100$; Table 5.1b).

5.5 DISCUSSION

Species displaying high ecological similarity are predicted to engage in strong interspecific competition (MacArthur & Levins 1967; Abrams 1983). In this study, stone loach and bullheads displayed moderate dietary overlap but there was little evidence for interspecific competition. In contrast to the competition hypothesis, growth in mass of stone loach was facilitated by the presence of bullheads. This effect was not mirrored by the survival and growth in TL of stone loach, suggesting that these metrics are less sensitive measures of fish performance. Positive interactions between potential competitors are common among plants and sessile animals (Bertness & Callaway 1994; Callaway 1995) and although examples of facilitative feeding have begun to emerge in mobile animals (Soluk & Collins 1988; Losey & Denno 1998; Swisher *et al.* 1998) few studies have shown one species to produce a quantifiable improvement in performance of another (Brönmark *et al.* 1991; Resetarits 1997; Soluk & Richardson 1997; Eklov & van Kooten 2001).

The mechanism causing this facilitation is difficult to resolve with the available data, since stomach contents data provide only a snapshot of foraging behaviour at the end of the experiment and because the system may not have reached equilibrium. Predator mediated changes in behaviour or microhabitat use of prey can enhance the foraging efficiency of a second predator species by increasing prey availability (Soluk & Collins 1988; Soluk 1993; Losey & Denno 1998; Eklov & van Kooten 2001). Benthic fish are known to affect the activity levels of benthic macroinvertebrate prey (Andersson *et al.* 1986; Wooster &

Sih 1995), and stone loach and bullheads have contrasting foraging strategies that could theoretically lead to facilitation (Matsuda *et al.* 1993; Sih *et al.* 1998). Thus, bullheads may have facilitated stone loach if anti-predator strategies of chironomid larvae towards bullheads made them more susceptible to stone loach. Alternatively, bullheads may have increased densities of chironomid larvae indirectly by reducing numbers of intermediate consumers and initiating a trophic cascade, although there was no evidence for this from measurements of macroinvertebrate densities taken at the end of the experiment (see Chapter 6). This facilitation model predicts that prey consumption will be higher in the presence of heterospecifics, but this was not upheld by the data. It is possible, however, that facilitative feeding occurred earlier in the experiment. This interpretation runs counter to the observation of Welton *et al.* (1991) that foraging rates of stone loach on chironomid larvae were reduced when held together with bullheads under controlled laboratory conditions, although the competitive interactions observed could have been an artefact of the unnaturally high fish densities used. However, alternative explanations for facilitation, such as increased foraging efficiency through improved detection of patchily distributed prey (Street & Hart 1985) or reduced energetic costs, seem unlikely.

Facilitation, in the form of enhanced growth rate, has the potential to impact the population dynamics of stone loach, since body size is positively correlated with female fecundity (Mills *et al.* 1983). However, if bullheads were facilitating stone loach by enhancing consumption rates of chironomid larvae, this is unlikely to be sustainable. At end of the experiment, loach consumed fewer chironomids in the presence of bullheads, suggesting that facilitation may have accelerated the depletion of prey. Stone loach did not switch to alternative food sources to maintain prey intake in response to declining intake of preferred prey. This restricted and inflexible foraging behaviour is thought to be due to the tactile foraging strategy of stone loach which limits them to taking small prey species with low mobility (Smyly 1955; Welton *et al.* 1983). Thus, the specialised dietary niche of stone loach appears to prevent interspecific competition but may also render them vulnerable to strong exploitation competition from conspecifics (A. Davey, *unpublished data*), which will probably override any short-term positive effects of bullheads.

Bullheads displayed a strong dietary shift in the presence of stone loach. Exploitation competition is able to account for the reduced consumption of chironomid larvae and

Ancylus fluviatilis, which were both reduced in density in enclosures containing stone loach (see Chapter 6). Predation by stream fish can exert strong top-down effects on densities of benthic invertebrate prey (Wooster 1994; Dahl & Greenberg 1996) but this is the first study to provide evidence that one species can affect the prey intake of a sympatric predator species through exploitation competition. The corresponding increase in consumption of *Potamopyrgus jenkinsi* by bullheads is thought to be a compensatory response to declining availability of preferred prey species and may reflect a change in dietary preference or foraging strategy. As a result bullheads were able to maintain prey biomass intake, and consequently survival and growth in body size were unaffected by the presence of stone loach. Bullheads are generalist predators, adopting an opportunistic foraging strategy in response to fluxes of key invertebrate groups (Hartley 1948; Mann & Orr 1969; Welton *et al.* 1983; Michel & Oberdorff 1995). This flexible behaviour may ameliorate interspecific competitive interactions, at least in the short term, by partitioning prey resources between the two species. Flexibility is thought to be an adaptation to life in a variable environment (Gorman 1988), and has been identified as a potential mechanism for co-existence in other stream fishes (Nakano *et al.* 1999; Katano *et al.* 2000). The potential for niche divergence to mitigate interspecific competition cautions against inferring population-level consequences of competition from niche shifts alone (MacNally 1983; Schoener 1983).

In conclusion, traditional measures of ecological similarity such as dietary overlap are a poor indicator of the nature and strength of interspecific interactions. Morphologically dissimilar species can engage in exploitation competition when resource use is independent of trophic morphology (Baltz *et al.* 1982; Resetarits 1995; Hesthagen & Heggenes 2003) and this study, conversely, reveals that small ecological differences among species can eliminate competitive interactions (Schlosser & Toth 1984) and may even lead to facilitation. The concept of limiting similarity may therefore be of limited value for predicting species co-existence (Abrams 1983; Resetarits 1995). Furthermore, indirect trophic interactions can produce positive as well as negative effects and result in complex, asymmetrical interactions (Soluk & Collins 1988; Brönmark *et al.* 1991; Resetarits 1997). The lack of evidence for competitive structuring in stream fish at the population and community level may therefore be due to the compensating effects of facilitation (Schluter 1984).

- 6 -

CONTRASTING AND ADDITIVE EFFECTS OF ECOLOGICALLY SIMILAR PREDATORS

6.1 ABSTRACT

Predation is one of the key processes governing patterns in ecological communities. By assigning species to trophic levels, theories of trophic interactions in food webs assume that predator species are functionally equivalent and independent. Interspecific differences in predator attributes can, however, cause idiosyncratic predator impacts and give rise to non-additive multiple predator effects as a result of direct and indirect interactions amongst predators. The aim of this study was to investigate the influence of predator attributes on top-down predation impacts by examining the independent and interactive effects of two benthic fish predators, bullheads *Cottus gobio* and stone loach *Barbatula barbatula*, on invertebrate and epilithic algae communities in a chalk stream. Presence and absence of each predator was manipulated in a 2x2 factorial design using cage enclosures. Bullheads had a negligible impact upon invertebrates, suppressing densities of only *Pisidium* spp., and had no significant effect on epilithic algae. In contrast, stone loach significantly reduced total invertebrate density and indirectly increased the standing crop of epilithic algae by suppressing the densities of two important herbivores, chironomid larvae and *Ancylus fluviatilis*. Predators generally functioned independently, with combined predator effects simply the sum of the impacts of the component species in isolation. This study demonstrates that in some circumstances multiple predator effects are additive despite complementary foraging modes that theoretically could facilitate or inhibit foraging efficiency. It also shows, however, that differences in predator attributes such as degree of specialisation and foraging mode can translate into quantitative and qualitative differences in effects upon herbivores and contrasting strengths of cascading effects on primary producers. Aggregating superficially similar predator species into a single functional unit therefore risks oversimplifying food webs. Focusing instead on attributes of predators that allow *a priori* predictions of independent and interactive effects should provide a more profitable approach to analysing complex trophic interactions.

6.2 INTRODUCTION

Predation is one of the key processes governing patterns in ecological communities. Almost all prey face a simultaneous predation threat from many species, yet the majority of experimental studies to date have only examined the effect of one predator species in isolation, or considered different predators one at a time (Sih *et al.* 1998). Perhaps because of this, theories of trophic interactions in food webs often assume that predator species can be treated collectively as a single functional unit such as a guild or trophic level (Hairston *et al.* 1960; Oksanen *et al.* 1981; Carpenter *et al.* 1985; Menge & Sutherland 1987), implying that different predator species are functionally equivalent and act independently.

Simplification of food webs by aggregating species into trophic levels has been criticised, however, because it does not adequately address the complexity of natural systems (Polis 1994; Polis & Strong 1996; Persson 1999). Firstly, predators often differ in a number of attributes such as foraging strategy, degree of specialisation and pattern of prey selection. These interspecific differences may translate into differential direct and indirect effects on lower trophic levels (McIntosh & Townsend 1996; Dahl 1998a, 1998b; Schmitz & Suttle 2001). Secondly, multiple predators do not function in isolation, but may interact with each other directly via interference competition, group searching or intraguild predation (Wissinger & McGrady 1993; Snyder & Ives 2001) and indirectly, via changes in prey density or behaviour (Matsuda *et al.* 1993). Interactions between predators can therefore facilitate or inhibit predation rates, resulting in risk enhancement or risk reduction for prey (Soluk 1993; Losey & Denno 1998). The outcome of these interactions is that the effects of multiple predators are non-additive. Thus, predators may have combined effects that cannot be predicted simply by summing the effects of each species in isolation (Sih *et al.* 1998; Swisher *et al.* 1998).

Experimental manipulations of predators have demonstrated top-down control of prey abundance in a range of ecosystems (for reviews see Sih *et al.* 1985; Pace *et al.* 1999; Schmitz *et al.* 2000; Shurin *et al.* 2002). Where there are strong interactions among species, predator effects can trigger a trophic cascade (*sensu* Carpenter *et al.* 1985) of alternating positive and negative effects between successive trophic levels (Shurin *et al.* 2002). The conceptual simplicity and elegance of trophic cascades has elevated them to a

paradigm in food-web science (Persson 1999; Polis *et al.* 2000) despite considerable variation in the magnitude of top-down predation effects within and between ecosystems (Sih *et al.* 1985; Shurin *et al.* 2002). To some extent, apparent disparities between previous studies may reflect a failure to appreciate the complexities of trophic interactions. The magnitude of predator impacts and the extent to which effects are propagated through food webs will depend upon the attributes of the predators concerned. Strong trophic interactions are considered to be more likely in simple food webs with specialist predators, low connectivity and strong linkages. In contrast, top-down predator effects will be limited in reticulate food webs where generalist or omnivorous predators produce weak, diffuse interactions (Polis & Strong 1996; Pace *et al.* 1999; Polis *et al.* 2000).

The aim of this study was to assess the influence of predator attributes on top-down predation impacts by examining the independent and interactive effects of ecologically similar predators with contrasting foraging strategies. Densities of two stream fish species, bullheads (*Cottus gobio*) and stone loach (*Barbatula barbatula*), were simultaneously manipulated *in situ* using cage enclosures to evaluate their effects on benthic invertebrate and epilithic algae communities. This is a particularly appropriate model system for a number of reasons. Firstly, fish-invertebrate-algae interactions in stream benthic communities have been classically documented as an example of a trophic cascade (Wooster 1994; Shurin *et al.* 2002). Secondly, bullheads and stone loach conform to the concept of distinct trophic levels. Both are small nocturnal, benthic species that feed almost exclusively on a common resource base of macroinvertebrate prey (Smyly 1955, 1957; Welton *et al.* 1983). Because they share a superficial ecological similarity, bullheads and stone loach are generally considered as members of the same guild or trophic level. Thirdly, bullheads and stone loach have contrasting foraging strategies that are theoretically likely to produce contrasting independent top-down effects and non-additive multiple predator effects (Sih *et al.* 1998). Stone loach are tactile foragers that actively seek out prey using their barbels and are restricted to taking small prey species with low mobility (Smyly 1955; Welton *et al.* 1983). Bullheads, in contrast, are visual ambush predators that feed opportunistically on a variety of large mobile invertebrate prey (Smyly 1957; Welton *et al.* 1983). Specifically, the objectives of this study were (i) to quantify and compare the impact of bullheads and stone loach upon invertebrate and epilithic algae communities and (ii) to test for non-additive multiple predator effects.

6.3 METHODS

6.3.1 Study site

The study was conducted on the Brandy Stream (see section 1.5.2 for details). Water temperature ranged from 11.7 to 17.6 °C (mean 14.1 °C) during the experiment (Seamon mini temperature recorder, Húgrún, Reykjavik, Iceland), and discharge was near baseflow.

6.3.2 Experimental enclosures

The experiment was conducted using an array of 20 replicate enclosures each 1.4 m long, 0.8 m wide (1.12 m²) and 0.3 m high. Enclosures had solid metal sides and base and 6 mm wire-mesh on the up- and down-stream ends to permit water to flow through the structure. Enclosures were designed to simulate a gravel riffle mesohabitat and were established on 26 July 2001 in water 0.14-0.23 m deep with velocity 0.18-0.37 m/s. Enclosures were placed approximately 4 m apart and staggered to reduce upstream enclosure effects. The base of each enclosure was covered with 30 kg of 40-120 mm gravel and cobbles and 30 kg of 10 mm gravel, creating a substrate approximately 25 mm depth. Plastic netting was placed over the open top of each enclosure to deter avian predators. Invertebrates were allowed to colonise the enclosures for 30 days prior to the start of the experiment by lowering the up- and down-stream wire meshes. The enclosures were rapidly colonised by benthic invertebrates and supported an assemblage of species similar to that found in the surrounding stream. Once raised to enclose the fish, the wire meshes were cleaned every 12 hours during the experiment to remove accumulated plant debris and maintain water flow through the enclosures.

6.3.3 Experimental design

A 2x2 factorial design was used, crossing presence and absence of bullheads with presence and absence of stone loach. The four treatments were each replicated five times and randomly assigned to enclosures. Each species was stocked at a density of 4.5 fish/m² (5 fish per enclosure). This is within the range of densities recorded for both bullheads and stone loach in chalk streams (Mann 1971; Prenda *et al.* 1997). Using equal densities of each predator species permits the per capita effect of bullheads and stone loach to be compared and standardises the effect of interactions between them. This design holds the

density of each component species constant to test for additive effects of fish predators (Sih *et al.* 1998). However, because the combined predator treatment is confounded with total predator density, it is not possible to determine if within and between species effects are equal and, thus, whether predators have substitutable effects (Sih *et al.* 1998).

6.3.4 Experimental protocol

All experimental fish were collected locally from the Brandy Stream by electrofishing on 22 and 24 August. On 25 August, 50 adult fish of each species were weighed to 0.01 g, measured to 0.1 mm (total length, TL) and randomly assigned to treatments. Bullheads ranged in initial mass from 2.67 g to 10.15 g (mean 4.98 g) and in TL from 62.1 mm to 92.5 mm (mean 72.9 mm). Stone loach ranged in initial mass from 2.02 g to 9.41 g (mean 4.40 g) and in TL from 68.1 mm to 105.9 mm (mean 84.3 mm). Fish were held in the enclosures for 21 days. Fish that died during the experiment were replaced with fish of a similar size to maintain the treatments.

Artificial substrata were used to measure the standing crop of epilithic algae inside the enclosures. On 7 August, six 25 x 25 mm unglazed ceramic tiles were placed in each enclosure. Three tiles were sampled at random on 31 August and 12 September (6 and 18 days into the experiment), wrapped in aluminium foil, placed on ice and transported immediately to the laboratory. Estimates of chlorophyll-*a* density were used as a measure of epilithic algae abundance following the method of Thompson (1999). Tiles were rinsed with distilled water to remove dirt, macroalgae and macroinvertebrates. Photosynthetic pigments were then extracted in 100 % methanol at room temperature (20°C) in the dark for 6.5 h. The concentration of chlorophyll-*a* in the resulting supernatant was determined by measuring absorbance (\AA) at 665 nm, and at 750 nm to correct for turbidity (Philips Unicam SP6-250 spectrophotometer). Chlorophyll-*a* biomass density was then calculated as:

$$\text{Chlorophyll-}a \text{ (}\mu\text{g/cm}^2\text{)} = \frac{13.0 \times \text{\AA}_{\text{net}} \times v}{d \times a} \quad (6.1)$$

where 13.0 is a constant for methanol, $\text{\AA}_{\text{net}} = \text{\AA}_{665} - \text{\AA}_{750}$, v = volume of methanol (ml), d = path length of cell (cm) and a = surface area of tile (cm^2). No correction can be made for

degradation products (phaeopigments) or chlorophylls *b* and *c* using methanol extraction (HMSO 1983; Thompson *et al.* 1999).

At the termination of the experiment on 15 September, benthic invertebrates were sampled using a 0.25 x 0.25 m surber sampler. Three samples were taken from each enclosure using a systematic sampling scheme, designed to reduce bias in estimates of invertebrate density arising from within-enclosure positional effects, and preserved in 0.1 g/l paraformaldehyde. In the laboratory, samples were screened with a 710 μm sieve and pooled for each enclosure. Invertebrates were then identified and counted under x40 magnification using a dissecting microscope. Densities (individuals/m²) were calculated for total invertebrates, and for the 26 most abundant invertebrate taxa.

After invertebrate sampling, the enclosures were searched and fish removed with a dip net. Bullheads and stone loach were killed by an overdose of anaesthetic (2-phenoxyethanol) and preserved in 70% ethanol solution. In the laboratory, stomachs of experimental fish were dissected out and contents examined under x40 magnification using a dissecting microscope. Prey items were identified to the lowest possible taxonomic level and counted.

6.3.5 Statistical analysis

Analyses of response variables were performed on the means from each enclosure ($n = 20$). Response variables were tested for homogeneity of variances using Cochran's C-test and analysed by two-way ANOVA with presence and absence of bullheads and stone loach as fixed factors. Using this factorial design, a significant main effect would indicate an effect of a given predator species, whilst a non-additive (emergent) multiple predator effect would be identified by a significant interaction term.

A multiplicative risk model was used to examine multiple predator effects on invertebrate densities. If predators A and B have independent, additive effects, then the density of prey that survive both predators combined is expected to be:

$$N(1 - p_a)(1 - p_b) = N(1 - p_a - p_b + p_a p_b) \quad (6.2)$$

where N is the initial (control) prey density and p_a and p_b are the proportional reductions in prey density caused by predators A and B alone, respectively (Soluk & Collins 1988). This model overcomes the limitations of simple additive models of predator interactions by constraining the proportion of prey remaining ≥ 0 , and is the most appropriate null model for prey response variables (Sih *et al.* 1998). All invertebrate density data were therefore $\log(x + 10)$ transformed prior to analysis to change the null model of multiple predator effects from an additive to a multiplicative risk model (Sih *et al.* 1998). This transformation also served to normalise distributions and stabilise variances. Average water velocity was included as a covariate in the ANOVA model to account for differences in physical conditions between enclosures. The assumption of homogeneous regressions was validated by checking for a non-significant velocity x bullhead x loach interaction term.

Chlorophyll-*a* density was analysed by repeated measures two-way ANOVA, with presence and absence of bullhead and stone loach as fixed factors and sampling date as the repeated measure. To identify important herbivorous species, partial correlations were used to examine relationships between invertebrate density and chlorophyll-*a* density whilst controlling for the confounding effects of water velocity. SPSS v.10.0 (SPSS Inc., Chicago) was used for all statistical procedures and significance evaluated at $\alpha = 0.05$.

Dietary composition of fish was expressed as the mean (\pm standard deviation) number of each invertebrate taxon per fish stomach across all treatments. Percentages were used to indicate relative abundance in the diet.

6.4 RESULTS

6.4.1 Invertebrates

The manipulation of fish predators had profound effects on the invertebrate assemblages within the enclosures. Bullheads had no effect upon total invertebrate density, but reduced the abundance of *Pisidium* bivalves by 42 % (Table 6.1; Figure 6.1). Stone loach had a

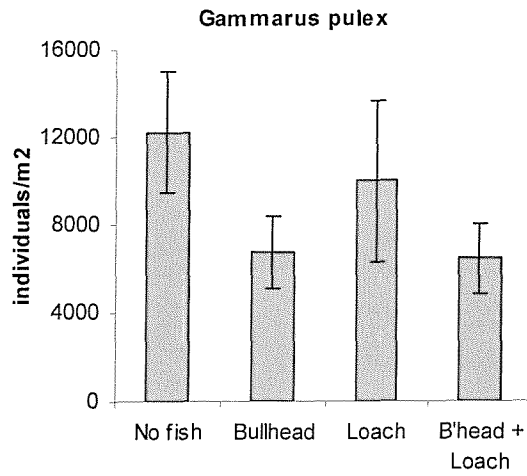
Table 6.1 Two-way ANCOVA of log-transformed invertebrate densities in cage enclosures. Enclosures were stocked with and without bullheads and stone loach in a 2x2 factorial design to assess the effect of each predator species separately (main effects) and to test for non-additivity (interaction term). Water velocity was included as a covariate to account for differences in physical conditions between enclosures. Five replicates were performed for each combination of treatments, giving a total of 20 data points.

Taxon	Bullhead	Stone loach	Bullhead x Loach	Water velocity	R ²
Oligochaeta	NS	NS	NS	-	0.241
<i>Glossiphonia complanata</i>	NS	NS	NS	-	0.316
<i>Erpobdella octoculata</i>	NS	NS	NS	NS	0.163
Ostracoda	NS	NS	NS	---	0.548
<i>Gammarus pulex</i>	NS	NS	(+)	+++	0.660
<i>Asellus aquaticus</i>	NS	NS	(+)	NS	0.327
<i>Elmis aenea</i> larvae	NS	NS	NS	NS	0.129
<i>Limnius volckmari</i> larvae	NS	NS	NS	-	0.309
Leuctridae	NS	NS	NS	+	0.379
<i>Baetis</i> spp.	NS	NS	NS	NS	0.217
<i>Ephemera danica</i>	NS	NS	NS	--	0.473
<i>Ephemerella ignata</i>	NS	NS	NS	NS	0.166
Chironomidae	NS	---	NS	--	0.737
Ceratopogonidae	NS	NS	NS	--	0.438
<i>Agapetus fuscipes</i>	NS	NS	NS	NS	0.211
<i>Silo nigricornis</i>	NS	NS	NS	NS	0.213
Rhyacophilidae	NS	NS	NS	++	0.459
Hydropsychidae	NS	-	NS	++	0.582
Leptoceridae	NS	NS	NS	---	0.550
<i>Polycentropus flavomaculatus</i>	NS	NS	NS	NS	0.280
<i>Hydroptila</i> sp.	NS	-	NS	NS	0.278
Acari	NS	-	NS	NS	0.356
<i>Potamopyrgus jenkinsi</i>	NS	NS	NS	-	0.379
<i>Valvata cristata</i>	NS	-	NS	NS	0.368
<i>Ancylus fluviatilis</i>	NS	-	NS	NS	0.387
<i>Pisidium</i> spp.	-	NS	NS	-	0.411
All invertebrates	NS	--	NS	NS	0.571

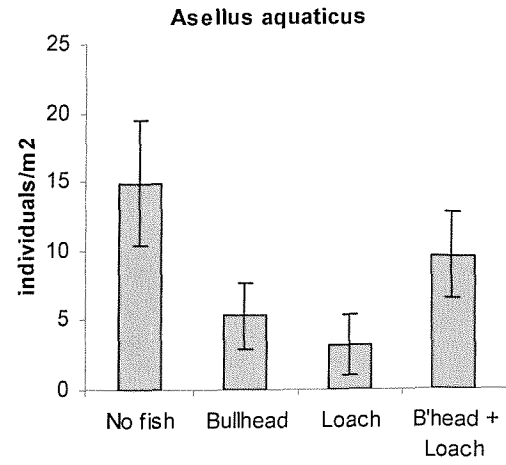
All *F*-values tested with 1 and 15 degrees of freedom. Symbols + and - denote positive and negative effects on density respectively. Significance of *F*: (+)/(-) *P* < 0.10, +/- *P* < 0.05, ++/- *P* < 0.01, +++/- *P* < 0.001, NS = not significant.

much greater impact, significantly reducing densities of chironomid larvae (-43 %), the caddis larvae Hydropsychidae (-49 %) and *Hydroptila* sp. (-43 %), Acari mites (-27 %), *Valvata cristata* (-45 %) and *Ancylus fluviatilis* (-51 %) (Table 6.1; Figure 6.1).

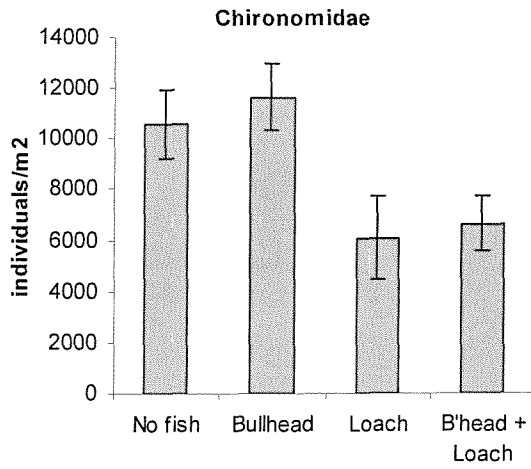
(a)



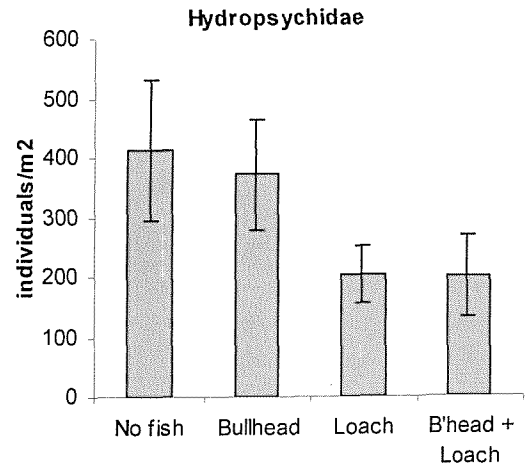
(b)



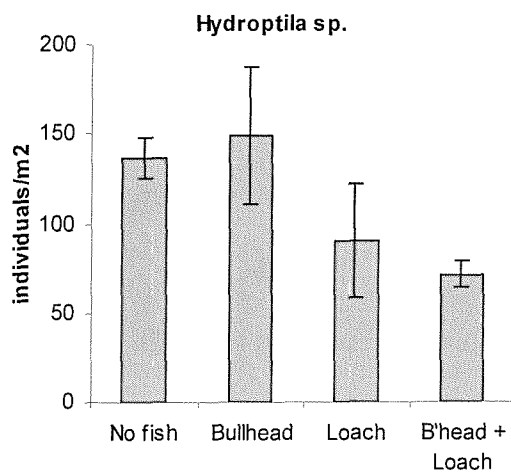
(c)



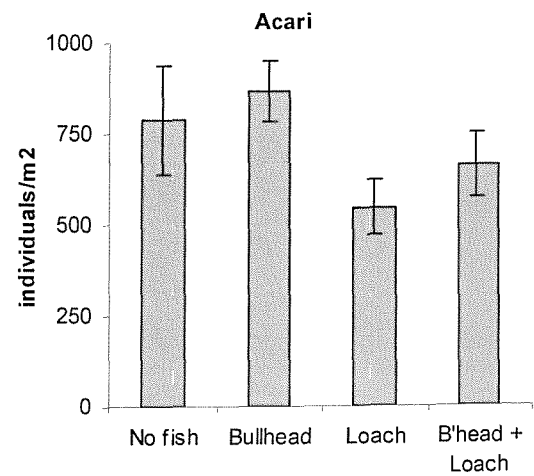
(d)



(e)



(f)



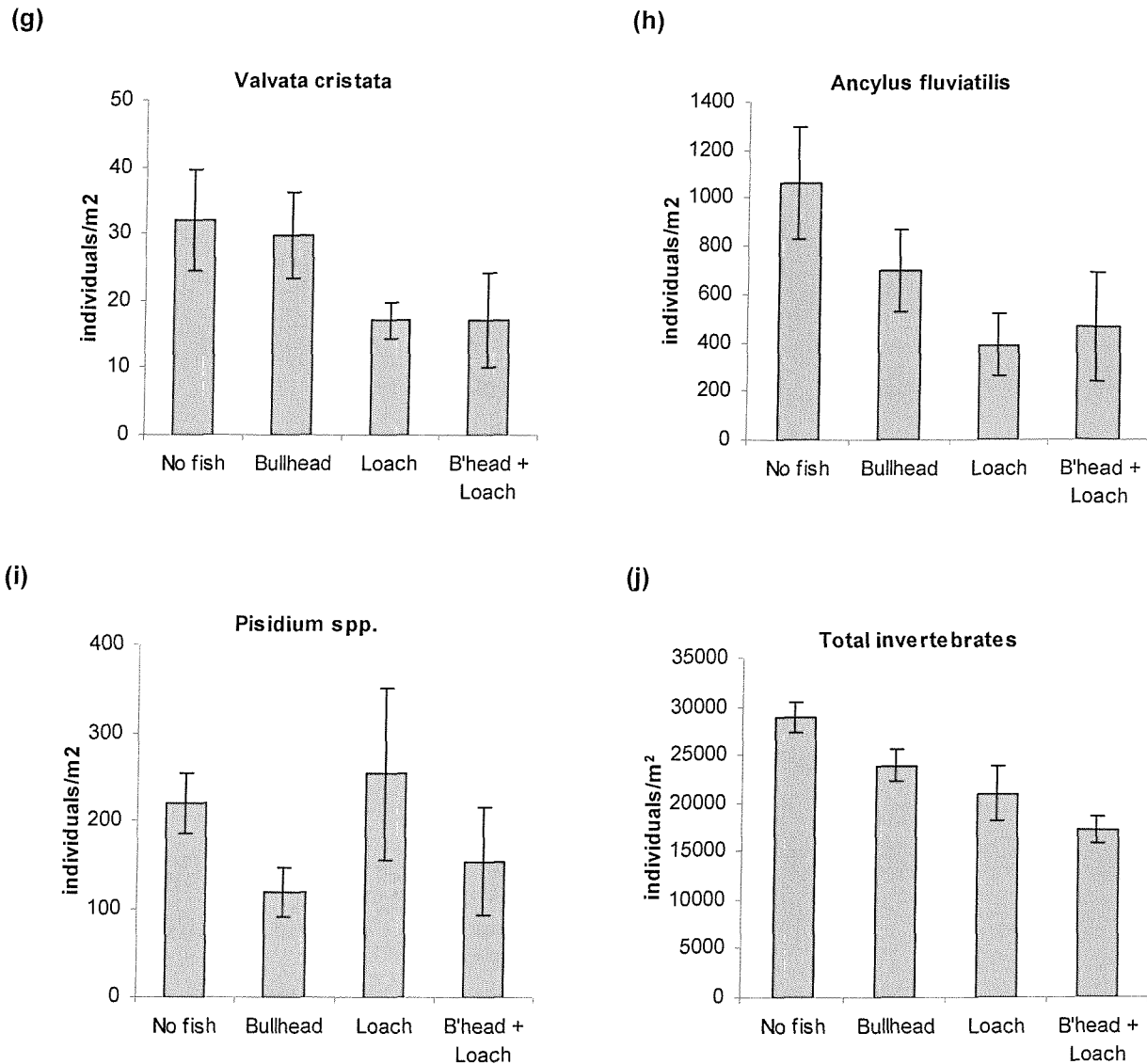


Figure 6.1 Mean (± 1 S.E.) densities of (a) *Gammarus pulex*, (b) *Asellus aquaticus*, (c) Chironomidae, (d) Hydropsychidae, (e) *Hydroptila* sp., (f) Acari, (g) *Valvata cristata*, (h) *Ancylus fluviatilis* and (i) *Pisidium* spp. and (j) total invertebrates in cage enclosures stocked with and without bullheads and stone loach in a 2x2 factorial design. Means are based on five enclosures per treatment.

Since these taxa comprised 46 % of the invertebrate community, total invertebrate density was reduced by over 40 %. Neither bullheads nor stone loach had any positive effects on invertebrate densities.

Overall, there was little evidence for non-additive predator effects. In most cases, combined effects of multiple predators were simply the sum of the effects of the component species in isolation (Table 6.1). There was a suggestion that the combined

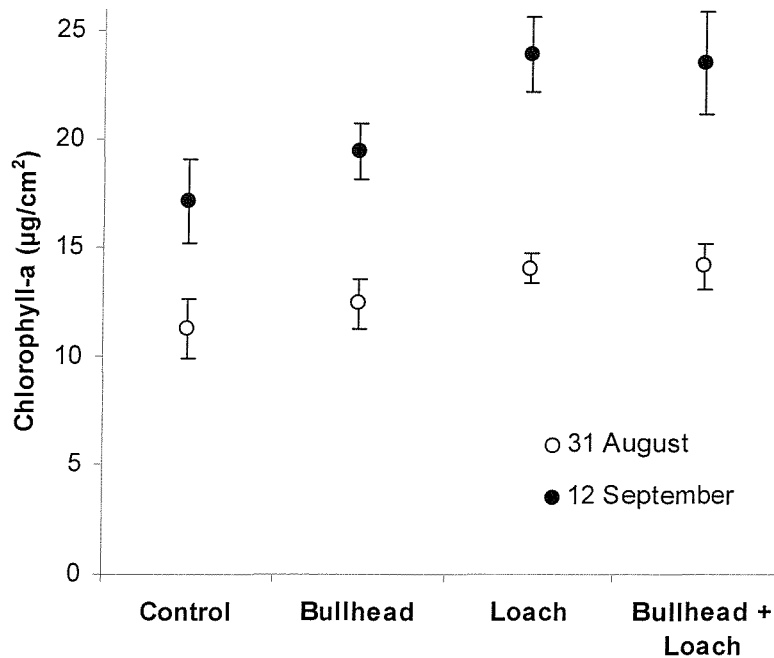


Figure 6.2 Mean (± 1 S.E.) chlorophyll-*a* biomass density of epilithic algae in cage enclosures stocked with and without bullheads and stone loach in a 2x2 factorial design. Epilithic algae were sampled from artificial substrata on 31 August and 12 September, 6 and 18 days into the 21 day experiment respectively. Means are based on 5 replicate enclosures per treatment.

impact of bullheads and stone loach on *Gammarus pulex* and *Asellus aquaticus* was weaker than the sum of their effects when held alone (Figure 6.1), but the interaction terms were marginally non-significant ($F_{1,15} = 3.138$, $P = 0.097$ and $F_{1,15} = 4.077$, $P = 0.062$ respectively; Table 6.1).

6.4.2 Epilithic algae

Chlorophyll-*a* density increased across all treatments during the experiment as the artificial substrata were colonised by epilithic algae ($F_{1,16} = 153.7$, $P < 0.001$; Figure 6.2, Table 6.2). Chlorophyll biomass was 26 % higher in enclosures with stone loach ($F_{1,16} = 7.855$, $P = 0.013$). In contrast bullheads had no effect upon the standing crop of epilithic algae ($F_{1,16} = 0.343$, $P = 0.566$). There was no also evidence for an interaction between bullheads and stone loach ($F_{1,16} = 0.460$, $P = 0.507$). Chlorophyll-*a* density on 12 September was negatively correlated with densities of chironomid larvae ($r = -0.517$, $P = 0.024$, $n = 20$) and *Ancylus fluviatilis* ($r = -0.484$, $P = 0.036$, $n = 20$) after partialling out

Table 6.2 Repeated-measures two-way ANOVA of chlorophyll-a biomass density of epilithic algae in cage enclosures stocked with and without bullheads and stone loach in a 2x2 factorial design. Epilithic algae were sampled from artificial substrata 6 and 18 days into the 21 day experiment. Five replicate enclosures were used for each combination of treatments, giving a total of 20 data points.

Source of variation	SS	df	MS	F	P
Between subjects					
Bullhead	6.480	1	6.480	0.343	0.566
Loach	148.379	1	148.379	7.855	0.013
Bullhead x Loach	8.686	1	8.686	0.460	0.507
Error	302.237	16	18.890		
Within subjects					
Date	641.761	1	641.761	153.715	<0.001
Date x Bullhead	0.253	1	0.253	0.061	0.809
Date x Loach	25.345	1	25.345	6.071	0.025
Date x Bullhead x Loach	1.632	1	1.632	0.391	0.541
Error	66.800	16	4.175		

Note: Repeated measures ANOVA assumes that there is no significant interaction of subject (enclosure) with date, which is untestable because it is the within-subject error term.

the effect of water velocity, but not significantly correlated with any other invertebrate taxon (all $P > 0.10$).

6.4.3 Fish diets

Bullheads and stone loach fed exclusively on benthic invertebrates (Table 6.3). Bullheads consumed a range of invertebrates, particularly large or mobile prey such as *Gammarus pulex*, chironomid larvae, *Ancylus fluviatilis*, *Potamopyrgus jenkinsi* and *Baetis* nymphs. Stone loach, in contrast, had a highly specialised diet, with chironomid larvae accounting for 93 % of all prey items.

6.5 DISCUSSION

6.5.1 Predator effects

In this study, bullheads and stone loach had contrasting effects on benthic invertebrate and epilithic algae communities. Bullheads had a negligible impact upon invertebrate densities and epilithic algae biomass. Previous studies have reported strong effects of bullheads on

Table 6.3 Dietary composition of bullheads and stone loach across treatments. Data are mean (\pm 1 S.D.) number of prey items per stomach and relative abundance in diet.

	Bullhead ($n = 50$)		Stone loach ($n = 48$)	
	Mean \pm S.D.	%	Mean \pm S.D.	%
Oligochaeta	$< 0.1 \pm 0.2$	0.5	0.3 ± 0.7	0.5
<i>Glossiphonia complanata</i>	$< 0.1 \pm 0.1$	0.3	0.0 ± 0.0	0.0
<i>Erpobdella octoculata</i>	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Ostracoda	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
<i>Gammarus pulex</i>	2.7 ± 2.8	34.7	2.2 ± 2.2	4.1
<i>Asellus aquaticus</i>	$< 0.1 \pm 0.1$	0.3	0.0 ± 0.0	0.0
<i>Elmis aenea</i> (larvae)	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
<i>Limnius volckmari</i> (larvae)	0.0 ± 0.0	0.0	$< 0.1 \pm 0.1$	< 0.1
Leuctridae	0.0 ± 0.0	0.0	$< 0.1 \pm 0.1$	< 0.1
<i>Baetis</i> spp.	0.5 ± 1.3	6.0	0.4 ± 0.9	0.7
<i>Ephemera danica</i>	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
<i>Ephemerella ignata</i>	0.1 ± 0.3	1.3	0.1 ± 0.2	0.1
Chironomidae	1.4 ± 2.4	18.7	50.0 ± 36.0	92.3
Ceratopogonidae	0.0 ± 0.0	0.0	0.1 ± 0.4	0.2
<i>Agapetus fuscipes</i>	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
<i>Silo nigricornis</i>	$< 0.1 \pm 0.1$	0.3	$< 0.1 \pm 0.1$	< 0.1
Rhyacophilidae	0.1 ± 0.3	1.0	$< 0.1 \pm 0.1$	< 0.1
Hydropsychidae	0.1 ± 0.3	1.0	0.3 ± 0.6	0.5
Leptoceridae	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
<i>Polycentropus flavomaculatus</i>	0.0 ± 0.0	0.0	$< 0.1 \pm 0.1$	< 0.1
<i>Hydroptila</i> sp.	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Acari	$< 0.1 \pm 0.1$	0.3	0.2 ± 0.4	0.3
<i>Potamopyrgus jenkinsi</i>	0.7 ± 1.9	8.5	$< 0.1 \pm 0.1$	< 0.1
<i>Valvata cristata</i>	0.0 ± 0.0	0.0	$< 0.1 \pm 0.1$	< 0.1
<i>Ancylus fluviatilis</i>	1.2 ± 2.4	16.1	0.0 ± 0.0	0.0
<i>Pisidium</i> spp.	$< 0.1 \pm 0.1$	0.3	$< 0.1 \pm 0.1$	< 0.1
Other taxa	0.8 ± 1.3	10.7	0.5 ± 0.9	0.9
TOTAL	7.7 ± 4.7	100.0	54.2 ± 35.4	100.0

lower trophic levels both directly through consumption and indirectly via interactions among prey species (Dahl 1998a; Englund & Evander 1999). In contrast, stone loach directly reduced total invertebrate density and indirectly increased the standing crop of epilithic algae by suppressing the densities of two important herbivores, chironomid larvae and *Ancylus fluviatilis*, which in turn released epilithic algae from grazing pressure. This is a clear example of a trophic cascade. The alternative mechanism, that excretion of nutrients by stone loach fertilised the algal biofilm, is unlikely since any accumulation of nutrients would be negligible compared to the input of nutrients from outside the enclosures. This is the first study to examine the impact of stone loach on community structure. Multiple predator effects were generally additive, with combined effects that were simply the sum of the effects of the component species in isolation.

These results concur with previous manipulations of stream fish, which report highly variable effects of predation on benthic communities. Some studies have shown weak or no effects of fish on invertebrates (Allan 1982; Culp 1986; Reice & Edwards 1986) whereas others have revealed strong impacts (Gilliam *et al.* 1989; Bechara *et al.* 1992; Forrester 1994). Where strong predator effects have been reported, they are often propagated down the food chain producing trophic cascades (McIntosh & Townsend 1996; Dahl 1998; Golden & Deegan 1998; see Shurin *et al.* 2002 for review). The underlying causes of inconsistent predator effects have been the subject of much debate (Polis & Strong 1996; Pace *et al.* 1999). Exogeneous factors such as productivity (Menge & Sutherland 1987), habitat complexity (Diehl 1992; Holomuzki & Stevenson 1992; Power 1992) and intraguild predation (Snyder & Wise 2001) have been shown to modulate the strength of trophic interactions, but endogenous factors such as predator attributes may also account for some of the discrepancies between previous studies of predator impacts.

6.5.2 Contrasting effects of ecologically similar predators

Although almost all food webs contain multiple predators, the majority of experimental studies to date have only examined the effect of one predator species in isolation, or considered different predators one at a time (Sih *et al.* 1998). This study demonstrates that superficially similar predator species can produce contrasting effects on lower trophic levels. Manipulations of multiple predators, although not always explicitly testing for interspecific differences, have frequently demonstrated quantitative and qualitative differences in predator impact upon intermediate consumers and contrasting strengths of cascading effects on primary producers (Brönmark 1994; Flecker & Townsend 1994; McIntosh & Townsend 1996; Dahl 1998a; Nyström *et al.* 1999; Stelzer & Lamberti 1999; Biggs *et al.* 2000; Nyström *et al.* 2001; Schmitz & Suttle 2001; Shurin 2001; Snyder & Wise 2001).

Species-specific predator effects are to be expected given the variety of foraging behaviour exhibited in natural systems. Indeed, resource partitioning in response to interspecific competition over ecological and evolutionary timescales means that functional equivalence of sympatric predators is likely to be the exception rather than the rule. The ultimate goal, however, is not to simply document this variation, but to draw generalisations from predator manipulations and identify attributes that allow *a priori* predictions of the impact

of a given predator to be made (Wootton 1994; Sih *et al.* 1998). The strength of trophic interactions has been suggested to depend upon foraging strategy (McIntosh & Townsend 1995), diel pattern of foraging (McIntosh & Townsend 1995; Pringle & Hamazaki 1998), feeding efficiency (Nyström *et al.* 1999) and co-evolutionary history (Rosenfeld 2000; Townsend 2003). However, these attributes are often confounded, making it difficult to assess the contribution of a single factor. By simultaneously manipulating two similar predator species under identical physical conditions, this study was able to isolate and evaluate the effect of a single endogenous factor, predator foraging strategy, on top-down predator effects.

Bullheads are opportunistic sit-and-wait, ambush predators, whilst stone loach are more specialised active foragers. These differences have been shown to produce different patterns of prey selection in the field (Welton *et al.* 1983) and may account for the greater impact of stone loach on invertebrate densities. Firstly, by preying upon a limited range of prey, in this case chironomid larvae, consumptive effects of stone loach are more concentrated than those of bullheads and will be more likely to result in significant reductions in prey density. This interpretation is consistent with the prediction that top-down predator effects will be promoted by simple food webs with strong linkages and low connectivity and limited in reticulate food webs with weak, diffuse interactions (Polis & Strong 1996; Pace *et al.* 1999). Secondly, the active foraging strategy of stone loach is likely to be more efficient than the passive ambush approach of bullheads (Dahl 1998a). Furthermore, disturbance caused by active searching may reduce prey densities locally by stimulating increased downstream emigration of invertebrates in the drift (Huhta *et al.* 2000). This latter process may account for the effect of stone loach on non-prey species such as *Ancylus fluviatilis* and *Valvata cristata*. Dahl & Greenberg (1996) showed by meta-analysis of predator manipulations that benthic feeding fishes have a greater impact on benthic invertebrate densities than drift-feeding species. The contrasting effects of two benthic predators observed in this experiment caution against generalising in this way and suggest that active and passive foraging modes provide a more generic distinction.

Evidence of idiosyncratic functionality in this study highlights the limitations of grouping species into trophic levels to predict trophic interactions (Polis 1994; Polis & Strong 1996; Persson 1999). Treating predator species collectively as a single functional unit means that

the importance of species identity in trophic interactions is likely to have been underestimated to date. A cross-ecosystem comparison of the strength of trophic cascades found that ecosystem type explained only 35 % of variation in the effects of predators on herbivores and 29 % of the variation in plant response (Shurin *et al.* 2002), suggesting that endogenous factors such as predator foraging strategy may play a significant role in determining the magnitude of predator effects.

6.5.3 Multiple predator effects

This study found little evidence for non-additive effects of two predatory fish species on densities of benthic invertebrates and epilithic algae. Although other studies have demonstrated risk enhancement and risk reduction for prey (Soluk 1993; Sih *et al.* 1998) and non-additive multiple predator effects on prey densities in the field indicative of complex species interactions (Stelzer & Lamberti 1999), this study shows that multiple predator systems can also conform to predictions of simple additive models whereby the combined effect is simply the sum of the effects of the component species in isolation (Brönmark 1994; Weissberger 1999; Schmitz & Sokol-Hessner 2002). Thus, the combined effect reflected responses to the more dangerous predator (Sih *et al.* 1998; Nyström *et al.* 2001).

Risk enhancement is theoretically likely when prey are threatened by multiple predators with contrasting foraging modes, since behavioural responses of prey species to one predator may increase their vulnerability to other predator species (Soluk & Collins 1988; Matsuda *et al.* 1993; Sih *et al.* 1998). The absence of facilitative effects in this study is thought to be due to differential prey selection and resource partitioning among bullheads and stone loach that acts to minimise trophic interactions between them. An alternative explanation is that prey adopt non-specific anti-predator defences that are effective against both predator species (Matsuda *et al.* 1993). Benthic invertebrates often respond to fish predation risk by decreasing activity (Wooster & Sih 1995), although it is unclear whether this anti-predator behaviour is effective against both sit-and-wait and active predators. Although bullheads increased consumption of *Potamopyrgus jenkinsi* in the presence of stone loach (Chapter 5), this dietary switch did not translate into a significant effect on *P. jenkinsi* densities, probably because of the limited duration of the experiment.

Risk reduction occurs when predator-predator interactions or indirect interactions among prey reduce predation efficiency (Soluk & Collins 1988; Sih *et al.* 1998). Bullheads are known to behave aggressively towards conspecifics (Smyly 1957; Ladich 1989) suggesting that interference competition could also occur between bullheads and stone loach. Welton *et al.* (1991) observed reduced per capita foraging rates of bullheads and stone loach on chironomid larvae and *Asellus aquaticus* when held together in aquaria under controlled laboratory conditions. However, the unnaturally high fish densities used suggest that any competitive interactions were an artefact of high stocking densities. Given that trophic interactions do occur between bullheads and stone loach (Chapter 5), the absence of risk reduction in the present study indicates either that these have a negligible effect on prey densities in the field or that the power of the experiment to detect subtle changes in community composition was low.

6.5.4 Conclusions

This study demonstrates that similar predator species can have contrasting, idiosyncratic effects upon community organisation and that in some circumstances, multiple predator effects are additive despite complementary foraging modes that theoretically could lead to risk enhancement or risk reduction. Whilst strong cascading trophic interactions do occur under certain conditions, generalising by aggregating apparently similar predator species into trophic levels should be done with caution since subtle differences in foraging behaviour of predators can lead to species-specific direct and indirect effects. Future work should address on heterogeneity in food webs by focusing on attributes of predators that determine the degree to which sympatric predator species are functionally equivalent and the pervasiveness of non-additive multiple predator effects.

- 7 -

GENERAL DISCUSSION

7.1 INTRODUCTION

The overall aim of this thesis was to examine the role of competition in structuring stream fish communities using bullheads and stone loach in chalk streams as a model system. Specifically, I performed a series of manipulative field and laboratory experiments and integrated the results with field surveys to identify the mechanisms and consequences of intraspecific and interspecific competitive interactions. This chapter discusses the limitations of adopting an experimental approach before summarising the main results from these investigations and suggesting further lines of enquiry. I then discuss the implications of these results for understanding of stream fish ecology, drawing comparisons with previous theoretical and empirical studies to generalise from the model system, and highlighting key issues and challenges for future research.

7.2 LIMITATIONS OF PRESENT STUDY

Evidence for competition cannot easily be obtained without experiments, and field experiments hold much potential to provide controlled tests of mechanisms of competition (Connell 1983; Gurevitch *et al.* 1992). The utility of experiments is substantially diminished, however, by poor experimental design (Underwood 1986; Fausch 1988), incorrect statistical analysis (Hurlbert 1984) or false interpretation (Bender *et al.* 1984). Field experiments on competition also face the particular problem of determining how responses of individual animals translate into quantifiable effects at the population and community level (MacNally 1983; Schoener 1983). Ideally, one would measure changes in fitness directly by monitoring reproduction and survival over several generations, but the practicalities of doing so are often prohibitive. Instead researchers frequently conduct single generation experiments and estimate fitness indirectly from performance indicators such as growth, habitat use or foraging behaviour that can be measured over short timescales (Fausch 1988). The relevance of short-term niche shifts or behavioural changes

for individual fitness and population dynamics is uncertain, however, because deviations from “normal” behaviour in control treatments do not necessarily result in reduced reproductive fitness (Katano *et al.* 2000). The use of individual growth rate is a better measure of competitive impact because body size is strongly correlated with fecundity in most fish species, including bullheads (Mann 1971; Marconato & Bisazza 1988) and stone loach (Mills *et al.* 1983). Changes in individual growth are therefore expected to translate into effects on demographic parameters.

A further drawback is that field experiments are generally conducted over limited spatial and temporal scales. This can, firstly, limit the generality of field experiments (Diamond 1986; Keddy 1989; Thrush *et al.* 2000). Tilman (1987) suggests, however, that the lack of generality is caused by a lack of emphasis upon mechanisms. Field experiments that adopt a phenomenological approach and do not consider the biological mechanisms underlying species interactions simply generate a sea of observations which are difficult to interpret and from which it is even more difficult to draw generalisations (Keddy 1989). A mechanistic approach, in contrast, has greater predictive power and provides an opportunity to consider how competitive interactions are likely to vary with intrinsic life history traits and along extrinsic environmental gradients (Tilman 1987). Secondly, a narrow focus introduces uncertainty when scaling up results to larger spatial and temporal scales (Cooper *et al.* 1998; Raffaelli & Moller 2000). It is widely acknowledged that as ecological patterns change with scale of investigation, so do the processes causing those patterns (Fisher 1994; Cooper *et al.* 1998). Small-scale manipulations using enclosures generally show stronger competitive effects than studies using unenclosed organisms (Gurevitch *et al.* 1992). This apparent scale-dependence in the strength of competition could be an artefact of high stocking densities, the result of complex interactions between competition and predation (Gurevitch *et al.* 1992), or due to greater spatial heterogeneity at larger spatial scales that reduces the power of an experiment to detect competition.

Despite these shortcomings, the careful design, analysis and interpretation of manipulative field experiments in this study to test specific hypotheses has provided clear insight into the mechanisms and consequences of intraspecific and interspecific competition in chalk stream fish communities.

7.3 SYNTHESIS OF MAIN FINDINGS

7.3.1 Intraspecific competition among bullheads

This study found evidence for strong intraspecific competition among bullheads for both food and shelter. Growth of adult bullheads was negatively density dependent (Chapters 2 and 4) with exact density compensation in biomass production, i.e. perfect density dependence. Growth of bullheads was limited by food availability and parallel dietary shifts induced by manipulation of both fish density and resource availability indicated that exploitation competition for preferred *Gammarus pulex* prey was the primary mechanism responsible for density dependent growth (Chapter 2). Bullheads reduced densities of *Gammarus pulex* in the stream bed by almost 50 %, although this effect was not statistically significant (Chapter 6) unless the effect of stone loach was ignored. The occurrence of exploitation competition despite a high standing crop of macroinvertebrates suggests that only a small fraction of the total prey population is accessible to predators, either because they are hidden in interstitial crevices (Power 1992) or because of specific anti-predator behaviour (Andersson *et al.* 1986). It would be interesting to investigate whether exploitative competitive interactions are more pronounced in patches with low habitat complexity. Bullheads were able to maintain prey biomass intake through a dietary shift, but flexible foraging behaviour was unable to fully compensate for effects of exploitation competition on growth rate. There was no evidence that consumption of prey was affected by interference competition, despite the fact that bullheads are known to behave aggressively towards conspecifics (Smyly 1957; Ladich 1989).

In the field, bullheads selected microhabitats such as cobbles and vegetation margins that provided shelter from predators (Chapter 4). Under experimental conditions, use of artificial shelters was density dependent as a result of both exploitation competition (shelter defence) and interference competition (reduced colonisation efficiency) (Chapter 3). That bullheads engaged in interference competition for shelter but not food is consistent with the predictions of resource defence theory which states that aggressive competitive interactions are more profitable when resources are discrete and spatially aggregated. In contrast to Fischer (2000) who showed that fish without adequate shelter become stressed and suffer reduced somatic growth, individual growth of bullheads was unaffected by shelter use (Chapter 3). Competitive interactions were asymmetrical, with

adult fish dominant over smaller juveniles (Chapters 3 and 4). Consequently, juvenile fish may be displaced from the shelter of cobbles onto finer substrata, resulting in some spatial segregation of size classes in the field (Chapter 4). Intraspecific competition for shelter may be light dependent (Chapter 4), but further studies are needed to clarify why microhabitat partitioning is more pronounced in unshaded reaches. Unsheltered fish are likely to be more vulnerable to predators, but this study was unable to test whether intraspecific competition increased the mortality risk of subordinate fish. Competition for shelter in coral reefs can lead to density dependent predation mortality in juvenile damselfishes (Holbrook & Schmitt 2002), and similar experiments on benthic stream fish are now needed to determine the full consequences of density dependent shelter use.

Given that bullheads compete for both food and shelter, it would be interesting to explore how availability of one resource affects competition for the other. For example, exploitation competition for food may be more intense if bullheads have a clumped distribution as a result of positive selection for coarse substrates. Alternatively, food availability may be correlated with substrate size, and hence shelter availability. Under these circumstances, individuals may be forced to trade-off the use of these resources, either accepting lower rates of food intake where shelter affords protection from predators or risking being unsheltered in order to maximise prey consumption (Grand & Dill 1997).

Density dependence in the individual growth rate of adult fish is likely to have important consequences for population dynamics via effects on demographic parameters such as fecundity and survival. However, the high fecundity of fishes means that any stabilising effects of adult competition on population size may be obscured by high stochastic variation in recruitment. Furthermore, detecting density dependence only identifies exploitation competition among adults as a potential regulating factor. Heavy mortality during early life-stages (Fox 1978a, 1978b) could hold populations below carrying capacity and preclude the occurrence of intraspecific competition amongst adults. Despite this, local densities of adult bullheads in chalk streams often exceed 2 fish/m² (Mann 1971; Green 1975; Fox 1978a), suggesting that exploitation competition among adult fish is a widespread phenomenon.

7.3.2 Interspecific competition between bullheads and stone loach

Evidence for interspecific competition between bullheads and stone loach was limited in this study. Despite a high degree of ecological similarity (Chapter 1), there were significant interspecific differences in both microhabitat use (Chapter 4) and dietary composition (Chapter 5). Subtle differences in morphology and behaviour may therefore translate into pronounced ecological differences. High intraspecific variation in resource use, however, meant that there was still considerable niche overlap between bullheads and stone loach and so simple comparisons of mean resource use may give a misleading indication of the extent of interspecific resource partitioning. Thus, although dietary and habitat partitioning may moderate the strength of interspecific competition, neither of these mechanisms is sufficient to eliminate all interspecific interactions.

Stone loach caused a pronounced dietary shift in bullheads as a result of exploitation competition. However, flexible foraging behaviour of bullheads successfully maintained prey biomass intake which offset any impact of heterospecifics on individual growth and survival (Chapter 5). Niche divergence during periods of low food availability is well documented in stream fish (Zaret & Rand 1971; Magalhães 1993; Gray *et al.* 1997) but this is the first study to demonstrate that dietary partitioning is a direct response to interspecific competition and that niche divergence is able to moderate the strength of the competitive impact. In contrast to *a priori* predictions of interspecific competition, growth of stone loach was higher in the presence of bullheads (Chapter 5). This enhanced performance was probably caused by bullheads making prey more vulnerable to predation by loach (see Soluk 1993; Swisher *et al.* 1998; Eklov & van Kooten 2001 for examples in freshwater fish), but the exact mechanism of facilitation remains uncertain and warrants further study. Facilitation has the potential to affect population dynamics via effects on fecundity (Mills *et al.* 1983), but is unlikely to be sustainable since exploitation of preferred chironomid larvae (Chapter 6) is likely to result in strong intraspecific competition.

Bullheads and stone loach had contrasting top-down effects on densities of benthic invertebrates and epilithic algae (Chapter 6), demonstrating that subtle interspecific differences in foraging behaviour and prey selection can generate idiosyncratic predator effects. Aggregating superficially similar predator species into a single functional unit

therefore risks oversimplifying food webs (Polis 1994; Polis & Strong 1996; Persson 1999). Combined effects of bullheads and stone loach on lower trophic levels were simply the sum of the effects of the component species in isolation (Chapter 6), although trophic interactions between the two species (Chapter 5) suggest that interspecific interactions may produce non-additive multiple predator effects. It would be interesting to repeat the experiment over longer timescale and monitor temporal patterns of community change in response to predation.

7.4 IMPLICATIONS FOR STREAM FISH COMMUNITIES

The application of an experimental approach to the study of a tractable model system has provided insight into the strength, mechanisms and consequences of intraspecific and interspecific competitive interactions in a benthic chalk stream fish community. The ultimate aim of ecology, however, is not to simply accumulate and document specific examples but to derive general predictions about the structure and function of ecological communities (Keddy 1989; Thrush *et al.* 1997). To achieve this, it is necessary to provide a comparative context by considering how the life history and behavioural strategies of the species under investigation influence their competitive dynamics and assessing the degree to which the processes described are applicable to the broader system. The aim of this section is therefore to evaluate the generality of these findings to other stream fish communities.

7.4.1 Intraspecific competition

Studies of intraspecific competition have, to date, been biased towards commercially important species such as brown trout *Salmo trutta* and Atlantic salmon *S. salar* (Le Cren 1965; Elliott 1985; Kennedy & Strange 1986a; Jenkins *et al.* 1999; Keeley 2001). On the basis of this limited empirical evidence, recent reviews have concluded that population regulation in fish occurs almost exclusively at the larval or early juvenile stage as a result of density dependent mortality (Charnov 1986; Sinclair 1989; Shepherd & Cushing 1990). However, competition for food and, possibly, shelter may regulate populations of stream fish at the adult stage via density dependence in growth in body size and, ultimately, fecundity (Chapters 2 and 3). The only previous study documenting density dependence in

adult fish comes from key-factor analysis of resident brown trout in a Lake District stream, where the number of spawning females produced in each year-class was strongly density dependent on the initial number of females that laid eggs at the start of that year class (Elliott & Hurley 1998), although the mechanism responsible was unclear. Clearly, all stages of the life cycle need to be taken into account when assessing the role of intraspecific competition in population regulation.

Intraspecific competitive interactions are likely to be more prevalent in adult fish than currently believed for two reasons. Firstly, fish typically increase in size by several orders of magnitude during their lifespans and consequently display marked ontogenetic changes in dietary composition and habitat use (Werner & Gilliam 1984). For example, individuals may select larger prey and outgrow interstitial shelters with increasing body size. These marked quantitative and qualitative changes in resource requirements provide the necessary conditions for the development of demographic bottlenecks after sexual maturity (Werner 1986; Beck 1995). Secondly, temperate rivers are subject to predictable seasonal variation in prey abundance, with large fluxes in the densities of key macroinvertebrate prey taxa (Magalhães 1993), and water temperature, which influences metabolic rate and hence energy requirements of fish. These seasonal patterns are predicted to reinforce the importance of competition in the structuring of freshwater fish communities by causing periodic bouts of intraspecific competition when food availability is low relative to the metabolic demands of the population (Persson & Johansson 1992; Gasith & Resh 1999) - the “competitive crunch” model of community organisation (Wiens 1977). Seasonal changes in behaviour in response to changes in water temperature could also lead to intraspecific competition in older fish. For example, Atlantic salmon become nocturnal in winter when water temperature falls, and seek shelter in interstitial spaces during the day to reduce vulnerability to endothermic predators (Valdimarsson & Metcalfe 1998; Heggenes *et al.* 1999). Competition for shelter can result in density dependent refuge use (Rangeley & Kramer 1998; Armstrong & Griffiths 2001) and shelter availability may therefore act as a bottleneck for salmonid populations during the winter.

The extent to which these competitive mechanisms apply to other stream fish will depend largely upon the traits of the species concerned. Predation by fish frequently has strong effects of on local prey densities through a combination of direct and indirect effects

(Wooster 1994; Wooster & Sih 1995; Shurin *et al.* 2002). Exploitation competition for food is likely to be more intense for benthic fish than for drift-feeding species (Chapman 1966) because their active foraging has a greater impact on prey densities (Dahl & Greenberg 1996). Specialist predators may be particularly susceptible to intraspecific competition for food because they are more likely to reduce prey densities (Chapter 6) and less able to exploit alternative food sources when availability of preferred prey becomes limiting (Polis & Strong 1996; Chapter 5). Competition for shelter will be most intense in species that behave aggressively towards conspecifics, such as salmonids, and negligible in group living species such as cyprinids. The exact consequences for population dynamics will depend on species-specific responses to shelter availability (Fischer 2000) and vulnerability to predation.

The influence of intraspecific competition on population dynamics will depend upon the relative strength of density independent processes (Townsend *et al.* 2003). Where stochastic disturbance events occur with sufficient frequency to restrict populations below the level at which resources become limiting, competition will be weak or absent (Horwitz 1978; Grossman *et al.* 1982; Moyle & Vondracek 1985; but see Matthews *et al.* 2001). The hydrological stability and high productivity of chalk streams suggest *a priori* that their fish communities should be deterministically structured by strong competition (Horwitz 1978; Schlosser 1982; Menge & Sutherland 1987). Furthermore, in chalk streams, bullheads lay several batches of eggs each year (Mills & Mann 1983). This extended reproductive window makes populations less susceptible to unfavourable flow or temperature conditions (Angermeier & Schlosser 1989). The intraspecific competitive interactions observed in this study are, therefore, likely to be stronger than those in most other stream systems. However, interplay between competition and physical factors has been demonstrated to generate complex community patterns (Hart 1992) and simple statements such as “competition is, or is not, important” are likely to be incorrect (Fisher 1994). Rather, density dependent and density independent processes interact to determine community structure (May 1986). For example, drought may have density dependent effects on fish populations by reducing habitat volume and food availability and increasing competition (John 1964; Magalhães 1993; Pires *et al.* 1999). Simulation modelling of fish community composition under flow-driven recruitment variation also indicates that

assemblage structure will depend upon how disturbance events affect density dependent processes (Strange *et al.* 1993).

7.4.2 Interspecific competition

The role of interspecific competition in structuring ecological communities has been the subject of intense debate (Schoener 1982; Connell 1983). The practical difficulties of performing manipulative experiments in flowing water have meant that knowledge of interspecific competition in stream fish is limited. Interspecific competition is predicted to be strongest between closely related and morphologically similar species because of greater overlap in resource use (MacArthur & Levins 1967; Abrams 1983). Although strong interspecific competition has been reported for some species (Le Cren 1965; Fausch & White 1986; Kennedy & Strange 1986a), subtle differences in resource use (Schlosser & Toth 1984) or flexible foraging behaviour (Angermeier 1987; Nakano *et al.* 1999; Katano *et al.* 2000) can be sufficient to prevent interspecific competition impacting demographic parameters. A high degree of specialisation is not an appropriate ecological trait for species persistence in fluctuating stream environments (Gorman 1988) and fishes often show generalist, opportunistic resource use (Dill 1983; Magalhães 1993; Gray *et al.* 1997). Dynamic niche partitioning in response to heterospecifics may therefore be a widespread and important mechanism of co-existence in stream fish (Nakano *et al.* 1999). Some morphologically specialised species such as stone loach, however, appear to be relatively limited in their resources use (Chapter 5) and may have less potential to respond to interspecific competition through niche shifts.

Models of community organisation have focused predominantly on competitive interactions among species and how they are modified by predation (Gause 1934; Hairston *et al.* 1960; MacArthur & Levins 1967; Menge & Sutherland 1987). More recent research indicates that interspecific interactions are not always negative (Connell 1983; Bertness & Callaway 1994; Bruno *et al.* 2003). Amongst populations of mobile animal predators, indirect trophic interactions can lead to facilitation as well as competition (Resetarits 1997; Swisher *et al.* 1998; Eklov & van Kooten 2001; Chapter 5) and result in complex asymmetrical interactions (Soluk & Collins 1988; Brönmark *et al.* 1991; Holzapfel & Mahall 1999). The direction of interspecific interactions may vary with identity of intermediate prey species (Soluk & Collins 1988) or temporally as a result of fluctuations

in environmental conditions or ontogenetic changes in resource use (Bruno *et al.* 2003). The prevalence of facilitation in stream fish communities is difficult to gauge from the limited number of studies performed to date, but it is possible that the failure of population and community scale analyses to find strong evidence of interspecific competition is because positive and negative interactions cancel each other out (Schluter 1984; Tilman 1987). The influence of competitive interactions on community structure may only be assessed, therefore, by incorporating facilitation into future models of community organisation (Bruno *et al.* 2003).

Interspecific competition has been conclusively shown in a number of studies of stream fish (Fausch & White 1981; Baltz *et al.* 1982; Dewald & Wilzbach 1992). However, the consequences of interspecific competitive interactions for population abundance and community structure will depend on the strength of interspecific competition relative to intraspecific competition (Gause 1934; Underwood 1986; Fausch 1988). Although interspecific competition can be more intense than intraspecific competition (Resetarits 1995), the weight of evidence from field experiments suggests that intraspecific competition is generally stronger than interspecific competition (Le Cren 1965; Connell 1983; this study). Thus, sympatric species are able to co-exist because competition amongst conspecifics limits their ability to competitively exclude heterospecifics. It is not surprising, therefore, that macroecological analyses which attempt to detect non-random assemblage composition by examining patterns of species have found little evidence of ecological saturation in stream fish (Angermeier & Winston 1995; Hugueny & Paugy 1995; Oberdorff *et al.* 1998). Interspecific competitive interactions appear to operate over small spatial and temporal scales, with distributional patterns at the landscape level influenced by other factors such as water temperature and connectivity (Fausch *et al.* 1994).

Models of trophic interactions in food webs often assume that predator species within a guild or trophic level are functionally equivalent and act independently (Hairston *et al.* 1960; Oksanen *et al.* 1981; Carpenter *et al.* 1985; Menge & Sutherland 1987). However, species-specific predator effects are to be expected given the variety of foraging behaviour exhibited in natural systems. Indeed, resource partitioning in response to interspecific competition over ecological and evolutionary timescales means that functional equivalence

of sympatric predators is likely to be the exception rather than the rule (Chapter 6). Interspecific interactions among predators can have consequences for lower trophic levels by enhancing or inhibiting predation rates (Soluk 1993; Sih *et al.* 1998; Swisher *et al.* 1998; Eklov & van Kooten 2001). Where species partition resources, however, multiple predator systems can also conform to predictions of simple additive models whereby the combined effect is simply the sum of the effects of the component species in isolation (Brönmark 1994; Weissberger 1999; Schmitz & Sokol-Hessner 2002; Chapter 6).

Although active interspecific competition may be weak in contemporary fish assemblages, it cannot be excluded as a driving force shaping these communities in evolutionary time. Observed morphological and ecological differences between component species are often assumed to be the result of divergent evolution in response to interspecific competition (Gatz 1979; Moyle & Senanayaka 1984; Winemiller 1991). This interpretation should be applied with caution, however, since the resultant pattern of selective segregation cannot be unambiguously attributed to the “ghost of competition past” (Connell 1980). This process of evolutionary resource partitioning may be particularly important in tropical fish assemblages where high species diversity is paralleled by high ecomorphological diversity (Winemiller 1991). In contrast, the stream fish communities of northern European are species poor and contain few congeneric species compared to those of the Mediterranean and North America (Oberdorff *et al.* 1997; Greenhalgh 1999). The apparent absence of strong interspecific competition in chalk stream fish communities is therefore probably due, at least in part, to their biogeographic history (Wheeler 1977).

7.5 WIDER PERSPECTIVES

Intraspecific competition is a key process by which populations are regulated (Sinclair 1989) but the influence of competition in nature has been the subject of considerable debate (Andrewartha & Birch 1954; Nicholson 1954; Turchin 1999). This study supports the idea that species in stable, predictable environments will engage in strong competition (Wiens 1977, 1984; DeAngelis & Waterhouse 1987) but is contrary to predictions that species with *r*-selected life history traits (rapid development, early maturity, high fecundity and short lifespans) will experience only weak or sporadic competition (MacArthur &

Wilson 1967; Pianka 1970). This could indicate an overriding influence of environmental stability, but may also reflect a life history adaptation to size-specific mortality factors in some stream fish (Fox 1978c; Mills & Mann 1983) that runs counter to established rK -selection theory.

Explaining the maintenance of species diversity is another major challenge in ecology. In systems such as forests, rocky shores and coral reefs, where patches can be occupied by only one species at a time, high species diversity is frequently observed with little or no niche differentiation (Silvertown & Law 1987). Under such circumstances, coexistence of potential competitors is thought to be maintained by unpredictable external forces that prevent competitive exclusion running its course. These models propose that spatial and temporal variation in environmental conditions achieves coexistence by (i) limiting the abundance of dominant competitors (disturbance hypothesis, Huston 1979; Wiens 1984), (ii) alternately favouring recruitment of different species (storage dynamics, Chesson & Warner 1981; Kelly & Bowler 2002) or (iii) generating vacant patches that are colonised at random (lottery model, Sale 1977) or by fugitive species (Paine 1979; Nee & May 1992). In contrast, this study provides evidence that species may coexist through intrinsic processes such as niche differentiation, dynamic resource partitioning (Lack 1946) and intraspecific competition (Gause 1934). Thus, traditional models of community organisation based on division of resources may be sufficient to explain coexistence of mobile consumers in systems with low species diversity and high resource heterogeneity.

7.6 CONCLUDING REMARKS

Competition is a fundamental process shaping stream fish communities. This study has shown that strong intraspecific competition for essential resources such as food and shelter can determine spatial distribution of fish in the field and potentially regulate population size via density dependent individual growth and fecundity. Competition may occur after sexual maturity as a result of ontogenetic niche shifts and temporal variation in resource availability. Interactions with conspecifics may be context-dependent and highly asymmetrical, favouring larger adults. In contrast, interspecific competitive interaction actions are weak as a result of dietary and microhabitat partitioning. Although competition

from heterospecifics may affect individuals in the short term, indirect facilitative interactions and strong intraspecific competition combine to limit the impact of interspecific competition at higher levels of ecological organisation.

Significant advances have been made in understanding the processes shaping stream fish communities but there is still much to learn about the relative importance of competition (Fausch *et al.* 1994). Although manipulative field experiments hold much potential for providing rigorous tests of competitive interactions and elucidating the underlying biological mechanisms (Gurevitch *et al.* 1992), there is a growing consensus that pluralistic models, linking experimental and field sampling approaches, are essential to explain the relative importance of different processes and ecological factors in governing community organisation at multiple spatial and temporal scales. Within hierarchically organised systems such as streams, the influence of competition on community structure will vary across habitats and catchments, and will also change in explanatory power over time, from scales of a few days to seasons and even years. Thus, the scale at which we study the lotic environment becomes of crucial importance. The challenge for future work is therefore not to determine which of several competing processes control patterns of interest, but to resolve the spatial and temporal boundaries of each and the causes of transitions among them (Fisher 1994).

- APPENDIX A -

PROCEDURE FOR PERFORMING *A PRIORI* CONTRASTS

Consider a balanced ANOVA of variable Y , with I levels of factor 1 and J levels of factor 2.

FOR MAIN EFFECTS

1. Omit data not required in analysis.
2. Compute the global mean (\bar{Y}) of remaining data.
3. Arrange data into I treatment groups.
4. Compute means (\bar{Y}_i) for each treatment.
5. Calculate main effect sum of squares as:

$$SS_{main} = \sum_{i=1}^I n_i (\bar{Y}_i - \bar{Y})^2$$

where n_i = number of data points in treatment i .

6. Divide SS_{main} by $i-1$ degrees of freedom to give MS_I and test over MS_{error} .

FOR 2-WAY INTERACTIONS

1. Omit data not required in analysis.
2. Compute the global mean (\bar{Y}) of remaining data.
3. Arrange data into ij treatment groups.
4. Compute means (\bar{Y}_i) for each level of factor I .
5. Compute means (\bar{Y}_j) for each level of factor J .
6. Compute means (\bar{Y}_{ij}) for each combination of treatments.
7. Calculate interaction sum of squares as:

$$SS_{int} = \sum_{j=1}^J \sum_{i=1}^I n_{ij} (\bar{Y}_{ij} - \bar{Y}_i - \bar{Y}_j + \bar{Y})^2$$

where n_{ij} = number of data points in treatment ij .

8. Divide SS_{int} by $(i-1)(j-1)$ degrees of freedom to give MS_{IJ} and test over MS_{error} .

REFERENCES

- Abel R. (1973) *The trophic ecology of Cottus gobio* (L.). PhD Thesis, University of Oxford.
- Abrams P.A. (1983) The theory of limiting similarity. *Annual Review of Ecology and Systematics*, **14**, 359-376.
- Abramsky Z., Rosenweig M.L. & Subach A. (1998) Do gerbils care more about competition or predation? *Oikos*, **83**, 75-84.
- Alanara A., Burns M.D. & Metcalfe N.B. (2001) Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *Journal of Animal Ecology*, **70**, 980-986.
- Allan J.D. (1982) The effects of reduction in trout density on the invertebrate community of a mountain stream. *Ecology*, **63**, 1444-1455.
- Allouche S. & Gaudin P. (2001) Effects of avian predation threat, water flow and cover on growth and habitat use by chub, *Leuciscus cephalus*, in an experimental stream. *Oikos*, **94**, 481-492.
- Allouche S. (2002) Nature and functions of cover for riverine fish. *Bulletin Français de la Pêche et de la Pisciculture* 297-324.
- Andersson K.G., Brönmark C., Herrmann J., Malmqvist B., Otto C. & Sjöström P. (1986) Presence of sculpins (*Cottus gobio*) reduces drift and activity of *Gammarus pulex* (Amphipoda). *Hydrobiologia*, **133**, 209-215.
- Andreasson S. (1969a) Locomotory activity patterns of *Cottus poecilopus* Heckel and *C. gobio* L. (Pisces). *Oikos*, **20**, 78-94.
- Andreasson S. (1969b) Interrelationships between *Cottus poecilopus* and *C. gobio* L. (Pisces) in a regulated northern Swedish river. *Oikos*, **20**, 540-546.
- Andreasson S. (1971) Feeding habits of a sculpin (*Cottus gobio*) population. *Report Institute of Freshwater Research Drottningholm*, **51**, 5-30.
- Andrewartha H.G. & Birch L.C. (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago, USA.
- Angermeier P.L. (1987) Spatiotemporal variation in habitat selection by fishes in small Illinois streams. In: W.J. Matthews & D.C. Heins, eds., *Community and Evolutionary Ecology of North American Stream Fishes*. University of Oklahoma Press, Norman. pp. 52-60.
- Angermeier P.L. & Schlosser I.J. (1989) Species-area relationships for stream fishes. *Ecology*, **70**, 1450-1462.
- Angermeier P.L. & Winston M.R. (1995) Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology*, **79**, 911-927.
- Arlettaz R. (1999) Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology*, **68**, 460-471.
- Armstrong J.D., Huntingford F.A. & Herbert N.A. (1999) Individual space use strategies of wild juvenile Atlantic salmon. *Journal of Fish Biology*, **55**, 1201-1212.
- Armstrong J.D. & Griffiths S.W. (2001) Density-dependent refuge use among over-wintering wild Atlantic salmon juveniles. *Journal of Fish Biology*, **58**, 1524-1530.
- Arthur W. & Mitchell P. (1989) A revised scheme for the classification of population interactions. *Oikos*, **56**, 141-143.
- Aström M., Lundberg P. & Lundberg S. (1996) Population dynamics with sequential density-dependencies. *Oikos*, **75**, 174-181.
- Ault T.R. & White R.W.G. (1994) Effects of habitat structure and the presence of brown trout on the population density of *Galaxias truttaceus* in Tasmania, Australia. *Transactions of the American Fisheries Society*, **123**, 939-949.
- Baltz D.M., Moyle P.B. & Knight N.J. (1982) Competitive interactions between benthic stream fishes, riffle sculpin, *Cottus gulosus*, and speckled dace, *Rhinichthys osculus*. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 1502-1511.
- Barr G.E. & Babbitt K.J. (2002) Effects of biotic and abiotic factors on the distribution and abundance of larval two-lined salamanders (*Eurycea bislineata*) across spatial scales. *Oecologia*, **133**, 176-185.
- Bass J.A.B. (1976) Studies on *Ephemerella ignata* (Poda) in a chalk stream in southern England. *Hydrobiologia*, **49**, 117-121.

- Bechara J., Moreau A.G. & Planas D. (1992) Top-down effects of brook trout (*Salvelinus fontinalis*) in a boreal forest stream. *Journal of Animal Ecology*, **62**, 451-464.
- Beck M.W. (1995) Size-specific shelter limitation in stone crabs - a test of the demographic bottleneck hypothesis. *Ecology*, **76**, 968-980.
- Bender E.A., Case T.J. & Gilpin M.E. (1984) Perturbation experiments in community ecology - theory and practice. *Ecology*, **65**, 1-13.
- Benke A.C., Huryn A.D., Smock L.A. & Wallace J.B. (1999) Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, **18**, 308-343.
- Berrie A.D. (1992) The chalk-stream environment. *Hydrobiologia*, **248**, 3-9.
- Bertness M.D. & Callaway R.M. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191-193.
- Biggs B.J.F., Francoeur S.N., Huryn A.D., Young R., Arbuckle C.J. & Townsend C.R. (2000) Trophic cascades in streams: effects of nutrient enrichment on autotrophic and consumer benthic communities under two different fish predation regimes. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1380-1394.
- Boaventura D., Da Fonseca L.C. & Hawkins S.J. (2003) Size matters: competition within populations of the limpet *Patella depressa*. *Journal of Animal Ecology*, **72**, 435-446.
- Bohlin T. (1977) Habitat selection and intercohort competition of juvenile sea-trout *Salmo trutta*. *Oikos*, **29**, 112-117.
- Bohlin T. (1978) Temporal changes in the spatial distribution of juvenile sea trout in a small stream. *Oikos*, **30**, 114-120.
- Bohlin T. (1989) Electrofishing - theory and practice with special emphasis on salmonids. *Hydrobiologia*, **173**, 9-43.
- Bohnsack J.A. (1989) Are high densities of fishes at artificial reefs the result of habitat limitation or behavioural preferences? *Bulletin of Marine Science*, **44**, 631-645.
- Boss S.M. & Richardson J.S. (2002) Effects of food and cover on the growth, survival, and movement of cutthroat trout (*Oncorhynchus clarki*) in coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1044-1053.
- Boussu M.F. (1954) Relationship between trout populations and cover on a small stream. *Journal of Wildlife Management*, **18**, 229-239.
- Britz P.J. & Pienaar A.G. (1992) Laboratory experiments on the effect of light and cover on the behavior and growth of African catfish, *Clarias gariepinus* (Pisces, Clariidae). *Journal of Zoology*, **227**, 43-62.
- Brönmark C., Rundle S.D. & Erlandsson A. (1991) Interactions between freshwater snails and tadpoles - competition and facilitation. *Oecologia*, **87**, 8-18.
- Brönmark C. (1994) Effects of tench and perch on interactions in a freshwater, benthic food chain. *Ecology*, **75**, 1818-1828.
- Brooker M.P., Morris D.L. & Hemsworth R.J. (1977) Mass mortalities of adult salmon, *Salmo salar*, in the River Wye 1976. *Journal of Applied Ecology*, **14**, 409-417.
- Brown L. & Downhower J.F. (1982) Summer movements of mottled sculpins, *Cottus bairdi* (Pisces: Cottidae). *Copeia*, **1982**, 450-453.
- Brown L.R. (1991) Differences in habitat choice and behavior among 3 species of sculpin (*Cottus*) in artificial stream channels. *Copeia*, **1991**, 810-819.
- Bruno J.F., Stachowicz J.J. & Bertness M.D. (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, **18**, 119-125.
- Bult T.P., Riley S.C., Haedrich R.L., Gibson R.J. & Heggenes J. (1999) Density-dependent habitat selection by juvenile Atlantic salmon (*Salmo salar*) in experimental riverine habitats. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1298-1306.
- Butler M.J. & Herrnkind W.F. (1997) A test of recruitment limitation and the potential for artificial enhancement of spiny lobster (*Panulirus argus*) populations in Florida. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 452-463.
- Callaway R.M. (1995) Positive interactions among plants. *Botanical Review*, **61**, 306-349.
- Carpenter S.R., Kitchell J.F. & Hodgson J.R. (1985) Cascading trophic interactions and lake productivity. *Bioscience*, **35**, 634-639.
- Cattaneo F., Lamouroux N., Breil P. & Capra H. (2002) The influence of hydrological and biotic processes on brown trout (*Salmo trutta*) population dynamics. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 12-22.

- Chapman D.W. (1962)** Aggressive behaviour in juvenile coho salmon as a cause of emigration. *Journal of the Fisheries Research Board of Canada*, **19**, 1047-1080.
- Chapman D.W. (1966)** Food and space as regulators of salmonids populations in streams. *American Naturalist*, **100**, 345-357.
- Chapman L.J. & Kramer D.L. (1991)** The consequences of flooding for the dispersal and fate of Poeciliid fish in an intermittent tropical stream. *Oecologia*, **87**, 299-306.
- Charnov E.L. (1986)** Life history evolution in a recruitment population: why are adult mortality rates constant? *Oikos*, **47**, 129-134.
- Chesson P.L. & Warner R.R. (1981)** Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist*, **117**, 923-943.
- Colwell R.K. & Futuyma D.J. (1971)** On the measurement of niche breadth and overlap. *Ecology*, **52**, 567-576.
- Colwell R.K. & Fuentes E.R. (1975)** Experimental studies of the niche. *Annual Review of Ecology and Systematics*, **6**, 281-310.
- Connell J.H. (1961)** The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, **42**, 710-723.
- Connell J.H. (1980)** Diversity and the evolution of competitors, or the ghost of competition past. *Oikos*, **35**, 131-138.
- Connell J.H. (1983)** On the prevalence and relative importance of interspecific competition - evidence from field experiments. *American Naturalist*, **122**.
- Coon T.G. (1987)** Responses of benthic riffle fishes in variation in stream discharge and temperature. In: W.J. Matthews & D.C. Heins, eds., *Community and Evolutionary Ecology of North American Stream Fishes*. University of Oklahoma Press, Norman. pp. 77-85.
- Cooper S.D., Diehl S., Kratz K. & Sarnelle O. (1998)** Implications of scale for patterns and processes in stream ecology. *Australian Journal of Ecology*, **23**, 27-40.
- Copp G.H., Warrington S. & de Bruine Q. (1994)** Comparison of diet in bullhead, *Cottus gobio* and stone loach, *Barbatula barbatula* in a small English lowland river. *Folia Zoologica*, **43**, 171-176.
- Copp G.H. & Garner P. (1995)** Evaluating the microhabitat use of freshwater fish larvae and juveniles with point abundance sampling by electrofishing. *Folia Zoologica*, **44**, 145-158.
- Cowan J.H., Rose K.A. & DeVries D.R. (2000)** Is density-dependent growth in young-of-the-year fishes a question of critical weight? *Reviews in Fish Biology and Fisheries*, **10**, 61-89.
- Cowx I.G., Young W.O. & Hellawell J.M. (1984)** The influence of drought on the fish and invertebrate populations of an upland stream in Wales. *Freshwater Biology*, **14**, 165-177.
- Crisp D.T. (1993)** Population densities of juvenile trout (*Salmo trutta*) in five upland streams and their effects upon growth, survival and dispersal. *Journal of Applied Ecology*, **30**, 759-771.
- Crowl T.A. & Schnell G.D. (1990)** Factors determining population density and size distribution of a freshwater snail in streams - effects of spatial scale. *Oikos*, **59**, 359-367.
- Culp J.M. (1986)** Experimental evidence that stream macroinvertebrate community structure is unaffected by different densities of coho salmon fry. *Journal of the North American Benthological Society*, **5**, 140-149.
- Cunjak R.A. & Power G. (1986)** Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1970-1981.
- Cunjak R.A. (1988)** Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 2156-2160.
- Cushing D.H. (1981)** *Fisheries Biology*. University of Wisconsin Press, Madison, USA.
- Dahl J. & Greenberg L.A. (1996)** Impact on stream benthic prey by benthic vs. drift feeding predators: a meta-analysis. *Oikos*, **77**, 177-181.
- Dahl J. (1998a)** Effects of a benthivorous and a drift-feeding fish on a benthic stream assemblage. *Oecologia*, **116**, 426-432.
- Dahl J. (1998b)** The impact of vertebrate and invertebrate predators on a stream benthic community. *Oecologia*, **117**, 217-226.
- Dahlgren C.P. & Eggleston D.B. (2000)** Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology*, **81**, 2227-2240.
- Darwin C. (1859)** *The Origin of Species by Means of Natural Selection*. Penguin Books, Harmondsworth (reprint 1968).
- Dawson H. (1976)** The organic contribution of stream edge forest litter fall to the chalk stream ecosystem. *Oikos*, **27**, 13-18.

- DeAngelis D.L. & Waterhouse J.C. (1987) Equilibrium and non-equilibrium concepts in ecological models. *Ecological Monographs*, **57**, 1-21.
- Degerman E. & Sers B. (1993) A study of interactions between fish species in streams using survey data and the PCA-hyperspace technique. *Nordic Journal of Freshwater Research*, **68**, 5-13.
- Dewald L. & Wilzbach M.A. (1992) Interactions between native brook trout and hatchery brown trout - effects on habitat use, feeding, and growth. *Transactions of the American Fisheries Society*, **121**, 287-296.
- Diamond J. (1986) Overview: laboratory experiments, field experiments, and natural experiments. In: J. Diamond & T.J. Case, eds., *Community Ecology*. Harper & Row, New York. pp. 3-22.
- Diehl S. (1992) Fish predation and benthic community structure - the role of omnivory and habitat complexity. *Ecology*, **73**, 1646-1661.
- Dill L.M. (1983) Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 398-408.
- Doncaster C.P. (1999) A useful phenomenological difference between exploitation and interference in the distribution of ideal free predators. *Journal of Animal Ecology*, **68**, 836-838.
- Doncaster C.P. & Gustafsson L. (1999) Density dependence in resource exploitation: empirical test of Levins' metapopulation model. *Ecology Letters*, **2**, 44-51.
- Doncaster C.P., Pound G.E. & Cox S.J. (2003) Dynamics of regional coexistence for more or less equal competitors. *Journal of Animal Ecology*, **72**, 116-126.
- Dubs D.O.L. & Corkum L.D. (1996) Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). *Journal of Great Lakes Research*, **22**, 838-844.
- Egglishaw H.J. & Shackley P.E. (1982) Influence of water depth on dispersion of juvenile salmonids, *Salmo salar* L. and *Salmo trutta* L., in a Scottish stream. *Journal of Fish Biology*, **21**, 414-155.
- Eklöv A.G. & Greenberg L.A. (1998) Effects of artificial instream cover on the density of 0+ brown trout. *Fisheries Management and Ecology*, **5**, 45-53.
- Eklöv A.G., Greenberg L.A., Brönmark C., Larsson P. & Berglund O. (1999) Influence of water quality, habitat and species richness on brown trout populations. *Journal of Fish Biology*, **54**, 33-43.
- Eklov P. & van Kooten T. (2001) Facilitation among piscivorous predators: effects of prey habitat use. *Ecology*, **82**, 2486-2494.
- Elliott J.M. (1984) Growth, size, biomass and production of young migratory trout *Salmo trutta* in a Lake District stream, 1966-83. *Journal of Animal Ecology*, **53**, 979-994.
- Elliott J.M. (1985) Population regulation for different life-stages of migratory trout *Salmo trutta* in a Lake District stream, 1966-83. *Journal of Animal Ecology*, **54**, 617-638.
- Elliott J.M. (1990) Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. III. The role of territorial behaviour. *Journal of Animal Ecology*, **59**, 803-818.
- Elliott J.M., Hurley M.A. & Elliott J.A. (1997) Variable effects of droughts on the density of a sea-trout *Salmo trutta* population over 30 years. *Journal of Applied Ecology*, **34**, 1229-1238.
- Elliott J.M. & Hurley M.A. (1998) Population regulation in adult, but not juvenile, resident trout (*Salmo trutta*) in a Lake District stream. *Journal of Animal Ecology*, **67**, 280-286.
- Elliott J.M. (2002) Shadow competition in wild juvenile sea-trout. *Journal of Fish Biology*, **61**, 1268-1281.
- Elton C. (1927) *Animal Ecology*. Sidgwick & Jackson, London.
- Elton C. (1939) On the nature of cover. *Journal of Wildlife Management*, **3**, 332-338.
- Englund G. & Olsson T. (1996) Treatment effects in a stream fish enclosure experiment: influences of predation rate and prey movements. *Oikos*, **77**, 519-528.
- Englund G. & Evander D. (1999) Interactions between sculpins, net-spinning caddis larvae and midge larvae. *Oikos*, **85**, 117-126.
- Everett R.A. & Ruiz G.M. (1993) Coarse woody debris as a refuge from predation in aquatic communities - an experimental test. *Oecologia*, **93**, 475-486.
- Facey D.E. & Grossman G.D. (1992) The relationship between water velocity, energetic costs and microhabitat use in four North American stream fishes. *Hydrobiologia*, **239**, 1-6.

- Fausch K.D. & White R.J. (1981)** Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 1220-1227.
- Fausch K.D. & White R.J. (1986)** Competition among juveniles of coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. *Transactions of the American Fisheries Society*, **115**, 363-381.
- Fausch K.D. (1988)** Tests of competition between native and introduced salmonids in streams: what have we learned? *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 2238-2246.
- Fausch K.D., Nakano S. & Ishigaki K. (1994)** Distribution of two congeneric charrs in streams of Hokkaido island, Japan - considering multiple factors across scales. *Oecologia*, **100**, 1-12.
- Figler M.H., Cheverton H.M. & Blank G.S. (1999)** Shelter competition in juvenile red swamp crayfish (*Procambarus clarkii*): the influence of sex differences, relative size and prior residence. *Aquaculture*, **178**, 63-75.
- Finger T.R. (1982)** Interactive segregation among three species of sculpins (*Cottus*). *Copeia*, **1982**, 680-694.
- Fischer P. (2000)** An experimental test of metabolic and behavioural responses of benthic fish species to different types of substrate. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2336-2344.
- Fisher S.G. (1994)** Pattern, process and scale in freshwater systems: some unifying thoughts. In: P.S. Giller, A.G. Hildrew & D.G. Raffaelli, eds., *Aquatic Ecology*. Blackwell Scientific, Oxford. pp. 575-592.
- Flecker A.S. & Townsend C.R. (1994)** Community-wide consequences of trout introduction in New Zealand streams. *Ecological Applications*, **4**, 798-807.
- Forrester G.E. (1994)** Influences of predatory fish on the drift dispersal and local density of stream insects. *Ecology*, **75**, 1208-1218.
- Forrester G.E., Chace J.G. & McCarthy W. (1994)** Diel and density-related changes in food consumption and prey selection by brook charr in a New Hampshire stream. *Environmental Biology of Fishes*, **39**, 301-311.
- Forrester G.E. & Steele M.A. (2000)** Variation in the presence and cause of density-dependent mortality in three species of reef fishes. *Ecology*, **81**, 2416-2427.
- Fox P.J. (1978a)** *The population dynamics of the bullhead (Cottus gobio L., Pisces), with special reference to spawning, mortality of young fish and homeostatic mechanisms*. Unpublished PhD Thesis, University of Reading, Reading, UK.
- Fox P.J. (1978b)** Caddis larvae (Trichoptera) as predators of fish eggs. *Freshwater Biology*, **8**, 343-345.
- Fox P.J. (1978c)** Preliminary observations on different reproduction strategies in the bullhead (*Cottus gobio* L.) in northern and southern England. *Journal of Fish Biology*, **12**, 5-11.
- Fraser D.F. & Sise T.E. (1980)** Observations on stream minnows in a patchy environment: a test of a theory of habitat distribution. *Ecology*, **61**, 790-797.
- Fraser N.H.C., Heggenes J., Metcalfe N.B. & Thorpe J.E. (1995)** Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. *Canadian Journal of Zoology*, **73**, 446-451.
- Freeman M.C. & Stouder D.J. (1989)** Intraspecific interactions influence size-specific depth distribution in *Cottus bairdi*. *Environmental Biology of Fishes*, **24**, 231-236.
- Fretwell S.D. & Lucas J.H.J. (1970)** On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16-36.
- Fretwell S.D. (1972)** *Populations in a Seasonal Environment*. Princeton University Press, Princeton.
- Gasith A. & Resh V.H. (1999)** Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics*, **30**, 51-81.
- Gaston K.J. & Lawton J.H. (1987)** A test of statistical techniques for detecting density dependence in sequential censuses of animal populations. *Oecologia*, **74**, 404-410.
- Gatz A.J. (1979)** Community organisation in fishes as indicated by morphological features. *Ecology*, **60**, 711-718.
- Gause G.F. (1934)** *The Struggle for Existence*. Hafner, New York.
- Gilliam J.F., Fraser D.F. & Sabat A.M. (1989)** Strong effects of foraging minnows on a stream benthic invertebrate community. *Ecology*, **70**, 445-452.

- Glova G.J. (1999)** A test for competition between two Gobiomorphus species (Teleostei : Elcotridae) in artificial channels. *Ecology of Freshwater Fish*, **8**, 70-77.
- Golden H.E. & Deegan L.A. (1998)** The trophic interactions of young Arctic grayling (*Thymallus arcticus*) in an Arctic tundra stream. *Freshwater Biology*, **39**, 637-648.
- Gorman O.T. (1987)** Habitat segregation in an assemblage of minnows in an Ozark stream. In: W.J. Matthews & D.C. Heins, eds., *Community and Evolutionary Ecology of North American Stream Fishes*. University of Oklahoma Press, Norman. pp. 33-41.
- Gorman O.T. (1988)** The dynamics of habitat use in a guild of Ozark minnows. *Ecological Monographs*, **58**, 1-18.
- Goss-Custard J.D., Caldow R.W.G., Clarke R.T. & West A.D. (1995)** Deriving population parameters from individual variations in foraging behaviour. II. Model tests and population parameters. *Journal of Animal Ecology*, **64**, 277-289.
- Goss-Custard J.D., West A.D., Stillman R.A., Durell S.E.A., Caldow R.W.G., McGrorty S. & Nagarajan R. (2001)** Density-dependent starvation in a vertebrate without significant depletion. *Journal of Animal Ecology*, **70**, 955-965.
- Grand T.C. & Dill L.M. (1997)** The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. *Behavioral Ecology*, **8**, 437-447.
- Grant J.W.A. & Kramer D.L. (1990)** Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 1724-1737.
- Gray E.V., Boltz J.M., Kellogg K.A. & Stauffer J.R. (1997)** Food resource partitioning by nine sympatric darter species. *Transactions of the American Fisheries Society*, **126**, 822-840.
- Green G.P. (1975)** *The food and production of the bullhead, Cottus gobio L., in the River Lambourn*. Unpublished PhD Thesis, University of Reading, Reading, UK.
- Greenberg L., Svendsen P. & Harby A. (1996)** Availability of microhabitats and their use by brown trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) in the River Vojmån, Sweden. *Regulated Rivers: Research and Management*, **12**, 287-303.
- Greenberg L.A. (1988)** Interactive segregation between the stream fishes *Etheostoma simotermum* and *E. rufilineatum*. *Oikos*, **51**, 193-202.
- Greenberg L.A. (1991)** Habitat use and feeding behaviour of thirteen species of benthic stream fishes. *Environmental Biology of Fishes*, **31**, 389-401.
- Greenberg L.A., Bergman E. & Eklov A.G. (1997)** Effects of predation and intraspecific interactions on habitat use and foraging by brown trout in artificial streams. *Ecology of Freshwater Fish*, **6**, 16-26.
- Greenberg L.A. (1999)** Effects of predation and discharge on habitat use by brown trout, *Salmo trutta*, and grayling, *Thymallus thymallus*, in artificial streams. *Archiv für Hydrobiologie*, **145**, 433-446.
- Greenhalgh M. (1999)** *Freshwater Fish*. Mitchell Beazley, London.
- Gregory J.S. & Griffith J.S. (1996a)** Aggressive behaviour of underyearling rainbow trout in simulated winter concealment habitat. *Journal of Fish Biology*, **49**, 237-245.
- Gregory J.S. & Griffith J.S. (1996b)** Winter concealment by subyearling rainbow trout: space size selection and reduced concealment under surface ice and in turbid water conditions. *Canadian Journal of Zoology*, **74**, 451-455.
- Grenouillet G., Huguency B., Carrel G.A., Oliver J.M. & Pont D. (2001)** Large-scale synchrony and inter-annual variability in roach recruitment in the Rhone River: the relative role of climatic factors and density-dependent processes. *Freshwater Biology*, **46**, 11-26.
- Gries G. & Juanes F. (1998)** Microhabitat use by juvenile Atlantic salmon (*Salmo salar*) sheltering during the day in summer. *Canadian Journal of Zoology*, **76**, 1441-1449.
- Griffith D.M. & Poulson T.L. (1993)** Mechanisms and consequences of intraspecific competition in a Carabid cave beetle. *Ecology*, **74**, 1373-1383.
- Griffiths S.W. & Armstrong J.D. (2002)** Rearing conditions influence refuge use among overwintering Atlantic salmon juveniles. *Journal of Fish Biology*, **60**, 363-369.
- Grossman G.D., Moyle P.B. & Whitaker J.O. (1982)** Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage - a test of community theory. *American Naturalist*, **120**, 423-454.
- Grossman G.D., De Sostoa A., Freeman M.C. & Lobón-Cerviá J. (1987)** Microhabitat use in a Mediterranean riverine fish assemblage - fishes of the Lower Matarraña. *Oecologia*, **73**, 490-500.

- Grossman G.D. & Freeman M.C. (1987) Microhabitat use in a stream fish assemblage. *Journal of Zoology*, **212**, 151-176.
- Grossman G.D. & Boule V. (1991) Effects of rosyside dace (*Clinostomus funduloides*) on microhabitat use of rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1235-1243.
- Grossman G.D., Ratajczak R.E., Crawford M. & Freeman M.C. (1998) Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecological Monographs*, **68**, 395-420.
- Guan R. & Wiles P.R. (1997) Ecological impact of introduced crayfish on benthic fishes in a British lowland river. *Conservation Biology*, **11**, 641-647.
- Gurevitch J., Morrow L.L., Wallace A. & Walsh J.S. (1992) A meta-analysis of competition in field experiments. *American Naturalist*, **140**, 539-572.
- Hairston N.G. (1980) Evolution under interspecific competition: field experiments on terrestrial salamanders. *Evolution*, **34**, 409-420.
- Hairston N.G.J., Smith F.E. & Slobodkin L.B. (1960) Community structure, population control, and competition. *American Naturalist*, **94**, 421-425.
- Hardin G. (1960) The competitive exclusion principle. *Science*, **131**, 1292-1297.
- Harrell H.L. (1978) Response of the Devil's River (Texas) fish community to flooding. *Copeia*, **1978**, 60-68.
- Harrison S. & Cappuccino N. (1995) Using density manipulation experiments to study population regulation. In: N. Cappuccino & P.W. Price, eds., *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, USA. pp. 131-147.
- Hart D.D. (1992) Community organisation in streams: the importance of species interactions, physical factors, and chance. *Oecologia*, **91**, 220-228.
- Hartley P.H.T. (1948) Food and feeding relationships in a community of fresh-water fishes. *Journal of Animal Ecology*, **17**, 1-14.
- Harvey B.C. & Stewart A.J. (1991) Fish size and habitat depth relationships in headwater streams. *Oecologia*, **87**, 336-342.
- Harvey B.C. & Nakamoto R.J. (1996) Effects of steelhead density on growth of coho salmon in a small coastal California stream. *Transactions of the American Fisheries Society*, **125**, 237-243.
- Harvey B.C. & Nakamoto R.J. (1997) Habitat-dependent interactions between two size-classes of juvenile steelhead in a small stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 27-31.
- Harwood A.J., Metcalfe N.B., Griffiths S.W. & Armstrong J.D. (2002) Intra- and inter-specific competition for winter concealment habitat in juvenile salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1515-1523.
- Hassell M.P. & Varley G.C. (1969) New inductive population model for insect parasites and its bearing on biological control. *Nature*, **223**, 1133-1136.
- Hassell M.P., Lawton J.H. & May R.M. (1976) Patterns of dynamical behaviour in single species populations. *Journal of Animal Ecology*, **45**, 471-486.
- Heggenes J. (1988) Effect of experimentally increased intraspecific competition on sedentary adult brown trout (*Salmo trutta*) movement and stream habitat choice. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 1163-1172.
- Heggenes J. & Saltveit S.J. (1990) Seasonal and spatial microhabitat selection and segregation in Young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in a Norwegian river. *Journal of Fish Biology*, **36**, 707-720.
- Heggenes J., Bagliniere J.L. & Cunjak R.A. (1999) Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in heterogeneous streams. *Ecology of Freshwater Fish*, **8**, 1-21.
- Heins D.C. & Matthews W.J. (1987) Historical perspectives on the study of community and evolutionary ecology of North American Stream Fishes. In: W.J. Matthews & D.C. Heins, eds., *Community and Evolutionary Ecology of North American Stream Fishes*. University of Oklahoma Press, Norman. pp. 3-7.
- Hellriegel B. (2000) Single- or multistage regulation in complex life cycles: does it make a difference? *Oikos*, **88**, 239-249.
- Hesthagen T. & Heggenes J. (2003) Competitive habitat displacement of brown trout by Siberian sculpin: the role of size and density. *Journal of Fish Biology*, **62**, 222-236.

- Hilborn R. & Mangel M. (1997) *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton, New Jersey.
- Hill J. & Grossman G.D. (1987) Home range estimates for three North American stream fishes. *Copeia*, **1987**, 376-380.
- Hill J. & Grossman G.D. (1993) An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology*, **74**, 685-698.
- Hixon M.A., Pacala S.W. & Sandin S.A. (2002) Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology*, **83**, 1490-1508.
- HMSO. (1983) *The determination of chlorophyll-a in aquatic environments 1980*. HMSO Publications, London.
- Holbrook S.J. & Schmitt R.J. (2002) Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology*, **83**, 2855-2868.
- Holomuzki J.R. & Stevenson R.J. (1992) Role of predatory fish in community dynamics of an ephemeral stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2322-2330.
- Holzapfel C. & Mahall B.E. (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. *Ecology*, **80**, 1747-1761.
- Hoopes R. (1975) Flooding as a result of Hurricane Agnes, and its effects on a native brook trout population in an infertile headwater stream in central Pennsylvania. *Transactions of the American Fisheries Society*, **104**, 96-99.
- Horwitz R.J. (1978) Temporal variability patterns and the distributional patterns of stream fishes. *Ecological Monographs*, **48**, 307-321.
- Hugueny B. & Paugy D. (1995) Unsaturated fish communities in African rivers. *American Naturalist*, **146**, 162-169.
- Huhta A., Muotka T. & Tikkanen P. (2000) Nocturnal drift of mayfly nymphs as a post-contact antipredator mechanism. *Freshwater Biology*, **45**, 33-42.
- Hurlbert S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187-211.
- Huston M.A. (1979) A general hypothesis of species diversity. *American Naturalist*, **113**, 81-101.
- Hutchinson G.E. (1957) Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology*, **22**, 415-427.
- Hyslop E.J. (1982) The feeding habits of 0+ stone loach, *Noemacheilus barbatula* (L.), and bullhead, *Cottus gobio* (L.). *Journal of Fish Biology*, **21**, 187-196.
- Imre I., Grant J.W.A. & Keeley E.R. (2002) The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 303-309.
- Jacobs J. (1974) Quantitative measurement of food selection, a modification of the forage ratio and Ivlev's selectivity index. *Oecologia*, **14**, 413-417.
- Jenkins T.M., Diehl S., Kratz K.W. & Cooper S.D. (1999) Effects of population density on individual growth of brown trout in streams. *Ecology*, **80**, 941-956.
- Jensen A.J. & Johnsen B.O. (1999) The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Functional Ecology*, **13**, 778-785.
- Jensen A.J., Forseth T. & Johnsen B.O. (2000) Latitudinal variation in growth of young brown trout *Salmo trutta*. *Journal of Animal Ecology*, **69**, 1010-1020.
- John K.R. (1964) Survival of fish in intermittent streams of the Chiricahua Mountains, Arizona. *Ecology*, **45**, 112-119.
- Johnsson J.I., Nobbelin F. & Bohlin T. (1999) Territorial competition among wild brown trout fry: effects of ownership and body size. *Journal of Fish Biology*, **54**, 469-472.
- Johnston T.A. & Cunjak R.A. (1999) Dry mass-length relationships for benthic insects: a review with new data from Catamaran Brook, New Brunswick, Canada. *Freshwater Biology*, **41**, 653-674.
- Jones A.N. (1975) A preliminary study of fish segregation in salmon spawning streams. *Journal of Fish Biology*, **7**, 95-104.
- Jonsson N., Jonsson B. & Hansen L.P. (1998) The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *Journal of Animal Ecology*, **67**, 751-762.
- Jorgensen L., Amundsen P.A., Gabler H.M., Halvorsen M., Erkinaro J. & Niemela E. (1999) Spatial distribution of Atlantic salmon parr (*Salmo salar* L.) and bullhead (*Cottus gobio* L.)

- in lotic and lentic habitats of a diversified watercourse in northern Fennoscandia. *Fisheries Research*, **41**, 201-211.
- Kalleberg H. (1958)** Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). *Report Institute of Freshwater Research Drottningholm*, **39**, 55-98.
- Katano O., Abe S., Matsuzaki K. & Iguchi K. (2000)** Interspecific interactions between ayu, *Plecoglossus altivelis*, and pale chub, *Zacco platypus*, in artificial streams. *Fisheries Science*, **66**, 452-459.
- Keddy P.A. (1989)** *Competition*. Chapman & Hall, London.
- Keeley E.R. (2000)** An experimental analysis of territory size in juvenile steelhead trout. *Animal Behaviour*, **59**, 477-490.
- Keeley E.R. (2001)** Demographic responses to food and space competition by juvenile steelhead trout. *Ecology*, **82**, 1247-1259.
- Kelly C.K. & Bowler M.G. (2002)** Coexistence and relative abundance in forest trees. *Nature*, **417**, 437-440.
- Kennedy G.J.A. & Strange C.D. (1982)** The distribution of salmonids in upland streams in relation to depth and gradient. *Journal of Fish Biology*, **20**, 579-591.
- Kennedy G.J.A. & Strange C.D. (1986a)** The effects of intra and interspecific competition on the survival and growth of stocked Atlantic salmon, *Salmo salar* L., and resident trout, *Salmo trutta* L., in an upland stream. *Journal of Fish Biology*, **28**, 479-489.
- Kennedy G.J.A. & Strange C.D. (1986b)** The effects of intra and interspecific competition on the distribution of stocked Atlantic salmon, *Salmo salar* L., in relation to depth and gradient in an upland trout, *Salmo trutta* L., stream. *Journal of Fish Biology*, **29**, 199-214.
- Kido M.H. (1996)** Diet and food selection in the endemic Hawaiian amphidromous goby, *Sicyopterus stimpsoni* (Pisces: Gobiidae). *Environmental Biology of Fishes*, **45**, 199-209.
- Kocik J.F. & Taylor W.W. (1995)** Effect of juvenile steelhead (*Oncorhynchus mykiss*) on age-0 and age-1 brown trout (*Salmo trutta*) survival and growth in a sympatric nursery stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 105-114.
- Krebs C.J. (1999)** *Ecological Methodology*. Benjamin Cummins, CA, USA.
- Kroon F.J., de Graaf M. & Liley N.R. (2000)** Social organisation and competition for refuges and nest sites in *Coryphopterus nicholsii* (Gobiidae), a temperate protogynous reef fish. *Environmental Biology of Fishes*, **57**, 401-411.
- Lack D. (1946)** Competition for food by birds of prey. *Journal of Animal Ecology*, **15**, 123-129.
- Ladich F. (1989)** Sound production by the river bullhead, *Cottus gobio* L. (Cottidae, Teleostei). *Journal of Fish Biology*, **35**, 531-538.
- Ladle M., Bass J.A.B. & Jenkins W.R. (1972)** Studies on production and food consumption by the larval Simuliidae (Diptera) of a chalk stream. *Hydrobiologia*, **39**, 429-448.
- Lande R., Engen S., Saether B.E., Filli F., Matthysen E. & Weimerskirch H. (2002)** Estimating density dependence from population time series using demographic theory and life-history data. *American Naturalist*, **159**, 321-337.
- Larkin P.A. (1956)** Interspecific competition and population control in freshwater fish. *Journal of the Fisheries Research Board of Canada*, **13**, 327-342.
- Law R. & Watkinson A.R. (1989)** Competition. In: J.M. Cherrett, ed., *Ecological concepts: the contribution of ecology to an understanding of the natural world*. Blackwell Science, Oxford. pp. 243-284.
- Le Cren E.D. (1965)** Some factors regulating the size of populations of freshwater fish. *Mitteilungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **13**, 88-105.
- Le Cren E.D. (1975)** The population dynamics of young trout (*Salmo trutta*) in relation to density and territorial behaviour. *Rapports et Procès-Verbaux des Réunions, Conseil International pour l'Exploration de la Mer*, **164**, 241-246.
- Le Cren E.D. (1987)** Perch (*Perca fluviatilis*) and pike (*Esox lucius*) in Windermere from 1940 to 1985: studies in population dynamics. *Canadian Journal of Fisheries and Aquatic Sciences*, **44** (Suppl. 2), 216-228.
- Lindroth A. (1955)** Distribution, territorial behaviour and movements of sea trout fry in the River Indalsälven. *Report Institute of Freshwater Research Drottningholm*, **36**, 104-119.
- Lomnicki A. (1978)** Individual differences between animals and the natural regulation of their numbers. *Journal of Animal Ecology*, **47**, 461-475.

- Losey J.E. & Denno R.F. (1998)** Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, **79**, 2143-2152.
- Lotka A.J. (1932)** The growth of mixed populations: two species competing for a common food supply. *Journal of the Washington Academy of Sciences*, **22**, 461-469.
- MacArthur R.H. & Levins R. (1967)** The limiting similarity, convergence and divergence of coexisting species. *American Naturalist*, **101**, 377-385.
- MacArthur R.H. & Wilson E.O. (1967)** *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- MacArthur R.H., Diamond J.M. & Karr J.R. (1972)** Density compensation in island faunas. *Ecology*, **53**, 330-342.
- MacKenzie A.R. & Greenberg L.A. (1998)** The influence of instream cover and predation risk on microhabitat selection of stone loach *Barbatula barbatula* (L.). *Ecology of Freshwater Fish*, **7**, 87-94.
- Mackey A.P. (1977)** Growth and development of larval Chironomidae. *Oikos*, **28**, 270-275.
- MacNally R.C. (1983)** On assessing the significance of interspecific competition to guild structure. *Ecology*, **64**, 1646-1652.
- Magalhães M.F. (1993)** Feeding of an Iberian stream cyprinid assemblage - seasonality of resource use in a highly variable environment. *Oecologia*, **96**, 253-260.
- Maitland P.S. (1965)** The feeding relationships of salmon, trout, minnows, stone loach and three-spined sticklebacks in the River Endrick, Scotland. *Journal of Animal Ecology*, **34**, 109-133.
- Maitland P.S. (1972)** *Key to British Freshwater Fishes*. Titus & Son, Kendal.
- Malthus T.R. (1798)** *An Essay on the Principle of Population*. Penguin Books, Harmondsworth (reprint 1982).
- Manly B.F.J. (1997)** *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman & Hall, London.
- Mann R.H.K. & Orr D.R.O. (1969)** A preliminary study of the feeding relationships of fish in an hard-water and soft-water stream in southern England. *Journal of Fish Biology*, **1**, 31-44.
- Mann R.H.K. (1971)** The populations, growth and production of fish in four small streams in southern England. *Journal of Animal Ecology*, **40**, 155-190.
- Mann R.H.K., Blackburn J.H. & Beaumont W.R.C. (1989)** The ecology of brown trout *Salmo trutta* in English chalk streams. *Freshwater Biology*, **21**, 57-70.
- Marconato A. & Rasotto M.B. (1983)** Mating preference for the female river bullhead, *Cottus gobio* (Cottidae, Teleostei). *Bollettino di Zoologia*, **50**, 51-54.
- Marconato A. & Bisazza A. (1988)** Mate choice, egg cannibalism and reproductive success in the river bullhead, *Cottus gobio* L. *Journal of Fish Biology*, **33**, 917-924.
- 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.
- Mason C.F. (1977)** Populations and production of benthic animals in two contrasting shallow lakes in Norfolk. *Journal of Animal Ecology*, **46**, 147-172.
- Matsuda H., Abrams P.A. & Hori M. (1993)** The effect of adaptive antipredator behavior on exploitative competition and mutualism between predators. *Oikos*, **68**, 549-559.
- Matthews W.J. (1985)** Critical current speeds and microhabitats of the benthic fishes *Percina roanoka* and *Etheostoma flabellare*. *Environmental Biology of Fishes*, **12**, 303-308.
- Matthews W.J. (1986)** Fish faunal structure in an Ozark stream: stability, persistence and a catastrophic flood. *Copeia*, **1986**, 388-397.
- Matthews W.J., Gido K.B. & Marsh-Matthews E. (2001)** Density dependent overwinter survival and growth of red shiners from a southwestern river. *Transactions of the American Fisheries Society*, **130**, 478-788.
- May R.M. (1986)** The search for patterns in the balance of nature: advances and retreats. *Ecology*, **67**, 1115-1126.
- McCree K.J. (1972)** Test of current definitions of photosynthetically active radiation against leaf photosynthesis data. *Agricultural Meteorology*, **10**, 443-453.
- McIntosh A.R., Townsend C.R. & Crowl T.A. (1992)** Competition for space between introduced brown trout (*Salmo trutta*) and a native galaxiid (*Galaxias vulgaris*) in a New Zealand stream. *Journal of Fish Biology*, **41**, 63-81.
- McIntosh A.R., Crowl T.A. & Townsend C.R. (1994)** Size-related impacts of introduced brown trout on the distribution of native common river galaxias. *New Zealand Journal of Marine and Freshwater Research*, **28**, 135-144.

- McIntosh A.R. & Townsend C.R. (1995)** Contrasting predation risks presented by introduced brown trout and native common river galaxias in New Zealand streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1821-1833.
- McIntosh A.R. & Townsend C.R. (1996)** Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish induced changes to grazer behaviour? *Oecologia*, **108**, 174-181.
- Menge B.A. & Sutherland J.P. (1987)** Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist*, **130**, 730-757.
- Mesick C.F. (1988)** Effects of food and cover on numbers of apache and brown trout establishing residency in artificial stream channels. *Transactions of the American Fisheries Society*, **117**, 421-431.
- Meyer E. (1989)** The relationship between body length parameters and dry mass in running water invertebrates. *Archiv für Hydrobiologie*, **117**, 191-203.
- Michel P. & Oberdorff T. (1995)** Feeding habits of fourteen European freshwater fish species. *Cybiurn*, **19**, 5-46.
- Mills C.A. & Mann R.H.K. (1983)** The bullhead *Cottus gobio*, a versatile and successful fish. *Freshwater Biological Association Annual Report*, **51**, 76-88.
- Mills C.A., Welton J.S. & Rendle E.L. (1983)** The age, growth and reproduction of the stone loach *Noemacheilus barbatula* (L.) in a Dorset chalk stream. *Freshwater Biology*, **13**, 283-292.
- Mills C.A. & Mann R.H.K. (1985)** Environmentally-induced fluctuations in year-class strength and their implications for management. *Journal of Fish Biology*, **27** (Suppl. A), 209-226.
- Mitchell W.A., Abramsky Z., Kotler B.P., Pinshow B. & Brown J.S. (1990)** The effect of competition on foraging activity in desert rodents - theory and experiments. *Ecology*, **71**, 844-854.
- Mittelbach G.G. & Osenberg C.W. (1993)** Stage-structured interactions in bluegill - consequences of adult resource variation. *Ecology*, **74**, 2381-2394.
- Morisita M. (1959)** Measuring of interspecific association and similarity between communities. *Memoirs of the Faculty of Science, Kyushu University, Series E. (Biology)*, **3**, 65-80.
- Morris V. (1965)** A comparison of the biology of the minnow, loach and bullhead from hard and soft waters. PhD Thesis, University of Liverpool.
- Mortensen E. (1977a)** Density-dependent mortality of trout fry (*Salmo trutta* L.) and its relationship to the management of small streams. *Journal of Fish Biology*, **11**, 613-617.
- Mortensen E. (1977b)** Population, survival, growth and production of trout *Salmo trutta* in a small Danish stream. *Oikos*, **28**, 9-15.
- Moyle P.B. & Senanayaka F.R. (1984)** Resource partitioning among the fishes of rainforest streams in Sri-Lanka. *Journal of Zoology*, **202**, 195-223.
- Moyle P.B. & Vondracek B. (1985)** Persistence and structure of the fish assemblage in a small Californian stream. *Ecology*, **66**, 1-13.
- Mullen D.M. & Barton T.M. (1995)** Size related habitat use by longnose dace (*Rhinichthys cataractae*). *American Midland Naturalist*, **133**, 177-183.
- Mullen D.M. & Burton T.M. (1998)** Experimental tests of intraspecific competition in stream riffles between juvenile and adult longnose dace (*Rhinichthys cataractae*). *Canadian Journal of Zoology*, **76**, 855-862.
- Murdoch W.W. (1994)** Population regulation in theory and practice. *Ecology*, **75**, 271-287.
- Nakano S. (1995)** Individual differences in resource use, growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. *Journal of Animal Ecology*, **64**, 75-84.
- Nakano S., Fausch K.D. & Kitano S. (1999)** Flexible niche partitioning via a foraging mode shift: a proposed mechanism for co-existence in stream-dwelling charrs. *Journal of Animal Ecology*, **68**, 1079-1092.
- Naslund I., Degerman E. & Nordwall F. (1998)** Brown trout (*Salmo trutta*) habitat use and life history in Swedish streams: possible effects of biotic interactions. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1034-1042.
- Natsumeda T. (2001)** Space use by the Japanese fluvial sculpin, *Cottus pollux*, related to spatio-temporal limitations in nest resources. *Environmental Biology of Fishes*, **62**, 393-400.
- Nee S. & May R.M. (1992)** Dynamics of metapopulations - habitat destruction and competitive coexistence. *Journal of Animal Ecology*, **61**, 37-40.
- Nicholson A.J. (1933)** The balance of animal populations. *Journal of Animal Ecology*, **2**, 132-178.

- Nicholson A.J. (1954) An outline of the dynamics of animal populations. *Australian Journal of Ecology*, **2**, 9-65.
- Nordwall F., Naslund I. & Degerman E. (2001) Intercohort competition effects on survival, movement, and growth of brown trout (*Salmo trutta*) in Swedish streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 2298-2308.
- Nunn A.D., Cowx I.G., Frear P.A. & Harvey J.P. (2003) Is water temperature an adequate predictor of recruitment success in cyprinid fish populations in lowland rivers? *Freshwater Biology*, **48**, 579-588.
- Nyström P., Brönmark C. & Graneli W. (1999) Influence of an exotic and a native crayfish species on a littoral benthic community. *Oikos*, **85**, 545-553.
- Nyström P., Svensson O., Lardner B., Brönmark C. & Graneli W. (2001) The influence of multiple introduced predators on a littoral pond community. *Ecology*, **82**, 1023-1039.
- Oberdorff T., Hugueny B. & Guegan J.F. (1997) Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America. *Journal of Biogeography*, **24**, 461-467.
- Oberdorff T., Hugueny B., Compin A. & Belmessam D. (1998) Non-interactive fish communities in the coastal streams of North-western France. *Journal of Animal Ecology*, **67**, 472-484.
- Oksanen L., Fretwell S.D., Arruda J. & Niemela P. (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, **118**, 240-261.
- Pace M.L., Cole J.J., Carpenter S.R. & Kitchell J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, **14**, 483-488.
- Paine R.T. (1979) Disaster, catastrophe and local persistence of the sea palm *Postelsia palmaeformis*. *Science*, **205**, 685-687.
- Park T. (1962) Beetles, competition and populations. *Science*, **138**, 1369-1375.
- Persson L. (1985) Asymmetrical competition - are larger animals competitively superior? *American Naturalist*, **126**, 261-266.
- Persson L. & Johansson L. (1992) On competition and temporal variation in temperate freshwater fish populations. *Netherlands Journal of Zoology*, **42**, 304-322.
- Persson L. (1999) Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. *Oikos*, **85**, 385-397.
- Petty J.T. & Grossman G.D. (1996) Patch selection by mottled sculpin (Pisces: Cottidae) in a southern Appalachian stream. *Freshwater Biology*, **35**, 261-276.
- Pianka E.R. (1970) On r-and K-selection. *American Naturalist*, **104**, 592-597.
- Pires A.M., Cowx I.G. & Coelho M.M. (1999) Seasonal changes in fish community structure of intermittent streams in the middle reaches of the Guadiana basin, Portugal. *Journal of Fish Biology*, **54**, 235-249.
- Polis G.A. (1984) Age structure component of niche width and intraspecific resource partitioning - can age-groups function as ecological species. *American Naturalist*, **123**, 541-564.
- Polis G.A. (1994) Food webs, trophic cascades and community structure. *Australian Journal of Ecology*, **19**, 121-136.
- Polis G.A. & Strong D.R. (1996) Food web complexity and community dynamics. *American Naturalist*, **147**, 813-846.
- Polis G.A., Sears A.L.W., Huxel G.R., Strong D.R. & Maron J. (2000) When is a trophic cascade a trophic cascade? *Trends in Ecology and Evolution*, **15**, 473-475.
- Pollard E.K., Lakhani H. & Rothery P. (1987) The detection of density-dependence from a series of annual censuses. *Ecology*, **68**, 2046-2055.
- Power M.E. (1992) Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology*, **73**, 1675-1688.
- Prejs A. & Prejs K. (1987) Feeding of tropical fresh-water fishes: seasonality of resource availability and resource use. *Oecologia*, **71**, 397-404.
- Prenda J., Armitage P.D. & Grayston A. (1997) Habitat use by the fish assemblages of two chalk streams. *Journal of Fish Biology*, **51**, 64-79.
- Pringle C.M. & Hamazaki T. (1998) The role of omnivory in a neotropical stream: separating diurnal and nocturnal effects. *Ecology*, **79**, 269-280.
- Raffaelli D.G. & Moller H. (2000) Manipulative field experiments in animal ecology: Do they promise more than they can deliver? *Advances in Ecological Research*, **30**, 299-338.
- Rangeley R.W. & Kramer D.L. (1998) Density-dependent antipredator tactics and habitat selection in juvenile pollock. *Ecology*, **73**, 943-952.

- Reice S.R. & Edwards R.L. (1986)** The effect of vertebrate predation on lotic macroinvertebrate communities in Quebec, Canada. *Canadian Journal of Zoology*, **64**, 1930-1936.
- Resetarits W.J. (1995)** Limiting similarity and the intensity of competitive effects on the mottled sculpin, *Cottus bairdi*, in experimental stream communities. *Oecologia*, **104**, 31-38.
- Resetarits W.J. (1997)** Interspecific competition and qualitative competitive asymmetry between two benthic stream fish. *Oikos*, **78**, 429-439.
- Riley S.C. & Fausch K.D. (1995)** Trout population response to habitat enhancement in six northern Colorado streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 34-53.
- Rincon P.A. & Grossman G.D. (1998)** The effects of rainbow trout (*Oncorhynchus mykiss*) on the use of spatial resources and behavior of rosyside dace (*Clinostomus funduloides*). *Archiv für Hydrobiologie*, **141**, 333-352.
- Rodriguez M.A. (1995)** Habitat-specific estimates of competition in stream salmonids - a field-test of the isodar model of habitat selection. *Evolutionary Ecology*, **9**, 169-184.
- Rosenblueth A. & Wiener N. (1945)** The role of models in science. *Philosophy of Science*, **12**, 316-321.
- Rosenfeld J.S. (2000)** Contrasting effects of fish predation in a fishless and fish-bearing stream. *Archiv für Hydrobiologie*, **147**, 129-142.
- Ross S.T. (1986)** Resource partitioning in fish assemblages: a review of field studies. *Copeia*, **1986**, 352-388.
- Ross S.T. (1991)** Mechanisms structuring stream fish assemblages: are there lessons from introduced species? *Environmental Biology of Fishes*, **30**, 359-368.
- Roughgarden J. (1979)** *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. MacMillan, New York.
- Roussel J.M. & Bardonnet A. (1997)** Diel and seasonal patterns of habitat use by fish in a natural salmonid brook: an approach to the functional role of the pool-riffle sequence. *Bulletin Française de la Pêche et de la Pisciculture*, **346**, 573-588.
- Roussel J.M., Bardonnet A., Haury J., Bagliniere J.L. & Prevost E. (1998)** Aquatic plant and fish assemblage: a macrophyte removal experiment in the stream riffle habitats in a lowland salmonid river (Brittany, France). *Bulletin Français de la Pêche et de la Pisciculture*, **350-351**, 693-709.
- Rundle S.D. & Hildrew A.G. (1992)** Small fish and small prey in the food webs of some southern English streams. *Archiv für Hydrobiologie*, **125**, 25-35.
- Sale P.F. (1974)** Overlap in resource use and interspecific competition. *Oecologia*, **17**, 245-256.
- Sale P.F. (1977)** Maintenance of high diversity in coral reef fish communities. *American Naturalist*, **111**, 337-359.
- Saunders J.W. & Smith M.W. (1962)** Physical alteration of stream habitat to improve trout production. *Transactions of the American Fisheries Society*, **91**, 185-188.
- Schlosser I.J. (1982)** Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs*, **52**, 395-414.
- Schlosser I.J. & Toth L.A. (1984)** Niche relationships and population ecology of rainbow (*Etheostoma caeruleum*) and fantail (*E. flabellare*) darters in a temporally variable environment. *Oikos*, **42**, 229-238.
- Schlosser I.J. (1987)** The role of predation in age- and size-related habitat use by stream fishes. *Ecology*, **66**, 651-659.
- Schlosser I.J. (1998)** Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. *Oecologia*, **113**, 260-268.
- Schluter D. (1984)** A variance test for detecting species associations, with some examples of applications. *Ecology*, **65**, 998-1005.
- Schluter D. & McPhail J.D. (1992)** Ecological character displacement and speciation in sticklebacks. *American Naturalist*, **140**, 85-108.
- Schmitz O.J., Hamback P.A. & Beckerman A.P. (2000)** Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist*, **155**, 141-153.
- Schmitz O.J. & Suttle K.B. (2001)** Effects of top predator species on direct and indirect interactions in a food web. *Ecology*, **82**, 2072-2081.
- Schmitz O.J. & Sokol-Hessner L. (2002)** Linearity in the aggregate effects of multiple predators in a food web. *Ecology Letters*, **5**, 168-172.
- Schoener T.W. (1974)** Resource partitioning in ecological communities. *Science*, **185**, 27-39.

- Schoener T.W. (1982)** The controversy over interspecific competition. *American Scientist*, **70**, 586-595.
- Schoener T.W. (1983)** Field experiments on interspecific competition. *American Naturalist*, **122**, 240-285.
- Schoener T.W. (1986)** Resource partitioning. In: J. Kikkawa & D.J. Anderson, eds., *Community Ecology: Pattern and Process*. Blackwell Scientific Publications. pp. 91-126.
- Sevenster J.G. & Bouton N. (1998)** The statistical significance of diets and other resource utilization patterns. *Netherlands Journal of Zoology*, **48**, 267-272.
- Shepherd J.G. & Cushing D.H. (1990)** Regulation in fish populations: myth or mirage? *Philosophical Transactions of the Royal Society of London, Series B*, **330**, 151-164.
- Shurin J.B. (2001)** Interactive effects of predation and dispersal on zooplankton communities. *Ecology*, **82**, 3404-3416.
- Shurin J.B., Borer E.T., Seabloom E.W., Anderson K., Blanchette C.A., Broitman B., Cooper S.D. & Halpern B.S. (2002)** A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, **5**, 785-791.
- Sih A., Crowley P., McPeck M., Petranks J. & Strohmeier K. (1985)** Predation, competition and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, **16**, 269-311.
- Sih A., Englund G. & Wooster D. (1998)** Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution*, **13**, 350-355.
- Silvertown J. & Law R. (1987)** Do plants need niches? Some recent developments in plant community ecology. *Trends in Ecology and Evolution*, **2**, 24-26.
- Sinclair A.R.E. (1989)** Population regulation in animals. In: J.M. Cherrett, ed., *Ecological Concepts*. Blackwell Scientific, Oxford, UK. pp. 197-241.
- Sloman K.A. & Armstrong J.D. (2002)** Physiological effects of dominance hierarchies: laboratory artefacts or natural phenomena? *Journal of Fish Biology*, **61**, 1-23.
- Smith R.W. & Griffith J.S. (1994)** Survival of rainbow trout during their first winter in the Henrys Fork of the Snake River, Idaho. *Transactions of the American Fisheries Society*, **123**, 747-756.
- Smyly W.J.P. (1955)** On the biology of the stone loach *Nemacheilus barbatula* (L.). *Journal of Animal Ecology*, **24**, 167-186.
- Smyly W.J.P. (1957)** The life-history of the bullhead or Miller's Thumb (*Cottus gobio* L.). *Proceedings of the Zoological Society of London*, **128**, 431-453.
- Snyder W.E. & Ives A.R. (2001)** Generalist predators disrupt biological control by a specialist parasitoid. *Ecology*, **82**, 705-716.
- Snyder W.E. & Wise D.H. (2001)** Contrasting trophic cascades generated by a community of generalist predators. *Ecology*, **82**, 1571-1583.
- Soderback B. (1994)** Interactions among juveniles of two freshwater crayfish species and a predatory fish. *Oecologia*, **100**, 229-235.
- Sogard S.M. (1997)** Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science*, **60**, 1129-1157.
- Sokal R.R. & Rohlf F.J. (1995)** *Biometry*. W.H. Freeman & Co., New York.
- Solomon D. (1985)** Salmon stock and recruitment, and stock enhancement. *Journal of Fish Biology*, **27** (Suppl. A).
- Soluk D.A. & Collins N.C. (1988)** Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. *Oikos*, **52**, 94-100.
- Soluk D.A. (1993)** Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. *Ecology*, **74**, 219-225.
- Soluk D.A. & Richardson J.S. (1997)** The role of stoneflies in enhancing growth of trout: a test of the importance of predator-predator facilitation within a stream community. *Oikos*, **80**, 214-219.
- Starrett W.C. (1951)** Some factors affecting the abundance of minnows in the Des Moines River. *Ecology*, **32**, 13-27.
- Steele M.A. (1999)** Effects of shelter and predators on reef fishes. *Journal of Experimental Marine Biology and Ecology*, **233**, 65-79.
- Steingrimsson S.O. & Grant J.W.A. (1999)** Allometry of territory size and metabolic rate as predictors of self-thinning in young-of-the-year Atlantic salmon. *Journal of Animal Ecology*, **68**, 17-26.

- Stelzer R.S. & Lamberti G.A. (1999)** Independent and interactive effects of crayfish and darters on a stream benthic community. *Journal of the North American Benthological Society*, **18**, 524-532.
- Stillman R.A., Goss-Custard J.D. & Caldow R.W.G. (1997)** Modelling interference from basic foraging behaviour. *Journal of Animal Ecology*, **66**, 692-703.
- Strange E.M., Moyle P.B. & Foin T.C. (1993)** Interactions between stochastic and deterministic processes in stream fish community assembly. *Environmental Biology of Fishes*, **36**, 1-15.
- Street N.E. & Hart P.J.B. (1985)** Group size and patch location by the stone loach, *Noemacheilus barbatulus*, a non-visually foraging predator. *Journal of Fish Biology*, **27**, 785-792.
- Sutherland W.J. (1996)** *From Individual Behaviour to Population Ecology*. Oxford University Press, Oxford, UK.
- Swisher B.J., Soluk D.A. & Wahl D.H. (1998)** Non-additive predation in littoral habitats: influences of habitat complexity. *Oikos*, **81**, 30-37.
- Taniguchi Y. & Nakano S. (2000)** Condition-specific competition: implications for the altitudinal distribution of stream fishes. *Ecology*, **81**, 2027-2039.
- Tansley A.G. (1917)** On competition between *Galium saxatile* L. (*G. hercynicum* Weig.) and *Galium sylvestre* Poll. (*G. asperum* Schreb.) on different types of soil. *Journal of Ecology*, **5**, 173-179.
- Taylor C.M. (1996)** Abundance and distribution within a guild of benthic stream fishes: local processes and regional patterns. *Freshwater Biology*, **36**, 385-396.
- Thompson R.C., Tobin M.L., Hawkins S.J. & Norton T.A. (1999)** Problems in extraction and spectrophotometric determination of chlorophyll from epilithic microbial biofilms: towards a standard method. *Journal of the Marine Biological Association of the United Kingdom*, **79**, 551-558.
- Thrush S.F., Schneider D.C., Legendre P., Whitlatch R.B., Dayton P.K., Hewitt J.E., Hines A.H., Cummings V.J., Lawrie S.M., Grant J., Pridmore R.D., Turner S.J. & McArdle B.H. (1997)** Scaling-up from experiments to complex ecological systems: Where to next? *Journal of Experimental Marine Biology and Ecology*, **216**, 243-254.
- Thrush S.F., Hewitt J.E., Cummings V.J., Green M.O., Funnell G.A. & Wilkinson M.R. (2000)** The generality of field experiments: Interactions between local and broad-scale processes. *Ecology*, **81**, 399-415.
- Tilman D. (1982)** *Resource Competition and Community Structure*. Princeton University Press, Princeton.
- Tilman D. (1987)** The importance of the mechanisms of interspecific competition. *American Naturalist*, **129**, 769-774.
- Toft C.A. (1985)** Resource partitioning in amphibians and reptiles. *Copeia* 1-21.
- Tonn W.M., Holopainen I.J. & Paszkowski C.A. (1994)** Density-dependent effects and the regulation of crucian carp populations in single species ponds. *Ecology*, **75**, 824-834.
- Townsend C.R. (2003)** Individual, population, community, and ecosystem consequences of a fish invader in New Zealand streams. *Conservation Biology*, **17**, 38-47.
- Townsend C.R., Begon M. & Harper J.L. (2003)** *Essentials of Ecology*. Blackwell Science, Malden, USA.
- Turchin P. (1999)** Population regulation: a synthetic view. *Oikos*, **84**, 160-163.
- Underwood A.J. (1978)** An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia*, **33**, 185-202.
- Underwood A.J. (1986)** The analysis of competition by field experiments. In: J. Kikkawa & D.J. Anderson, eds., *Community Ecology: Pattern and Process*. Blackwell, Melbourne, Australia. pp. 240-268.
- Usio N. & Townsend C.R. (2000)** Distribution of the New Zealand crayfish *Paranephrops zealandicus* in relation to stream physico-chemistry, predatory fish, and invertebrate prey. *New Zealand Journal of Marine and Freshwater Research*, **34**, 557-567.
- Valdimarsson S.K. & Metcalfe N.B. (1998)** Shelter selection in juvenile Atlantic salmon, or why do salmon seek shelter in winter? *Journal of Fish Biology*, **52**, 42-49.
- Valdimarsson S.K. & Metcalfe N.B. (2001)** Is the level of aggression and dispersion in territorial fish dependent on light intensity? *Animal Behaviour*, **61**, 1143-1149.
- van der Meer J. & Ens B.J. (1997)** Models of interference and their consequences for the spatial distribution of ideal and free predators. *Journal of Animal Ecology*, **66**, 846-858.
- van Snik Gray E. & Stauffer J.R. (1999)** Comparative microhabitat use of ecologically similar benthic fishes. *Environmental Biology of Fishes*, **56**, 443-453.

- Vehanen T., Maki-Petays A., Aspi J. & Muotka T. (1999)** Intercohort competition causes spatial segregation in brown trout in artificial streams. *Journal of Fish Biology*, **55**, 35-46.
- Volterra V. (1926)** Variations and fluctuations of the numbers of individuals in animal species living together. In: R.N. Chapman, ed., *Animal Ecology* (1931). McGraw Hill, New York. pp. 409-448.
- Vorburger C. & Ribí G. (1999)** Aggression and competition for shelter between a native and an introduced crayfish in Europe. *Freshwater Biology*, **42**, 111-119.
- Weissberger E.J. (1999)** Additive interactions between the moon snail *Euspira heros* and the sea star *Asterias forbesi*, two predators of the surfclam *Spisula solidissima*. *Oecologia*, **119**, 461-466.
- Welsh S.A. & Perry S.A. (1998)** Habitat partitioning in a community of darters in the Elk River, West Virginia. *Environmental Biology of Fishes*, **51**, 411-419.
- Welton J.S. (1979)** Life-history and production of the amphipod *Gammarus pulex* in a Dorset chalk stream. *Freshwater Biology*, **9**, 263-275.
- Welton J.S., Mills C.A. & Rendle E.L. (1983)** Food and habitat partitioning in two small benthic fishes, *Noemacheilus barbatulus* (L.) and *Cottus gobio* (L.). *Archiv für Hydrobiologie*, **97**, 434-454.
- Welton J.S., Mills C.A. & Pygott J.R. (1991)** The effect of interaction between stone loach *Noemacheilus barbatulus* (L.) and the bullhead *Cottus gobio* (L.) on prey and habitat selection. *Hydrobiologia*, **220**, 1-7.
- 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. (1986)** Species interactions in freshwater fish communities. In: J. Diamond & T.J. Case, eds., *Community Ecology*. Harper & Row, New York, USA. pp. 344-358.
- Westlake D.F., Casey H., Dawson H., Ladle M., Mann R.H.K. & Marker A.F.H. (1972)** The chalk stream ecosystem. In: Z. Kajak & A. Hillbricht-Ilkowska, eds., *Productivity Problems of Freshwaters*. PWN, Warsaw, Poland. pp. 615-635.
- Wheeler A. (1977)** The origin and distribution of the freshwater fishes of the British Isles. *Journal of Biogeography*, **4**, 1-24.
- Wheeler A. (1992)** A list of the common and scientific names of the Fishes of the British Isles. *Journal of Fish Biology*, **41**, 1-37.
- Wiens J.A. (1977)** On competition and variable environments. *American Scientist*, **65**, 590-597.
- Wiens J.A. (1984)** On understanding a non-equilibrium world: myth and reality in community patterns and processes. In: D.R. Strong, D. Simberloff, L.G. Abele & A.B. Thistle, eds., *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton, NJ. pp. 439-457.
- Wiens J.A., Stenseth N.C., Vanhorne B. & Ims R.A. (1993)** Ecological mechanisms and landscape ecology. *Oikos*, **66**, 369-380.
- Williams G.A. & Morritt D. (1995)** Habitat partitioning and thermal tolerance in a tropical limpet, *Cellana grata*. *Marine Ecology Progress Series*, **124**, 89-103.
- Williams J.B., Tieleman B.I. & Shobrak M. (1999)** Lizard burrows provide thermal refugia for larks in the Arabian Desert. *Condor*, **101**, 714-717.
- Winemiller K.O. (1991)** Ecomorphological diversification in lowland fresh-water fish assemblages from five biotic regions. *Ecological Monographs*, **61**, 343-365.
- Winterbottom J.H., Orton S.E., Hildrew A.G. & Lancaster J. (1997)** Field experiments on flow refugia in streams. *Freshwater Biology*, **37**, 569-580.
- Wissinger S. & McGrady J. (1993)** Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. *Ecology*, **74**, 207-218.
- Wolda H. & Dennis B. (1993)** Density-dependence tests, are they? *Oecologia*, **95**, 581-591.
- Wooster D. (1994)** Predator impacts on stream benthic prey. *Oecologia*, **99**, 7-15.
- Wooster D. & Sih A. (1995)** A review of the drift and activity responses of stream prey to predator presence. *Oikos*, **73**, 3-8.
- Wootton J.T. (1994)** Predicting direct and indirect effects - an integrated approach using experiments and path analysis. *Ecology*, **75**, 151-165.
- Young K.A. (2001)** Habitat diversity and species diversity: testing the competition hypothesis with juvenile salmonids. *Oikos*, **95**, 87-93.
- Zar J.H. (1999)** *Biostatistical Analysis*. Prentice Hall, NJ, USA.
- Zaret T.M. & Rand A.S. (1971)** Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology*, **52**, 336-342.