THE UNIVERSITY OF HULL

THE ECOLOGY OF LARVAL AND JUVENILE FISHES IN LOWLAND RIVERS, WITH PARTICULAR EMPHASIS ON FORAGING

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ABSTRACT

FEEDING ECOLOGY OF 0+ FISHES

There are numerous biotic and abiotic factors that affect the abundance of cyprinid fish stocks in rivers, many of which are poorly understood. The role of food availability during critical life stages is one of these factors that may determine the growth and survival of 0+ fishes, and ultimately their recruitment to adulthood. Until the main factors affecting recruitment of cyprinid fishes are better understood, informed/appropriate management actions cannot be undertaken. For this reason temporal, spatial and inter-specific influences affecting the prey availability, feeding ecology and condition of 0+ fishes were studied in experimental and wild conditions to improve the understanding of feeding ecology for 0+ fishes in rivers and the effect this has on the health of the individual fish.

This study revealed diel variation in fish species composition, prey availability, diet composition, feeding activity and prey selection of larval and 0+ juvenile fishes. Five surveys were carried out in total, until the fishes reached juvenile stage, in the River Trent. There was circumstantial evidence of zooplankton migration in some species, for example, densities of Rotifera in the margins declined at night, suggesting migration into open waters. Densities of 0+ fishes were generally higher at night in three surveys, but higher in daylight in two surveys. This may have been a result of predator avoidance as more >0+ pike and perch were found in the margins at night. There was also a significant increase in spined loach and bullhead at night compared to daylight. Gut fullness of 0+ juvenile roach and perch increased at night, but there was a reduction in gut fullness at night for larval roach and perch, suggesting a switch in feeding behaviour during ontogeny that was also evident in electivity indices and prey availability. Seasonal variations in prey availability and feeding ecology of 0+ roach and bream were studied on the River Trent, which revealed a significant reduction in feeding activity of both species from summer to winter, but this did not affect the condition of the fishes, which remained constant across all seasons. Significant seasonal differences in the diet composition were found in 0+ bream, but not 0+ roach.

Spatial variations in prey availability (composition, density and diversity), feeding ecology (diet composition, feeding activity and prey selection) and condition of 0+ fishes were studied using point abundance sampling on a mesohabitat scale in the River Ancholme to investigate the influence of habitat type (floating-leaved, emergent or submerged vegetation). The highest densities of most zooplankton taxa were found in emergent and floating-leaved vegetation (the least complex habitats) compared with submerged vegetation (the most complex). Feeding activity was higher for larval and 0+ juvenile roach than bream in all vegetation categories. Gut fullness of larval roach was highest in submerged vegetation, suggesting that the complex structure did not affect the feeding activity of 0+ roach. In general, selection was higher in simple vegetation categories than complex vegetation categories, even though the same prey was available in most habitats, indicating that prey availability was not the only factor influencing feeding ecology of 0+ roach and bream and that habitat complexity influences prey choice. Nonetheless, this did not influence the condition of roach and bream between the different vegetation categories, which remained constant.

The effects of interspecific interactions on the diet composition, prey selection, growth and condition of 0+ roach and bream were studied in allopatric (single-species) and sympatric (mixed-species) fish populations established in enclosures at Calverton Fish Farm, Nottinghamshire. This study found a significant influence of interspecific interactions on the diet composition and prey selection of 0+ fishes. There was evidence of resource partitioning when roach and bream larvae were in sympatry, which suggested that feeding behaviour of both species was negatively affected by interspecific interactions. By comparison, interspecific interactions had no significant influence on the length, weight or weight-length relationships of 0+ roach and bream. In addition, the condition of roach was not affected by the presence of bream, but there was a small but significant deterioration in the condition of bream in the presence of roach. These results were compared to wild conditions in the River Trent, which generally supported the findings at Calverton even though the densities at Calverton were higher. This information will improve understanding of the feeding ecology of 0+ fishes during early development, which can be used in the management and rehabilitation of fish populations and fluvial habitats, as well as improving growth and survival in aquaculture facilities, and inform research sampling strategies when studying juvenile fish populations.

CHAPTER ONE

1. INTRODUCTION AND OBJECTIVES

Fish larvae are subject to high mortality, averaging 96.4% for freshwater species over the whole larval period (Houde, 2002). Their survival is governed by many factors at a local and global scale, as a result of natural and anthropogenic pressures. Natural variables/events that influence the survival of larval fish include starvation, predation, floods, diseases and parasites, rapid changes in water quality, temperature and dissolved oxygen levels (Mills & Mann, 1985; Miller *et al*., 1988; Gliwicz, 1994; Houde, 2002; Ondračková *et al*., 2002; Nunn *et al*., 2003, Quist, 2004; Longshaw *et al*., 2005; Longshaw *et al*., 2010 Nunn *et al*., 2012). Flood events increase the risk of drift and 'wash out' for 0+ fishes in all rivers, especially ones that have been modified by man. Bischoff & Wolter, (2001) found a drastic decline in 0+ fishes after a summer flood on the River Oder in the Czech Republic. Similarly, Harvey, (1987) found that fish smaller than 10 mm were extremely susceptible to downstream displacement in flood conditions. This emphasises the importance of maintaining and where possible connecting back waters that provide essential refuge areas for 0+ fishes (Nunn *et al.*, 2007c) as the channelisation of many rivers for transport or flood defence has led to the loss or degradation of refuge or spawning habitats, as well as cutting the river off from its natural floodplain (Cowx & Welcomme, 1998). Temperature is another variable that can influence fish growth and subsequent recruitment to adulthood. Research indicated that large cohorts of adult cyprinid fishes often result from higher than average water temperature in the first summer of life (Mills & Mann, 1985; Cowx, 2001; Grenouillet *et al*., 2001). Mills & Mann, (1985) showed how roach grow little in length in water temperatures below 12^{o}C, which can increase predation risk for 0+ fishes because of their smaller size. Growth is also influenced by the foraging ecology of 0+ fishes; many studies have suggested that the abundance of suitable food available to the early life stages of fishes has a critical influence on their growth and, consequently, recruitment success (usually defined as the number of a cohort that joins the adult stock; Cushing & Horwood, 1994). Slow growth due to reduced feeding success would increase the period of vulnerability to predators (Miller *et al*., 1988; Cushing & Horwood 1994; Bremigan & Stein, 1994; Bass *et al*., 1997; Mayer & Wahl, 1997; DeVries *et al*., 1998; Garner, 1998; Graeb *et al*., 2004; Hoxmeier *et al*., 2004; King, 2004; Nunn *et al*., 2007a, b). The Growth-Mortality Hypothesis (Ware, 1975; Shepherd & Cushing, 1980) affirms that predation risk decreases with increasing size. Yet knowledge of the feeding ecology of 0+ fishes and the affect this has on recruitment success is relatively poor (Cryer *et al*., 1986; Cushing, 1990; Bremigan & Stein, 1994; Nunn *et al*., 2007a & b; Nunn *et al*., 2012). Hjort (1914) was the first to link larval survival and ultimately recruitment with food availability; he suggested the Critical Period Hypothesis, which has since been a key influence on further larval survival studies. This hypothesis suggests that if food is limiting during the transition from endogenous (yolk) to exogenous (planktonic or non-planktonic) feeding, many fish larvae will die from starvation, but if food availability is high, survival is likely to increase (Houde, 2002).

It is known that most fish species are initially planktivorous and that their small size and poor swimming ability (due to undeveloped fins) restricts the type (size, morphology and behaviour) of prey that they can ingest (Cushing, 1990; Mayer & Wahl, 1997; Mehner & Thiel, 1999; Nunn *et al*., 2007a & b; Stige *et al*., 2011; Nunn *et al*., 2012). As the larvae develop and increase in size, their swimming ability improves due to the formation of fins, their gape size increases and their vision improves, effectively increasing prey availability (Wanzenböck & Schiemer, 1989). A lack of suitable prey can reduce growth rates and possibly lead to starvation, and a reduction in energy intake may also cause swimming speeds to be reduced, further reducing foraging efficiency (Hoxmeier *et al*., 2004). This makes 0+ fishes particularly susceptible to temporal and spatial variations in prey availability.

Temporal differences in food availability may vary for a number of reasons, including diel (Dodson, 1990; Loose & Dawidowicz, 1994; Burks *et al.*, 2002), seasonal (Wilhm *et al.*, 1977; Gosselain *et al.*, 1994; van Dijk & van Zanten, 1995; Kobayashi *et al.*, 1998; Wolfinbarger, 1999; Viroux, 2002; Talling, 2003) and annual (Mayer & Wahl, 1997; Dickmann *et al*., 2007; Burrow *et al*., 2011; Stige *et al*., 2011, Nunn *et al*., 2012) differences in prey abundance. Diurnal fluctuations of zooplankton populations may occur due to vertical and horizontal migration of some zooplankton species into and out of the littoral zone to avoid predation and increase foraging efficiency (Gliwicz, 1989; Lauridsen *et al.*, 1996; Nunn *et al*., 2012). Consequently, diurnal fluctuations in fish species composition have been observed. Many studies have found evidence of diurnal migration of 0+ fishes into and out of the littoral zone to increase foraging success and avoid predation of piscivorous fish (Copp & Jurajda, 1993; Jacobson *et al*., 1997; Baras & Nindaba, 1999; Copp, 2004; Copp *et al*., 2005). Annual variations in recruitment success may also be governed by the feeding ecology of 0+ fishes. Cushing (1990) was the first to suggest a hypothesis that explains why successful first-feeding might vary annually. His Match-Mismatch Hypothesis states that "while annual spawning times in fish are constant, the onset of the annual primary production cycle is not, but a result of changing physical conditions" (e.g. irradiance and heat). Therefore, if the timing of phytoplankton population growth and subsequent zooplankton populations occurs too early or too late, then fish larvae may be "mismatched" to the peaks in abundance of food supply, resulting in starvation and ultimately death. This is supported by the Food Production Hypothesis (Anderson, 1988) that states that “the absolute magnitude of primary production varies annually, depending on certain physical conditions such as temperature”. Thus, when primary production is high, zooplankton abundance increases as they graze on plankton, making more zooplankton available to fish larvae, which increases their chances of survival.

Spatial variations in prey abundance can have important implications for the growth and survival of larval fishes as they are restricted to certain habitats due to their limited swimming ability. As a result, their diet is often limited to the prey available in their immediate habitat. There is limited research on how habitat structure influences prey availability, fish feeding ecology and their condition, especially on cyprinid fishes in natural riverine environments (Winfield, 1986; Diehl, 1988; Copp, 1992a, b; Garner, 1995; Miranda & Hodges, 2000; Agostinho *et al.*, 2007). Werner *et al*., (1983) demonstrated that higher growth rates were achieved if fish were able to switch habitats to maximise foraging success. Thus, understanding the habitats that larval and juvenile fishes occupy and the influence this has on prey availability, in addition to the feeding ecology (diet composition and prey selection) and condition of larval and juvenile fishes, will help improve river restoration projects and in turn enhance fish recruitment.

Interspecific interactions can also have important implications for the growth, survival and recruitment success of fishes, not only in the wild but also aquaculture conditions. For example, larval fishes may alter their diets, and have lower growth rates, in the presence of competing species, especially as they are restricted to a similar diet due to their limited movement and gape size (Garner, 1996a; Nunn *et al*., 2007b; Nunn *et al*., 2012). Interspecific competition for prey items in 0+ juvenile fishes has also been recorded; for example, the diets of juvenile Eurasian perch (*Perca fluviatilis* L.), pikeperch (*Sander lucioperca* (L.)), ruffe (*Gymnocephalus cernuus* (L.)), roach (*Rutilus rutilus* (L.)) and common bream (*Abramis brama* (L.)) overlapped significantly in a lowland reservoir (Matena 1998). Therefore, it is important to increase knowledge of the influence of interspecific interactions on the diet composition, prey selection, growth and subsequent condition of 0+ fishes, as this ultimately influences recruitment success (DeVries *et al.*, 1998).

Nonetheless, relatively little is known about temporal, spatial and interspecific influences on the diets and prey availability of 0+ fishes in rivers and the effect this has on the growth and condition of individual fish. To this end, this thesis aims to bridge these knowledge gaps by examining 0+ freshwater fishes from the UK that are typical of a lowland river system and also of angler interest, with chapters covering the following topics:

Chapter 2 reviews the current state of knowledge of diets and dietary preferences of 0+ fishes, the importance of abundance of particular food items for survival and growth of 0+ fishes and indicators of nutritional health of 0+ fishes.

Chapter 3 investigates temporal variations in the foraging ecology of 0+ fishes, with particular emphasis on diel changes in prey availability and selection, diet composition and fish species composition. In addition, seasonal variations in the diet composition, prey selection and condition of 0+ fishes were studied.

Chapter 4 investigates spatial variations in the foraging ecology of 0+ fishes, specifically the influence that macrophyte structure has on prey availability and the diet composition, prey selection and condition of 0+ fishes.

Chapter 5 investigates the effects of interspecific interactions on the diet composition, prey selection, growth and condition of 0+ fishes in experimental and natural conditions.

Chapter 6 brings together all the knowledge gained within the thesis and suggests recommendations for future research.

Objectives

The objectives of this thesis were to identify 1) any temporal variations (diel and seasonal) in prey availability that may influence feeding behaviour and diet composition, which could influence the condition of 0+ fishes 2) any affects of macrophyte structure on food availability and how this influences the diet composition, prey selection and condition of 0+ fishes 3) and compare the diet composition, prey selection, growth and condition of 0+ fishes in sympatry and allopatry in experimental conditions and compare these to samples from the wild. The knowledge obtained from this thesis will help transform understanding of the factors influencing the feeding ecology of 0+ fishes and is a vital stepping stone in understanding the factors influencing recruitment success. This will help guide future research, improving sustainable fish populations within aquatic environments.

Throughout this thesis 0+ fish/es is a term used frequently, which relates to all fish under one year old. This includes both the larval and juvenile stages of fish development, which are described below. In addition, these steps can be grouped into finfold (L1 – L3) and finformed (L4-L6) larvae and juvenile (known as ecospecies) when discussing feeding behaviour and diet, as these change with development.

Larval step 1 (L1) begins at the onset of exogenous feeding, and is characterised by a reduction of the yolk sac, a straight notochord, a rudiment of a swim bladder in percids, a single gas-filled chamber in the swim bladder of cyprinids, and development of objective vision and vaguely defined anal, dorsal and caudal finfolds.

Larval step 2 (L2) commences upon complete resorption of the yolk (transition to exclusively exogenous feeding), and is characterised by ossification of the vertebral bodies, further differentiation of the finfolds, a terminal closable mouth, increased diameter of the intestine, filling of the swim bladder in percids, and enlargement of the swim bladder in cyprinids.

Larval step 3 (L3) begins with development of the hypurals and mesenchymal lepidotrichia formation in the dorsal and anal finfolds, and is characterised by the posterior end of the notochord bending upwards at an obtuse angle, continued differentiation of the finfolds, formation of the first rays in the slightly heterocercal caudal fin, and the appearance of teeth in the jaws of percids.

Larval step 4 (L4) is characterised by the posterior end of the notochord bending sharply upwards so that the hypurals and caudal fin rays point backwards, ossification of the caudal fin rays, appearance of rays in the dorsal and anal finfolds, anlagen of pelvic fins, a two-chambered swim bladder in cyprinids, and development of the upper field of vision.

Larval step 5 (L5) is characterised by ossification of the rays of the dorsal and anal fins, formation of mesenchymal rays in the pectoral and pelvic fins, pelvic fins nearing the edge of the preanal finfold, and a deeply incised caudal fin which changes from trilobate to homocercal.

Larval step 6 (L6) is characterised by full development of rays in all fins, atrophy of the preanal finfold such that the pelvic fins of cyprinids surpass its margin, a marked increase in intestine length and development of the first pair of intestinal loops, and flexion of the myomeres into a zigzag formation.

Juvenile period (J) begins with disappearance of preanal finfold, complete differentiation of the fins, bifurcation of most fin rays, and differentiation of the nasal orifice and the onset of squamation.

CHAPTER TWO

THE DIETS AND DIETARY PREFERENCES OF 0+ FRESHWATER FISHES, WITH PARTICULAR REFERENCE TO RIVER HABITATS AND THE MAIN RIVERINE FISH SPECIES OF ANGLER INTEREST IN THE UK: A LITERATURE REVIEW

2.1 Introduction

Early development represents a critical period in the life cycle of fishes (Copp 1990a, 1992a; Baras *et al*., 1995; Garner 1996a; Mann 1997), with growth in the first few weeks after hatching key to survival and recruitment success (Mills & Mann 1985; Kubečka 1994; Grenouillet *et al*., 2001b; Nunn *et al*., 2003; Nunn *et al*., 2007d). One of the most important factors regulating the growth and survival of young fishes is food availability (Schiemer *et al*., 1989; Mann 1997; Mann *et al*., 1997; DeVries *et al*., 1998; Fiksen & MacKenzie 2002), with a lack of suitable prey potentially causing either reduced growth or starvation (Graeb *et al*., 2004; Hoxmeier *et al*., 2004; Tonkin *et al*., 2006). Knowledge of the dietary requirements of larval and juvenile fishes is essential for the management of their populations and habitats.

2.2 Diets of 0+ fishes in the UK

The diets of adult freshwater fishes present in the UK have been investigated extensively (Frost 1943; Hartley 1948; Frost 1950; Hynes 1950; Thomas 1962; Maitland 1965; Mann & Orr 1969; Hellawell 1971a, b, 1972; Mann 1973; Hellawell 1974; Mann 1974, 1976a, b, 1978; Bohl 1980, 1982; Haberlehner 1988; Cowx 1989; Giles *et al*., 1990; Specziár *et al*., 1997; Specziár *et al*., 1998; García-Berthou 1999; García-Berthou & Moreno-Amich 2000; García-Berthou 2001; Khan 2003) (Table 2.1). By comparison, there is limited information for some UK species and there are very few cases where diet has been related to food availability.

Roach (*Rutilus rutilus* (L.))

After hatching, roach larvae initially feed on copepod nauplii, rotifers and phytoplankton (Hammer 1985; Jelonek 1986; Townsend *et al*., 1986; Weatherley 1987; Reyesmarchant *et al*., 1992; Matěna 1995; Garner 1996a; Mann *et al*., 1997; Nunn *et al*., 2007b). As the larvae develop, cladocerans become important in the diet (Northcott 1979; Hammer 1985; Townsend *et al*., 1986; Horppila 1994; Matěna 1995; Simonian *et al*., 1995; Mann 1997; Mann *et al*., 1997; Mehner *et al*., 1997; Nunn *et al*., 2007b), although phytoplankton may dominate the diet if cladoceran abundance is low (Weatherley 1987; Kurmayer & Wanzenböck 1996). As 0+ juveniles, roach feed primarily upon zooplankton before switching to aufwuchs (Garner 1996a; Mann *et al*., 1997; Vašek *et al*., 2006; Nunn *et al*., 2007b, 2008a). The proportion of aufwuchs in the diet typically increases through the summer (Weatherley 1987; Matěna 1995; Nunn *et* *al*., 2007b), often coinciding with low availabilities of animal prey, particularly cladocerans (Persson 1983).

Dace (*Leuciscus leuciscus* (L.))

Dace larvae commence exogenous feeding 2-3 days after hatching, before the yolk sac is fully absorbed (Mann & Mills 1986). The initial diet consists mainly of rotifers and diatoms, with some copepod nauplii and copepodites (Mills *et al*., 1985; Weatherley 1987). Nunn *et al*., (2007b) found that the diets of young dace larvae in the River Trent were dominated by rotifers (primarily Brachionus spp., Euchlanis spp., Keratella spp.), with small numbers of cladocerans, such as *Bosmina* sp., *Ilyocryptus* sp. and chydorids, also eaten by many fish, along with early instar chironomid larvae, harpacticoid copepods and copepod nauplii. As they develop, dace larvae begin to feed upon cladocerans, copepods and chironomid larvae (Mills *et al*., 1985; Mann and Mills 1986; Nunn *et al*., 2007b), with aerial insects, chironomid pupae and tubificids increasing in importance towards the end of the larval period (Weatherley 1987). After approximately 10 weeks, the proportion of algae was found to increase rapidly to become the major component of the diet (Weatherley 1987). In the River Dee, the diets of juvenile dace were dominated by blue-green algae and detritus (Weatherley 1987), whereas in the River Trent, chironomids (larvae, adults) and aufwuchs (the periphyton and associated microfauna that grow on underwater surfaces) were the main food (Nunn *et al*., 2007b).

Chub (*Leuciscus cephalus* (L.))

During the early larval period, chub feed predominantly upon rotifers and diatoms (Garner 1996a). In the River Trent, for example, the diets of young chub larvae were dominated by rotifers (predominantly Keratella spp., Brachionus spp. and Euchlanis spp.), with smaller numbers of algae (mainly Closterium spp. and Pediastrum spp.), copepod nauplii and early instar chironomid larvae also eaten (Nunn *et al*., 2007b). By contrast, Mark *et al*., (1987) found that chub larvae rarely consumed rotifers and copepod nauplii, but preyed upon small crustaceans, adult copepods and chironomid larvae immediately after hatching. As the fish develop, small cladocerans, such as *Bosmina* sp., *Chydorus* spp. and *Alona* spp., become more frequent in the diet, along with larger chironomid larvae and cyclopoid copepods (Nunn *et al*., 2007b). In the late larval period there is a switch to Cladocera and chironomid larvae (Garner 1996a). In the River Trent, chub had more diverse diets than other cyprinid species, with older larvae consuming a range of prey, including chironomid larvae, *Scapholeberis mucronata*, *Polyphemus pediculus* (L.), *Bosmina* sp., *Chydorus spp*., *Pleuroxus spp*., *Alona* spp., copepod nauplii, cyclopoid copepods, rotifers, testate amoebae, adult dipterans and *Eurycercus lamellatus* (Müller). Juvenile chub mainly feed upon adult dipterans and chironomid larvae (Mark *et al*., 1987; Garner 1996a), although aufwuchs may also be important (Nunn *et al*., 2007b).

Table 2.1. Diet composition of lowland freshwater fish species of angler interest in the UK (adapted from Cowx 2001)

	Developmental period	
Species	Larvae and juveniles	Adults
Roach	Phytoplankton, zooplankton, benthic invertebrates, aufwuchs	Benthic invertebrates, zooplankton, aufwuchs, algae, macrophytes
Dace	Phytoplankton, zooplankton, benthic invertebrates, aufwuchs	Benthic invertebrates, aerial insects, aufwuchs, macrophytes
Chub	Zooplankton, benthic invertebrates, aufwuchs	Benthic invertebrates, aerial insects, aufwuchs, macrophytes, fishes
Bream	Zooplankton, benthic invertebrates, aufwuchs	Benthic invertebrates, zooplankton, aufwuchs
Rudd	Phytoplankton, zooplankton	Aerial insects, aufwuchs, algae, macrophytes
Barbel	Zooplankton, benthic invertebrates	Benthic invertebrates
Tench	Phytoplankton, zooplankton, benthic invertebrates	Benthic invertebrates
Carp	Zooplankton, benthic invertebrates	Benthic invertebrates, macrophytes
Bleak	Zooplankton	Zooplankton, aerial insects
Gudgeon	Zooplankton, benthic invertebrates	Zooplankton, benthic invertebrates
Pike	Zooplankton, benthic invertebrates, fishes	Fishes, amphibians, birds, mammals
Perch	Zooplankton, benthic invertebrates	Benthic invertebrates, fishes
Ruffe	Zooplankton, benthic invertebrates	Benthic invertebrates
Zander	Zooplankton, benthic invertebrates, fishes	Fishes
Crucian carp	Zooplankton	Zooplankton, benthic invertebrates

Bream (*Abramis brama* (L.))

Bream larvae subsist on the yolk sac until a length of ~8 mm, thereafter they begin to feed upon unicellular algae (Kennedy & Fitzmaurice 1968), before switching to rotifers, copepod nauplii and early instar chironomid larvae (Žiliukienė 2005; Nunn *et al*., 2007b). As the fish develop, small cladocerans, such as *Bosmina* spp., *Chydorus* spp. and *Alona* spp., become more frequent in the diet, along with larger chironomid larvae and cyclopoid copepods, followed by greater diversities of cladocerans and macroinvertebrates in the diets of older larvae (Kennedy & Fitzmaurice 1968; Peirson 1983; Mehner *et al*., 1997; Žiliukienė 2005; Nunn *et al*., 2007b). In the River Trent, bream continued to consume rotifers extensively towards the end of the larval period, with *Bosmina* sp., *Daphnia* spp., non-planktonic cladocerans (*Chydorus* spp., *Ceriodaphnia* spp., *Simocephalus* spp., *Alona* spp.), cyclopoid copepods, copepod nauplii and chironomid larvae also consumed by older bream larvae (Nunn *et al*., 2007b). Juvenile bream feed on benthic macroinvertebrates, non-planktonic cladocerans, copepods or aufwuchs (Peirson 1983; Winfield & Townsend 1988; Garner 1996a; Persson & Brönmark 2002; Vašek *et al*., 2006; Nunn *et al*., 2007b).

Rudd (*Scardinius erythrophthalmus* (L.))

Rudd larvae feed mainly on unicellular algae, while older 0+ individuals feed on cladocerans and copepods (Kennedy & Fitzmaurice 1974).

Barbel (*Barbus barbus* (L.))

The diets of larval and 0+ juvenile barbel are dominated by benthic organisms (e.g. chironomid and ephemeropteran larvae, non-planktonic cladocerans), with cyclopoid copepods, copepod nauplii and rotifers also consumed by some fish (Bischoff & Freyhof 1999; Nunn *et al*., 2007b).

Tench (*Tinca tinca* (L.))

Tench larvae subsist on the yolk sac until a length of 6-7 mm, thereafter they begin to feed upon protozoans, rotifers and unicellular algae (Kennedy & Fitzmaurice 1970; Lukowicz *et al*., 1986). As tench larvae develop, larger rotifers and small cladocerans begin to feature in the diet, before they switch to ostracods, larger cladocerans, copepods, water mites and aquatic insect larvae (Kennedy & Fitzmaurice 1972; Steffens 1995). In the River Great Ouse, the diet of young tench larvae was dominated by cladocerans, with cladocerans and copepods the principal prey of older larvae and 0+ juveniles (Copp & Mann 1993).

Carp (*Cyprinus carpio* L.)

Cladocerans, especially *Daphnia* spp., are usually the main food of carp larvae, although corixids, ostracods, copepods, seeds and insect larvae may also be eaten by some fish (Alikunhi 1966; Kokeš *et al*., 1984; Vilizzi 1998; Khan 2003; Nunn *et al*., 2007b). Cladocerans are also important in the diets of juvenile carp, although seeds, ostracods, hemipterans, chironomids, dipterans, oligochaetes, gastropods, trichopterans and decapods may also be eaten (Vilizzi 1998; Khan 2003). By contrast, the diet of juvenile carp in a waterbody connected to the River Trent consisted almost entirely of cyclopoid copepods, although this was probably due to the super-abundance of this prey item (Nunn *et al*., 2007b).

Bleak (*Alburnus alburnus* (L.))

The diets of bleak larvae are dominated by rotifers, with smaller numbers of copepod nauplii, *Bosmina* sp. and early instar chironomid larvae also eaten (Garner 1996a; Nunn *et al*., 2007b). As the fish develop, small cladocerans, such as *Bosmina* sp., *Chydorus* spp. and *Alona* spp., become more frequent in the diet, along with larger chironomid larvae and cyclopoid copepods. Unlike many other cyprinid species, bleak continue to be largely zooplanktivorous in the juvenile period (Schiemer *et al*., 1989), with *Bosmina* sp., copepod nauplii and rotifers the most frequent prey (Garner 1996a; Nunn *et al*., 2007b).

Gudgeon (*Gobio gobio* (L.))

Gudgeon larvae begin to feed 3 days after hatching, with the yolk fully absorbed after 5-6 days (Kennedy & Fitzmaurice 1972), although there appears to be little information on the prey consumed. In the River Trent, Alona spp., copepod nauplii and chironomid larvae were the most important prey in the diet of older gudgeon larvae (Nunn *et al*., 2007b). The diet of juvenile gudgeon is dominated by benthic organisms, such as molluscs, Gammarus sp., chironomid, ephemeropteran and trichopteran larvae, non-planktonic cladocerans (e.g. Alona spp.) and aufwuchs (Kennedy & Fitzmaurice 1972; Nunn *et al*., 2007b), although those in the River Great Ouse were found to consume mainly copepods (Garner 1996a).

Pike (*Esox lucius* L.)

Pike larvae initially feed upon rotifers and microcrustaceans (cladocerans and copepods), before switching to chironomids (larvae and pupae) and benthic invertebrates (Asellus sp. and Gammarus sp.) (Wright & Giles 1987; Bry *et al*., 1995; Mamcarz *et al*., 1998; Žiliukienė & Žiliukas 2006). Piscivory develops from a length of >20 mm, and cannibalism can occur from a length of >30 mm (Giles *et al*., 1986; Wright & Giles 1987; Alp *et al*., 2008).

Perch (*Perca fluviatilis* L.)

Perch larvae subsist on the yolk sac until the mouth becomes terminal at a length of 6-7 mm (Spanovskaya & Grygorash 1977), whereupon rotifers and copepod nauplii are the initial food items (Treasurer 1990; Mehner *et al*., 1997; Skrzypczak *et al*., 1998), with ciliates and algae eaten occasionally (Guma'a 1978). Small cladocerans are eaten as the larvae increase in size (Skrzypczak *et al*., 1998), while *Daphnia* spp. become important in the diet after perch exceed 10-15 mm, and Leptodora kindtii and Bythotrephes spp. are taken by >15 mm larvae (Guma'a 1978; Mehner *et al*., 1997). Copepods may also be common in the diet (Matěna 1995; Nunn *et al*., 2007b), and are sometimes favoured over cladocerans (Guma'a 1978). Perch larvae in the River Trent consumed a range of prey, including cyclopoid copepods, *Daphnia hyalina* (Leydig), copepod nauplii, *Bosmina* sp., *E. lamellatus* and *Alona* spp. (Nunn *et al*., 2007b). In still waters, juvenile perch consume mainly planktonic cladocerans, especially *Daphnia* spp., *Bosmina* spp. and *Leptodora kindtii* (Spanovskaya & Grygorash 1977; Vašek *et al*., 2006). Littoral forms, such as Sida crystallina and Chydorus spp., are generally of less importance, while copepods and chironomid larvae and pupae are more important than in larvae. By contrast, phytophilic and benthic invertebrates appear to be more important in rivers (Nunn *et al*., 2007b). In addition, some perch may become piscivorous (Deelder 1951; Guma'a 1978; Brabrand 1995; Mehner *et al*., 1995; Mehner *et al*., 1996; van Densen *et al*., 1996; Borcherding *et al*., 2000; Brabrand 2001; Beeck *et al*., 2002).

Ruffe (*Gymnocephalus cernuus* (L.))

Ruffe larvae initially feed upon rotifers and copepod nauplii (Ogle 1998 cited Johnsen 1965) before switching to copepods, *Daphnia* spp., *Bosmina* spp., chydorids and chironomid larvae (Boron & Kuklinska 1987; Matěna 1995; Mehner *et al*., 1997; Ogle *et al*., 2004). Juvenile ruffe are predominantly benthic feeders, with a diet dominated by chironomid larvae (Ogle *et al*., 1995; Tarvainen *et al*., 2008).

Zander (*Sander lucioperca* (L.))

Zander larvae begin to feed within 48 hours of hatching, at a size of approximately 5-6 mm (Linfield & Rickards 1979). The larvae initially feed on copepod nauplii before switching to copepods, then *Daphnia* spp. and other large cladocerans, with bosminids and chydorids usually forming only a minor part of the diet (Kokeš 1993; Frankiewicz *et al*., 1997; Mehner *et al.,* 1997; Peterka *et al*., 2003; Nunn *et al*., 2007b). Similarly, the main prey of 0+ juvenile zander are cladocerans and copepods, with piscivory occurring from a length of 20 mm (Mehner *et al*., 1996), although fish remain a relatively unimportant part of the diet until a length of >100 mm is reached (Willemsen 1969; Collette *et al*., 1977; Buijse & Houthuijzen 1992; Hansson *et al.,* 1997).

Crucian carp (*Carassius carassius* (L.))

The diets of larval and 0+ juvenile crucian carp consist of planktonic cladocerans (especially *Bosmina* spp.), with copepods, benthic cladocerans and chironomid larvae also eaten (Penttinen & Holopainen 1992).

2.3 Influence of food availability on the survival and growth of 0+ fishes

A range of factors influence the fish populations of rivers (Figure 2.1). The growth and survival of larval fishes can be highly susceptible to fluctuations in prey availability (Graeb *et al.*, 2004; Hoxmeier *et al.*, 2004), and knowledge of how such fluctuations influence growth and survival of larval fishes is imperative to understand recruitment processes (Welker *et al.*, 1994). Many fish species are zooplanktivorous at the onset of exogenous feeding (Whiteside *et al.*, 1985; Wanzenböck & Schiemer 1989), and the growth, survival and, ultimately, recruitment of such fishes during their early life history is often strongly linked with zooplankton availability (Schiemer *et al.*, 1989; Mann *et al.*, 1997). Indeed, the match/mismatch hypothesis (Cushing 1990) postulates that the survival of fish larvae will be highest when hatching coincides with peaks in plankton production (‘match’ scenario), with a mismatch in the timing of hatching and plankton blooms leading to high mortality (‘mismatch’ scenario). Early in fish ontogeny, food intake may be strictly governed by morphological and behavioural constraints (Mark *et al.*, 1987; Bremigan & Stein 1994). Food particles must therefore be available in both sufficient quantity and the correct size (Mills & Mann 1985; Mitra *et al.*, 2007), with a decline in abundance of appropriately-sized prey potentially causing either reduced growth or starvation (Graeb *et al.*, 2004; Hoxmeier *et al.*, 2004; Tonkin *et al.*, 2006).

Competitive effects on growth occur when behavioural interactions between fish cause an unequal distribution of a resource that is directly or indirectly related to growth (Wootton 1990). A number of studies have demonstrated a negative relationship between fish growth and fish density (e.g. Persson & Greenberg 1990; Byström & García-Berthou 1999; Dettmers & Wahl 1999; Cowan *et al.*, 2000; Feldlite & Milstein 2000; Pivnička & Švátora 2000; Romare 2000). Grenouillet *et al.*, (2001b) found that survival of roach in the first year of life was density-dependent, and stated that intraspecific competition within the 0+ cohort could influence recruitment to older age-classes. This may be of particular importance in years of good recruitment. Cryer *et al.*, (1986) and Perrow & Irvine (1992), studying lacustrine populations of roach, demonstrated that abundant 0+ roach can sometimes show poor growth as a result of depression of their prey populations. Competition for food resources may also influence winter mortality of 0+ fishes, as overwinter survival has been found by many studies to be positively related to fish length (≈ lipid content) (Miller *et al.*, 1988; Post & Evans 1989; Johnson & Evans 1990, 1991; Thompson *et al.*, 1991; Griffiths & Kirkwood 1995; Johnson & Evans 1996; Kirjasniemi & Valtonen 1997a, b; Copeland & Carline 1998; Garvey *et al.*, 1998; Hurst & Conover 1998; Post *et al.*, 1998; Schindler 1999; Lappalainen *et al.*, 2000; McCollum *et al.*, 2003; Eckmayer & Margraf 2004; Pangle *et al.*, 2004; Curry *et al.*, 2005; Hurst 2007).

2.4 Ontogenetic shifts in the diets of 0+ fishes

According to the theory of saltatory ontogeny (Balon 1979), during their first year of life, fishes with indirect development (i.e. those with a larval period) pass through a sequence of developmental steps characterised by biochemical, physiological, morphological, ethological and ecological traits that result in important shifts in resource use. With respect to the foraging ability of 0+ fishes, the key attributes are those pertaining to enhanced swimming performance, namely development of the fins, and improved vision (Wanzenböck & Schiemer 1989). Once fins are fully developed, associated improvements in swimming performance allow broadening and diversification of diet spectra, effectively increasing the efficiency of the fish in capturing prey. Similarly, improved vision increases the search volumes of 0+ fish, effectively increasing prey availability (Schiemer *et al*., 1989; Wanzenböck & Schiemer 1989; Keckeis & Schiemer 1992; Gliwicz 2001; Nunn *et al*., 2012).

First-feeding is considered a critical period in the early life of fish (Kamler 2002), with zooplankton serving as a vital food resource for the survival of newly-hatched fish of many species (Whiteside *et al*., 1985; Wanzenböck & Schiemer 1989). Poor feeding success of first-feeding larvae may result from low density of small, non-elusive/evasive prey (Krebs & Turingan 2003). After hatching, fish larvae grow rapidly, their mode of swimming changes and so does their food spectrum (Mark *et al*., 1987). Although many fish species are zooplanktivorous at the onset of exogenous feeding, distinct shifts in their foraging biology may occur during development (Werner & Gilliam 1984; Wanzenböck & Schiemer 1989; Anneville *et al*., 2007; Dauwalter & Fisher 2008; Nunn *et al*., 2008b; De Brabandere *et al*., 2009; Grohs *et al*., 2009; Specziár & Rezsu 2009). A general sequence of ontogenetic shifts in resource use often exists for the first weeks after hatching (Mark *et al*., 1987; Garner 1996a; Mann *et al*., 1997; Nunn *et al*., 2007b). Newly-hatched individuals of many fish species prey mainly upon pelagic rotifers and phytoplankton, because of their inability to catch and handle larger prey (Mark *et al*., 1987; Mark *et al*., 1989; Treasurer 1992), with microcrustaceans and chironomid larvae becoming more frequent in the diet as the fish develop (Broughton &

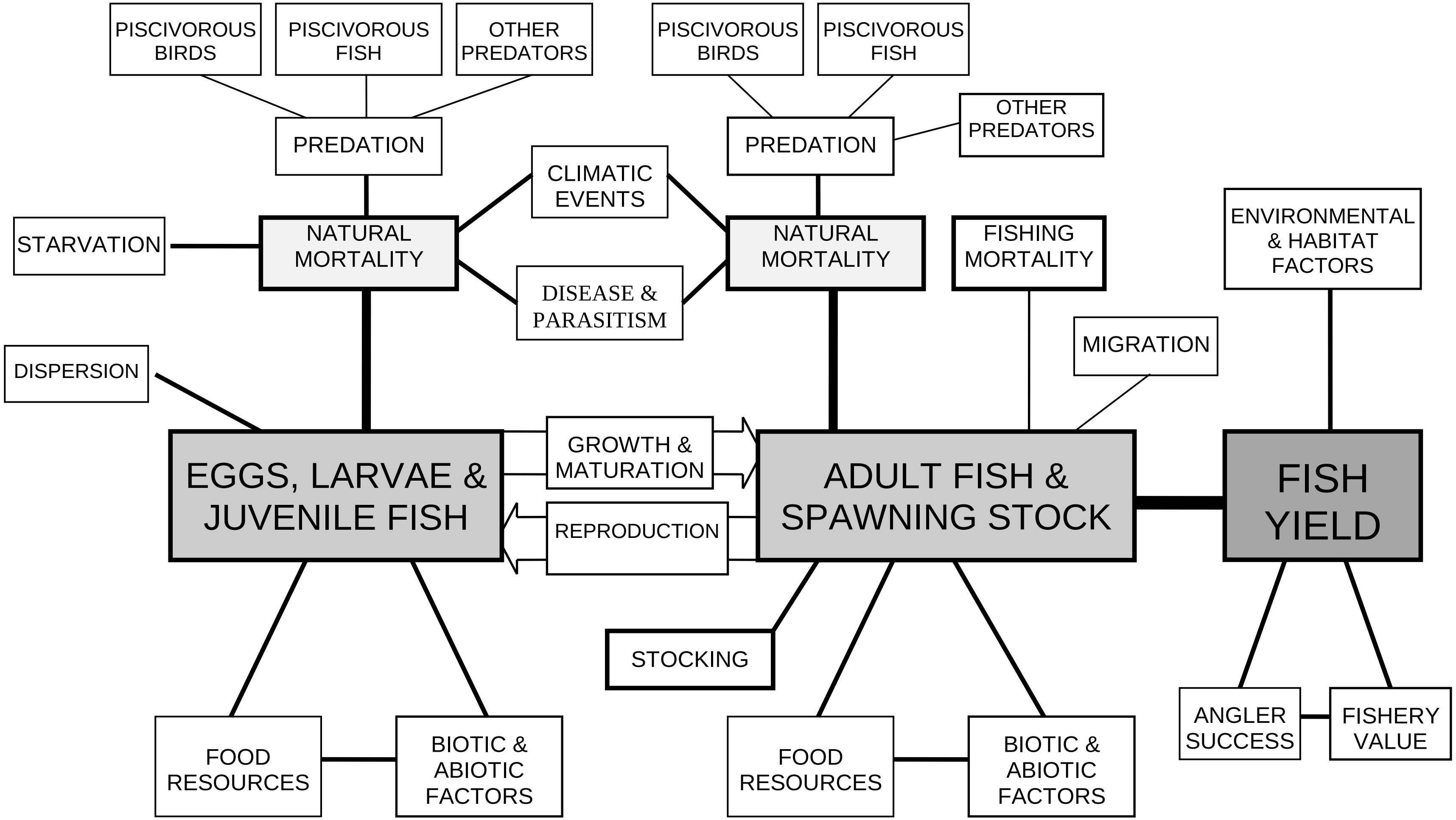


Figure 2.1. The complexity of the factors that influence fish populations in rivers (Cowx 2001).

Jones 1978; Garner 1996a; Lightfoot & Jones 1996; Mann *et al*., 1997). Nunn *et al*., (2007b) differentiated two main ontogenetic shifts in diet, corresponding with the transition from finfold to finformed larvae, and from the larval to the juvenile period.

2.5 Interspecific diet similarity in 0+ fishes

Dietary overlap can have implications for growth, survival and recruitment success. Interspecific overlap is often greatest among young larvae, suggesting that the fish are still morphologically and behaviourally undifferentiated during this period (Garner 1996a). Although the diets of the young larvae of many species are similar, they do not necessarily compete for resources, since many of them do not overlap spatially and temporally. In the River Trent, for example, dace hatch approximately two months earlier than chub, and by the time chub hatch, all dace are juveniles: dace and chub larvae, therefore, do not compete for resources (Nunn *et al*., 2007b). Similarly, barbel larvae rarely occur in the same habitats as tench larvae, and overlap between benthivorous and planktivorous or neuston-feeding species is likely to be limited (Nunn *et al.,* 2007a).

Many cyprinid larvae form mixed species shoals in the littoral zone after hatching (Rheinberger *et al*., 1987; Garner 1996a), and dietary overlap can be high (Matěna 1998). Overlap in diet is generally greatest between ecologically-similar species (Garner 1996a). The diets of dace larvae, for example, frequently overlap with those of sympatric roach larvae, and the diets of juvenile dace, roach and chub often overlap (Nunn *et al*., 2007b). In the Římov Reservoir, Matěna (1998) found that the diets of juvenile perch, zander, ruffe, roach and bream overlapped significantly, resulting from high preference for *Daphnia* spp., and it was assumed that there was strong interspecific competition for food resources. Overlap does not necessarily imply competition, however, since competition only occurs in situations where demand for a particular food item exceeds the immediate supply (Zaret & Rand 1971). Nunn *et al*., (2007b), for example, found that dietary overlap was greatest among 0+ fishes feeding upon rotifers and aufwuchs, which were invariably the most abundant food categories.

Interspecific competition often causes a narrowing of the niche widths of the competing species along one or more niche dimensions (Wootton 1990). Zaret & Rand (1971), studying competition in tropical stream fishes, demonstrated a change from distinct food niches during the dry season (limited food supply) to widely overlapping niches in the wet season (abundant food supply). Similarly, in the absence of roach, 0+ perch feed mainly upon planktonic cladocerans, whereas in the presence of roach they consume copepods and macroinvertebrates, and have lower growth rates (Persson

1987; Persson & Greenberg 1990). Likewise, Cowx (1989) found that where roach and dace coexisted in the River Exe, growth rates of one or both species were reduced, possibly due to reductions in feeding diversity. Matěna (1995) observed that resource partitioning was a characteristic feature in the littoral 0+ fish assemblages of the Římov Reservoir, with perch favouring pelagic copepods, and roach consuming periphytic organisms, such as chironomid larvae. The only significant overlap in diet occurred when *Polyphemus* sp. was eaten, when it formed up to 90% of the diet of both roach and perch, in spite of its low abundance in the zooplankton.

2.6 Prey selection by 0+ fishes

Foraging theory has received considerable attention across a diverse range of fauna over the last four decades (see Pyke 1984; Sih & Christensen 2001), including some classic work on fishes (e.g. Ivlev 1961; Werner & Hall 1974). Most of the work on larval and 0+ juvenile fishes has been conducted in either the marine environment (e.g. Fortier & Harris 1989; Gaughan & Potter 1997; Pepin & Penney 1997) or lakes and reservoirs (e.g. Mark *et al*., 1987; Bremigan & Stein 1994; Mayer & Wahl 1997; Matěna 1998), with rivers receiving comparatively little attention especially in the UK (Braga *et al*., 2012).

Optimal foraging theory predicts that predators should select prey that maximise the energetic gains available in relation to the energetic costs of capturing, ingesting and digesting the prey (Pyke 1984). For a fish predator, the energetic content of a given prey type increases with prey size, but there is also an associated increase in handling time (Gill & Hart 1994). Handling times also vary between prey taxa, although few studies have succeeded in isolating the effects of taxa (e.g. morphology, behaviour) and size in prey selection by 0+ fishes (Winfield *et al*., 1983; Ghan & Sprules 1993). Thus, prey selection is determined by the relative profitabilities of particular types and sizes of prey, with maximal profitabilities conferred by prey types and sizes that provide the maximum energy gain per unit handling time (Stephens & Krebs 1986). A key factor in prey selection is the relative availability (≈ search time) of particular prey. For example, Townsend *et al.,* (1986) observed that juvenile roach fed predominantly on planktonic cladocerans in late spring and summer, and non-planktonic cladocerans for the remainder of the year, with the switch from planktonic to non-planktonic cladocerans coinciding with low availabilities of planktonic prey (<40 plankters L-1). Similar responses have been observed for other fish species, such as perch (Persson & Greenberg 1990; Mehner *et al*., 1995) and yellow perch (*Perca flavescens* (Mitchill)) (Wu & Culver 1992). Another factor influencing prey selection is the dynamic change in the effective profitability of particular prey types and sizes in relation to fish gut fullness

(Gill & Hart 1994; Wanzenböck 1995). In a laboratory experiment, Gill & Hart (1998) demonstrated that three-spined stickleback (*Gasterosteus aculeatus* L.) fed upon prey of a specific size until the stomach was full; thereafter, similar-sized prey were rejected in favour of smaller prey.

The diet of freshwater fish in the first weeks of life can include both an increase in prey size and changes in prey species as the fish grow and develop (Ghan & Sprules 1993). Gape has often been identified as a key morphological trait limiting prey size of fish that swallow prey whole (e.g. Dąbrowski & Bardega 1984; DeVries *et al*., 1998; Mehner *et al.,* 1998; Sabatés & Saiz 2000; Krebs & Turingan 2003; Truemper & Lauer 2005; Makrakis *et al*., 2008).The small gape of 0+ fishes limits their prey size, yet within constraints set by gape, food eaten influences growth and, ultimately, survival (Bremigan & Stein 1994). Mayer & Wahl (1997) demonstrated that young walleye (*Sander vitreus* (Mitchill)) fed selectively and that, for at least some size classes, the selected prey conferred benefits in terms of greater growth or survival. Similarly, Graeb *et al*., (2004) found that fish size and prey availability affected the growth, survival, prey selection and foraging behaviour of yellow perch larvae.

The interactions between the relative importance of taxa and size of prey may be subtle. Gliwicz *et al*., (2004) found that, when studying smelt (*Osmerus eperlanus* (L.)), selection was similar for small- and large-bodied prey, but lower for elongated- (*Daphnia* spp., *Diaphanosoma* spp.) than for compact-bodied (*Bosmina* spp., *Chydorus* spp.) species. Furthermore, smelt selected later instars and females with the greatest clutches. Utilisation of cladocerans as a common food resource during the late larval and early juvenile periods of many freshwater fish species probably occurs as a result of their ease of capture compared with copepods (Winfield *et al*., 1983; Hammer 1985), even though the latter are often numerically abundant and of greater calorific value (Manatunge & Asaeda 1999; Mitra *et al*., 2007). 0+ juvenile roach and bream both find copepods more difficult to capture than cladocerans (Winfield *et al*., 1983; Winfield & Townsend 1988; Matěna 1998), since copepods are faster moving than cladocerans and have sensory hairs that enable them to detect the shock waves of approaching fish. Nevertheless, some studies, although almost exclusively of non-cyprinids, have reported a low importance of daphnids as food and a higher preference for copepods (e.g. Guma'a 1978; Treasurer 1990), perhaps because copepods, especially egg-bearing females, are more visible to young fish than cladocerans (Ghan & Sprules 1993) or due to the small sizes of fish investigated (Mehner *et al*., 1998).

A general sequence of ontogenetic shifts in food consumption is often reflected in the electivity indices for particular prey types. For example, Nunn *et al*., (2007a) noted that selection of rotifers and copepod nauplii by 0+ fishes declined with development, whereas cladocerans and copepods generally increased. This can be partly attributed to the restrictions imposed by the gape of 0+ fishes. However, certain taxa were consistently selected over others of the same size. For example, the majority of young cyprinid larvae selected rotifers over similar-sized copepod nauplii. Ghan & Sprules (1993) observed a similar phenomenon in young burbot (*Lota lota* (L.)) larvae, with the globular rotifer *Asplanchna* sp. selected over spined rotifers and copepod nauplii, perhaps due to differences in morphology or behaviour between taxa; copepod nauplii are faster moving than rotifers, while the protuberances of spined rotifers may hinder fish attempting to prey upon them and increase handling times. Similarly, in the marine environment, Pepin & Penney (1997) observed that the larvae of almost all of the 11 fish species they studied selected the nauplii and copepodites of calanoid copepods over those of cyclopoid copepods. As with copepods and cladocerans, this was attributed to differences in swimming behaviour between the prey, with calanoid copepods swimming more smoothly and consistently than cyclopoid copepods, making their capture easier.

In contrast to larvae, for which there was a positive relationship between prey (zooplankton) and gape size, that no relationship was found for 0+ juvenile fishes in an earlier study on the River Trent (Nunn *et al*., 2007a) suggests that the size of zooplankton consumed was limited by the small size of available zooplankton, rather than gape. Indeed, this supposition was supported by the fish consuming large benthic invertebrates. Similarly, Krebs & Turingan (2003) found little evidence that the size of prey consumed by red drum (*Sciaenops ocellatus* (L.)) larvae and juveniles was closely related to gape. Notwithstanding, variations in relative size-selectivity between larval and 0+ juvenile fishes may be related to ontogeny. For example, Wanzenböck (1995) found that the optimal prey size for 15 mm roach and bleak was ~100% of their gape width, but ~50% of the theoretical maximum for 40 mm fish.

Since the size distribution of zooplankton available to larval fishes influences their foraging success, growth and survival, an optimal prey size for larval fish may exist (Bremigan & Stein 1994). In the River Trent, the majority of fish consumed zooplankton substantially smaller than the maximum theoretically possible inferred from their gape (Nunn *et al*., 2007a). Similarly, Mehner *et al*., (1998) found that modal lengths of *Daphnia* spp. consumed by perch were substantially smaller than the fish were capable of consuming according to their gape size. Indeed, Scott (1987) found that juvenile dace and roach preferred prey approximately 60% of their maximum gape. The preference for prey that are smaller than the maximum theoretically ingestible is probably due to the increased handling time required for large prey (Wanzenböck 1995).

2.7 Spatial variations in the diets of 0+ fishes

The habitats used by fishes can have an important influence on prey availability and, therefore, their diets (Fig. 2; Garner 1998; Grenouillet *et al*., 2001a). Riverine zooplankton communities are invariably dominated by rotifers and small crustaceans throughout the year, with no marked development of large-bodied cladoceran and copepod populations (Basu & Pick 1996; Viroux 1997). By contrast, areas of reduced flow invariably provide superior conditions for plankton development due to increased water retention times, and may be important sources of drifting material in the main river channels (Bass *et al*., 1997a; Spaink *et al*., 1998). In addition, floodplain waterbodies frequently support substantial populations of aquatic macrophytes, which provide habitat for phytophilic zooplankton and refuge for planktonic species from fish predation (Northcott 1979; Garner *et al*., 1996; Bass *et al.,* 1997b; Mann *et al*., 1997; Stansfield *et al*., 1997; Gozlan *et al*., 1998; Grenouillet *et al.,* 2000, 2001a; Grenouillet & Pont 2001; Grenouillet *et al.,* 2002; Okun & Mehner 2005a, b; Cremona *et al*., 2008). Furthermore, plants invariably support greater numbers of species of animals, in larger numbers and with greater ranges of body size, than areas of open water (Northcott 1979; Whiteside *et al*., 1985).

A number of studies have demonstrated that zooplankton densities, notably of large-bodied cladocerans, are significantly higher at floodplain sites than at main river sites (Bass *et al*., 1997a; Spaink *et al*., 1998). Indeed, Nunn *et al*., (2007c) observed that densities of rotifers, bosminids, chydorids, daphnids, cyclopoids and copepod nauplii were all significantly higher at floodplain sites than at main river sites. Daphnids, for example, were recorded at maximum densities of over 900 L^{-1} at floodplain sites, compared with <10 L^{-1} at main river sites. Zooplankton populations often persist for longer in floodplain waterbodies than in lotic environments. For example, Bass *et al*., (1997a) found that whilst zooplankton populations declined after mid-summer in the River Great Ouse, high populations of rotifers and microcrustaceans persisted later into the year in an adjacent marina. Furthermore, Mann *et al*., (1997) noted that the switch in the diet of 0+ roach from zooplankton to aufwuchs observed in the River Great Ouse did not occur in an adjacent marina, where planktonic cladocerans dominated the diet. Similarly, Nunn *et al*., (2007b) observed that, compared with the River Trent, the switch to aufwuchs was delayed in a waterbody connected to the river, where large quantities of zooplankton (especially *Bosmina* sp. and cyclopoid copepods) were available later into the summer. Notwithstanding, comparatively little research has been conducted into the influence of spatial (within and between catchment) variations in prey availability on the diet composition and prey selection of 0+ fishes.

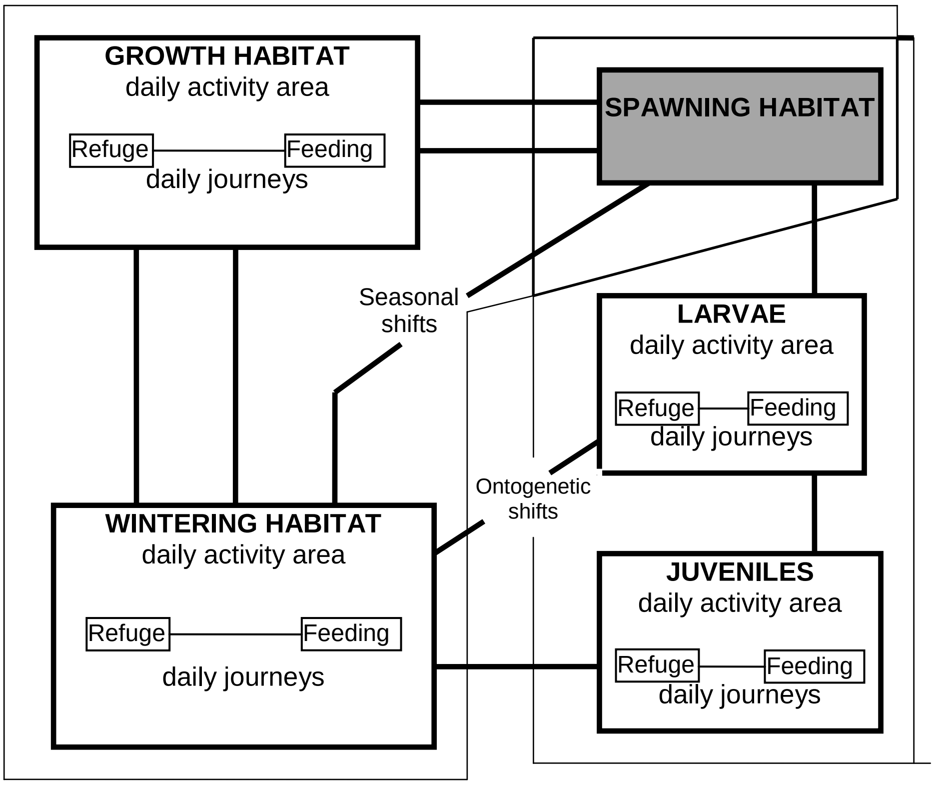


Figure 2.2. The functional unit concept for fish habitat requirements (Cowx 2001).

2.8 Temporal variations in the diets of 0+ fishes

Fishes may exhibit diel variations in feeding activity and diet composition (Johnson & Dropkin 1993; Haertel & Eckmann 2002; Alajärvi & Horppila 2004; Vašek & Kubečka 2004; Copp *et al*., 2005; Okun *et al*., 2005; Copp 2008; Hautala 2008; Kratochvil *et al.,* 2008; Medeiros & Arthington 2008). For example, Mills *et al*., (1985) observed that daytime gut contents of dace larvae averaged 3-4 times the volume present during 02.00-06.00 hours. Similarly, Garner (1996b) observed that the number of prey items and taxa found in the guts of 0+ juvenile roach and chub decreased at night. Both roach and chub consumed significantly fewer planktonic prey at night, whereas aufwuchs tended to be more abundant in the diet at night. Likewise, Horppila (1999), studying adult roach, found that zooplankton were consumed mostly during the day, whereas zoobenthos, plants and detritus were mainly consumed at night. By contrast, Weatherley (1987) reported that, in the first two months of life, peak gut fullness of dace occurred at night, and Winfield & Townsend (1988) observed that young bream largely feed in the hours of darkness. Diel shifts in diet composition are often linked to either changes in habitat use or prey availability (Bohl 1980; Gliwicz & Jachner 1992; Copp & Jurajda 1993; Jacobsen & Berg 1998; Hansen & Closs 2005). Although a substantial amount of research has investigated the diets of 0+ fishes during the summer (Mark *et al*., 1987; Mark *et al*., 1989; Garner 1996b, a, 1998; Nunn *et al*., 2007b, a), there is a lack of comparable information for the autumn and winter periods (but see Nunn *et al*., 2008a). Winter diet may be of particular importance as overwinter survival is often positively correlated with fish condition and food intake (Griffiths & Kirkwood 1995; Kirjasniemi & Valtonen 1997a; Pangle *et al*., 2004; Hurst 2007). In addition, little is known about the influence of seasonal and annual variations in prey availability on the diet composition and prey selection of 0+ fishes, and the interacting effects of temporal and ontogenetic factors.

2.9 Recommendations

The review of the literature identified a number of gaps in the knowledge of the feeding ecology of larval and 0+ juvenile fishes, some of which are recommended as areas for further research such as using RNA-DNA ratio analysis to determine the condition of fish:

- **Nutritional condition** – use RNA-DNA ratio analysis to compare the nutritional condition of cultured and wild fish larvae. It may also be possible to use multivariate morphometric methods based on Procrustes analysis. Where possible, nutritional condition should be linked to food availability/exploitation.

Many areas were discussed and explored in this thesis, such as the ones described below:

- **Spatial variations in the diets of 0+ fishes** – comparisons of diet composition, prey selection and food (e.g. zooplankton, benthos, aufwuchs) availability in various habitat types (e.g. contrasting river types, main river and floodplain areas, areas with and without aquatic macrophytes, and within beds of different macrophyte species). Spatial differences in diets should be examined for affects on growth and condition, enabling key foraging habitats to be identified in terms of both food resources and nutrition.

- **Temporal variations in the diets of 0+ fishes** – comparisons of feeding activity, diet composition, prey selection and food availability on a diel, seasonal and annual basis. Temporal variations in diets should be examined for the influence of habitat and ontogeny.

- **Ontogenetic shifts in the diets of 0+ fishes –** comparisons of diet between various developmental steps of key fish species, to investigate whether there are differences in diet that can be linked to ontogeny. This should include an assessment of the relative importance of ontogeny and food availability in the diet composition of 0+ fishes.

- **Interspecific similarity in the diets of 0+ fishes –** analysis of dietary overlap between species, to identify the species and developmental steps most likely to compete for food resources. This could include the use of experiments to examine the influence of interspecific interactions/competition on the diet composition, prey selection, growth and condition of fishes in single- and mixed-species enclosures.

- **Prey selection –** assessment of the relative importance of taxa- and size-specific characteristics in the prey selection process of various species and developmental steps.

CHAPTER THREE

TEMPORAL VARIATIONS IN FORAGING ECOLOGY OF 0+ RIVERINE FISHES

3.1 INTRODUCTION

Temporal variations in prey availability can influence the foraging ecology (diet composition and prey selection) of 0+ fishes, which in turn could affect their growth, survival and recruitment success (Cryer *et al.*, 1986; Bass *et al.*, 1997; Barriga *et al.*, 2011; Nunn *et al*., 2012). Temporal variations in prey availability may occur for a variety of reasons, including diel, seasonal and annual changes in environmental conditions, such as water temperature, oxygen saturation, light penetration and hydrological regime (flow and water depth), as well as habitat type and availability (May, 1983; Andrew & Fitzsimmons, 1992; Reckendorfer *et al.*, 1999; Baranyi *et al.*, 2002; Viroux, 2002).

Populations of many zooplankton species, for example, vary on a seasonal basis, frequently related to fluctuations in food availability, predation and environmental conditions (Wilhm *et al.*, 1977; Gosselain *et al.*, 1994; van Dijk & van Zanten, 1995; Kobayashi *et al.*, 1998; Wolfinbarger, 1999; Viroux, 2002; Talling, 2003). Well-documented examples include planktonic cladocerans, such as *Daphnia* spp., which usually increase in abundance during the spring before experiencing population ‘crashes’ in mid-summer (Hülsmann *et al.*, 1999; Benndorf *et al.*, 2001; Hülsmann, 2003; Wagner *et al.*, 2004). Comparable fluctuations in abundance or biomass are also a feature of many benthic invertebrate species, as well as phytoplankton, periphyton and macrophytes. River discharge is a key factor controlling the extent and timing of riverine phytoplankton and zooplankton populations, with reductions in abundance frequently coinciding with increases in river discharge (Bass *et al.*, 1997; Marker & Collett, 1997; Reckendorfer *et al.*, 1999; Baranyi *et al.*, 2002; Viroux, 2002). Diel fluctuations in zooplankton availability also occur due to a number of factors, such as migration to avoid predation or to improve feeding efficiency (Dodson, 1990; Loose & Dawidowicz, 1994; Burks *et al.*, 2002). In deep waterbodies, for example, many zooplankton species exhibit diel vertical migrations, seeking refuge in deep water from fish predation during daylight and grazing upon phytoplankton near the water surface at night (Gliwicz, 1986). By contrast, in shallow waterbodies zooplankton sometimes undertake horizontal migrations (Lauridsen *et al.*, 1996; Nunn *et al*., 2012).

In spite of the prevalence and magnitude of temporal variations in prey availability, relatively few studies have examined their effects on the feeding ecology of 0+ fishes. The aim of this study was thus to investigate temporal variations in the foraging ecology of 0+ fishes. Specifically, the objectives were to examine: (1) diel variations in prey availability, feeding activity, diet composition and prey selection of larval and 0+ juvenile fishes; and (2) seasonal variations in the diet composition and condition of larval and 0+ juvenile fishes. It was predicted that prey availability, feeding activity, diet composition and prey selection would vary temporally, which would be reflected in the condition of the 0+ juvenile fishes. This information will improve understanding of the temporal feeding behaviour and ecology of fishes during early development, which could be useful in river rehabilitation schemes and management plans, as well as aquaculture facilities, to enhance fish population abundance and community structure.

3.2 MATERIALS AND METHODS

3.2.1 DIEL VARIATIONS IN THE FORAGING ECOLOGY OF 0+ FISHES

Diel variations in the foraging ecology of 0+ fishes were examined in Colwick Marina, which is connected to the River Trent, Nottinghamshire (Plate 3.1). The River Trent (Fig. 2.1) is 274 km long from its source on the Staffordshire Moorlands to its confluence with the Humber Estuary, and is joined by a number of major tributaries in the central Midlands (Cowx, 1991). The Trent is the third largest river in England and Wales, with a catchment area of approximately 10 500 km^2. The lower Trent has been channelised in many areas and impounded by a number of large weirs and sluices, such as Holme Sluices and Cromwell Weir. Water depths are artificially maintained for the transport of freight and recreational boating by dredging, and parts of the floodplain have been claimed for urban development (Nunn, 2005).

The River Trent had abundant and well-renowned fish stocks, including Atlantic salmon (*Salmo salar* L.) (Jacklin, 1996), prior to the Industrial Revolution. Fish stocks began to decline within the river system because of poor water quality linked to reduced dissolved oxygen levels (Jacklin, 1996). A number of measures (diversion of industrial effluents and improved sewage treatment) by authorities such as the water companies have led to an improvement in water quality and, in turn, an improvement in the fish populations (Jacklin, 1996). The fish community of the lower Trent is characterised by typical lowland species such as roach, bream, chub, perch, bleak, dace and gudgeon (Whitton & Lucus, 1997, Tewson, *pers. obvs.*).

Colwick Marina (surface area ~1 ha) is located on the left-hand bank of the River Trent, approximately 300 m upstream of Holme Sluices, and is connected to the main river by a 30-m long, 20-m wide channel. The sampling area was situated in the south-eastern corner of the marina. This site was chosen as the fish populations there are representative of the river system and 0+ fishes use the area as refuge from the main river flow. Water depths in the sampling area varied from centimetres in the margins to approximately 1.2 m, and the gradient was steady (approximately 1:10). The substratum consisted of imprinted concrete, with an ephemeral covering of silt and filamentous algae, with gravel and silt to the left and right of the slipway, respectively. Aquatic vegetation (mainly sweet flag, Canadian pondweed (*Elodea canadensis* Michx.), reed sweet-grass, common duckweed (*Lemna minor* L.) and branched bur-reed) were present either side of the slipway. Riparian vegetation was limited to typical pioneer species and was mown periodically, although a number of small sallow (*Salix caprea* L.), osier (*Salix viminalis* L.) and alder (*Alnus glutinosa* L.) were present. Directional water movement within the marina was negligible.

A micromesh seine net (25 m long by 3 m deep, 3 mm hexagonal mesh) was used to capture fish every 3 h over a 24-h cycle on 3/4, 17/18 June and 1/2 July 2009, and 19/20 May, 2/3, 16/17, 30/1 June/July and 14/15 July 2010. The net was walked out into the river from the bank by two people, when approximately 5 metres out one person created a corner for the net by remaining stationary and the pulling the rest of the net from the bank, while the second person walked parallel to the bank and back in using the whole of the net to create a rectangle shape. The net was then pulled in using the leads first to prevent any fish escaping. A representative subsample of fish was then taken from the seine net using a hand net and the rest of the fish were returned safely to the river. Additional samples of the smallest larvae were obtained using a fine-meshed hand-net by walking with the net through the marginal areas of the sample site, as it was thought that the smaller larval stages of fishes may be under represented in the seine net. All larval and 0+ juvenile fishes were immediately preserved in 4% formalin solution. A 3-h interval between samples was considered sufficient for gut passage given the water temperature and sizes of the fish (Persson, 1986; Garner, 1996b; Horppila, 1999). Five of the samples were collected in daylight and three were collected at night.

Zooplankton populations were surveyed via five replicate samples collected concurrently with the fish samples, using a 10-L bucket (i.e. 50 L in total). Each zooplankton sample was sieved through a 100-μm-meshed net and preserved in the field using 4% formalin solution, and later stained with Rose Bengal to facilitate observation of small transparent organisms. Whilst the mesh size of the net likely underestimates the densities of the smallest rotifers, it was considered satisfactory for the sizes eaten by 0+ fishes (Bottrell *et al.*, 1976; Bass *et al.*, 1997).

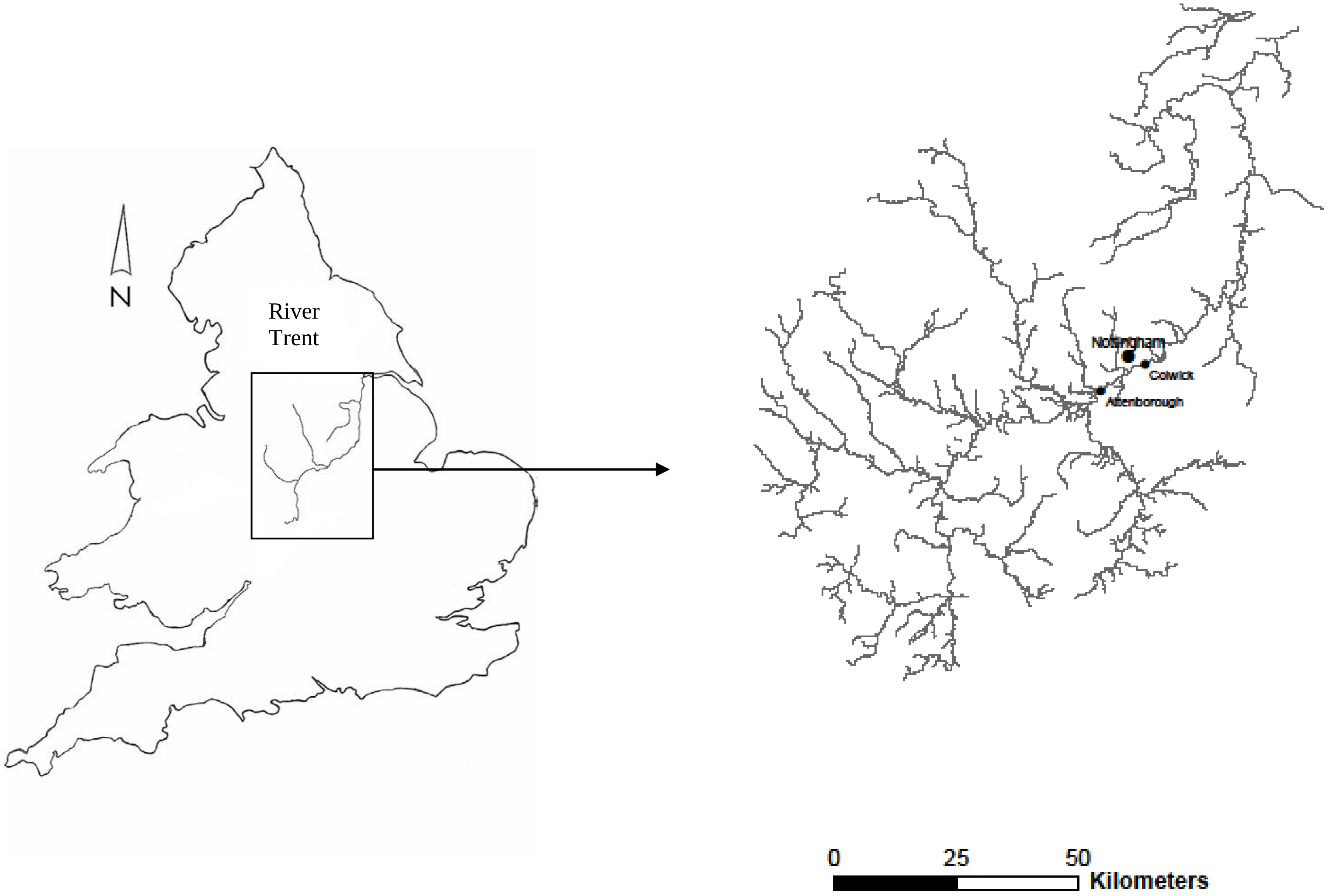


Fig. 3.1. Site location maps for Attenborough Nature Reserve and Colwick Marina.

Plate 3.1. Colwick Marina showing netted area. (——) Source: www.google.com/maps

In the laboratory, fish were identified to species (Pinder, 2001) and measured for total length (TL, nearest 0.1 mm). It can be deceptive to classify 0+ fishes based solely on length, as individuals of similar length may display differences in development (Copp, 1990a, b). For this reason, fish were separated into the following six larval (L1-L6) steps and one 0+ juvenile (J) step based on development rather than size (Copp, 1990a; Peňáz, 2001). Note, no finfold (larval steps 1-3) fishes were caught in this study only finformed (larval steps 4-6) and 0+ juveniles (see Chapter 1).

For each sampling occasion, the contents of the entire gastrointestinal tract were removed from a minimum of five specimens of each available ecospecies (see Chapter 1) of roach and perch for each sampling occasion (roach n = 95, perch n = 101). These species were chosen as they were the most abundant in all samples. Discrete food items (e.g. benthic invertebrates and zooplankton) were identified to the lowest practicable taxonomic level using various keys (e.g. Scourfield & Harding, 1966; Fitter & Manuel, 1986) and enumerated, while aufwuchs (the periphyton and associated microfauna that grow on underwater surfaces) was recorded as percent volume and converted to ‘number’ (to ensure that all prey categories were recorded using a common unit and scale) using the relationship between percent volume of aufwuchs and the number and percent volume of ‘non-aufwuchs’:

N aufwuchs = (N non-aufwuchs / V non-aufwuchs) x V aufwuchs

where N and V are the number and percent volume, respectively, of aufwuchs and non-aufwuchs in each fish (Nunn *et al.*, 2007a).

In the laboratory, each zooplankton sample was made up to 100 ml with 4% formalin solution and thoroughly mixed before withdrawing a 500 μl sub-sample with a wide-bore, automatic pipette. The sub-sample was emptied into a Sedgewick Rafter counting chamber, and all organisms were identified to appropriate taxonomic groups (Johnson, 1952; Scourfield & Harding, 1966; Harding & Smith, 1974; Pontin, 1978; Fitter & Manuel, 1986) and enumerated using a binocular microscope. Cladocerans, for example, were identified to either species or genus, while other taxa were typically identified to lower levels of taxonomic resolution. Three sub-samples were analysed for each zooplankton sample.

Diel variations in feeding activity were assessed using the points method (Hynes, 1950; Hyslop, 1980) with each fish being allocated points according to the fullness of its gut (0 points = empty gut, 2 = ¼ full, 4 = ½ full, 6 = ¾ full, 8 = completely full, 10 = distended), for all surveys combined in each year. Feeding activity was then compared between day and night using either independent samples t-tests or Mann-Whitney U tests (Dytham, 2003).

The number of each taxon in each sub-sample of zooplankton was used to calculate the mean (± SD) density of zooplankton (plankters L^{-1}) on each sampling occasion. Fish density was calculated by dividing the number of fishes caught by the area (96 m^2) sampled. Dietary and zooplankton data were used to calculate diel variations in the relative abundance (percent abundance) of particular taxa in the diet and in the zooplankton by dividing the number of a particular taxon by the total number of taxa found within the diet and then multiplying this by 100. Prey selection was investigated using the relativized electivity index (*E**) of Vanderploeg & Scavia (1979) comparing all surveys combined. Lechowicz (1982) reviewed the sampling characteristics of a range of electivity indices, and concluded that the relativized electivity index (*E**) of Vanderploeg & Scavia (1979) provides the single most useful index. *E** is calculated as:

$$E_i^* = \frac{W_i - \left(\frac{1}{n}\right)}{W_i + \left(\frac{1}{n}\right)}$$

where n is the number of prey types available and W_i is estimated by:

$$W_i = \frac{\left(\frac{r_i}{p_i}\right)}{\sum\left(\frac{r_i}{p_i}\right)}$$

where r_i and p_i are the percentage of prey type i in the diet and in the environment, respectively. E^* ranges from –1 to +1, with negative values indicating avoidance, positive values indicating selection, and 0 representing no preference. Occasionally a prey category occurred in the diet but not in the corresponding plankton samples. When such prey comprised ≥5% of the diet, their electivities were set at +1 since they were ingested despite not being detected in the environment (Ghan & Sprules, 1993; Nunn *et al.*, 2007d). When the relative proportion of such categories in the diet was <5%, electivity was set at 0.

Diel variations in fish species composition were also investigated by calculating the mean percent abundance of all species over each 24-h period. Fish size structure was assessed using length-frequency histograms and then compared between day and night samples using two-sample Kolmogorov-Smirnov tests. Density was also calculated for all species and ages of fish combined to identify any diel fish movement in and out of the littoral zone. The mean (± SD) length, density and relative abundance of 0+ and >0+ pike (*Esox lucius*, L.) were also calculated to investigate diel variations in predation risk, as these were the main predators of 0+ fishes found in the sampling area.

Although there were obvious differences in the abundance and size of pike between day and night, they were not statistically significant, probably due to the unequal number of day and night samples. The densities and mean lengths were therefore proportionalised and normalized by arcsine transformation, and mean densities and lengths were compared between day and night using one way Analysis of Variance (ANOVA) followed by a Games-Howell post hoc test (equal variances not assumed) (Fowler & Cohen, 1992). Length distributions between day and night were also compared using two-sample Kolmogorov-Smirnov tests).

3.2.2 SEASONAL VARIATIONS IN THE FORAGING ECOLOGY OF 0+ JUVENILE FISHES

Seasonal variations in the foraging ecology of 0+ juvenile fishes were examined by analysing the diet composition and condition of 0+ juvenile roach and bream in the River Trent at Attenborough (Fig. 3.1) over the summer, autumn and winter of 2010/11. These species were chosen as they were the most abundant in the samples; the study was conducted at Attenborough because sufficient fish were captured for analysis in all seasons (few fish were captured from Colwick Marina in the winter). The site at Attenborough Nature Reserve was situated on the left-hand back of the River Trent and has a natural bank, a width of approximately 100 m and a maximum depth of 3–4 m. The substratum mainly consists of sand and gravel, with macrophytes including sweet flag (*Acorus calamus* L.), reed sweet-grass and branched bur-reed (*Sparganium erectum* L.) (Nunn *et al.,* 2007c). Fish were captured approximately monthly between June and February using a micromesh seine net (25 m long by 3 m deep, 3 mm hexagonal mesh size) and preserved in 4% formalin solution. When available, the contents of the entire gastrointestinal tract were removed from a minimum of five individuals of each fish species for each sampling occasion (roach n = 66, SL range 18-56 mm; bream n = 58, SL range 20-69 mm). Gut contents were analysed as described previously (Section 3.2.1). Gut fullness (≈ feeding activity) was assessed for individual fish using the points method (Section 3.2.1).

Summer (June-August), autumn (September-November) and winter (December-February) diet composition was analysed using the graphical method of Costello (1990), as modified by Amundsen *et al*. (1996). This combines prey-specific abundance (the percentage a particular prey taxon comprised of all prey items, in only those fish in which that prey occurred) and frequency of occurrence (the number of fish in which a particular prey taxon occurred, divided by the total number of fish in which prey were present), and allows prey importance and feeding strategy to be explored. Prey points located at the upper left of the plots indicate specialisation by individual fish, and those in the upper right represent specialisation of the fish population. Points located in the lower right corner represent prey that has been eaten by most fish in small numbers, and those in the lower left represent rare prey. A more detailed explanation of interpretation of the plots can be found in Amundsen *et al*. (1996).

A Bray-Curtis similarity matrix (Czekanowski, 1913; Bray & Curtis, 1957) was calculated in the PRIMER (Plymouth Routines In Multivariate Ecological Research) statistical package, using the mean percent abundance of each zooplankton taxon in on each sampling occasion. The similarity matrices were then submitted to analysis of similarity (ANOSIM) to investigate monthly variations in the diet composition of 0+ juvenile roach and bream (Clarke & Warwick, 2001; Zuur *et al*., 2007). The ANOSIM test statistic (R) ranges from 0 (no differences in diet between months) to 1 (all inter-monthly dissimilarities in diet are larger than any intra-monthly dissimilarities). The Bray-Curtis similarity index (C_z) represents the overall similarity between each pair of samples, taking the abundance of all taxa into consideration, and is calculated as:

$$C_z = 2W/(a + b)$$

where *W* is the sum of the lesser percent abundance value of each taxon common to two samples (including tied values), and *a* and *b* are the sums of the percent abundances of taxa in samples *a* and *b*, respectively. The index ranges from 0 (no taxa in common) to 1 (identical composition). In addition, monthly variations in the diversity and evenness of 0+ juvenile roach and bream diets were calculated by applying the Shannon-Wiener diversity index (*H'*) and evenness (J') (Washington, 1984).

Gut fullness data were tested for normality and homogeneity of variances using one-sample Kolmogorov-Smirnov and Levene tests, respectively, and mean feeding activity was compared between summer, autumn and winter by one-way analysis of variance (ANOVA) followed by Games-Howell *post hoc* tests (Dytham, 2003). Fish were weighed (nearest 0.01 mg) by blotting of the excess moisture with tissue and putting them on a digital scale, then measured (TL). The weight-length relationships were then used to calculate the relative body condition factor (*K*) of roach and bream (Bagenal & Tesch, 1978) calculated using:

$$K= \frac{W}{\hat{W}}$$

where *W* is the observed weight of each individual and $\hat{W}$ is the expected weight using the weight-length relationships of roach and bream in the single-species enclosures. At the population level, the average *K* indicates whether a population is in better (*K*>1) or poorer (*K*<1) condition than an average population (Bagenal & Tesch, 1978).

3.3 RESULTS

3.3.1 DIEL VARIATIONS IN THE FORAGING ECOLOGY OF 0+ FISHES

3.3.1.1 PREY AVAILABILITY

Generally the most abundant taxa in the zooplankton were Rotifera and *Daphnia* spp. with the exception of some surveys (Figs 3.2 & 3.3); mean densities were generally high compared with other taxa, with a maximum of 40 Rotifera L^{-1} in 2009 and 63 L^{-1} in 2010 (Figs 3.4a & 3.5a), and 49 *Daphnia* spp. L^{-1} in 2009 and 106 L^{-1} in 2010 (Figs 3.4b & 3.5b). Other taxa recorded were cyclopoid copepods, copepod nauplii, *E. lamellatus, Simocephalus* spp., *Alona* spp., *P. pediculus*, *Pleuroxus* spp., *Chydorus* spp., *Bosmina* sp. and Ostracoda. The density of Rotifera generally declined at night with the exception of late June (Fig. 3.5a), whereas *Daphnia* spp. usually increased at night (3.5b). The mean percent abundance and densities of cyclopoid copepods were generally low, but numbers mostly increased at night, with a maximum density of 49 L^{-1}

at 02:00 on 19/20 May 2010 (Figs 3.4c & 3.5c). Although the mean percent abundance of copepod nauplii was comparatively high, the maximum density was only 21 L^{-1} (Fig. 3.4d), but there was generally an increase in density at night in 2009 and a decrease in density at night in 2010 (Fig. 3.5d). The mean percent abundances of *E. lamellatus* and *Simocephalus* spp. were low throughout the summer in 2009 with no diel pattern. The abundance of *Chydorus* spp. was low but increased at night in 2010 (Fig. 3.5e). No other consistent diel patterns in relative abundance or density were recorded for any other taxa.

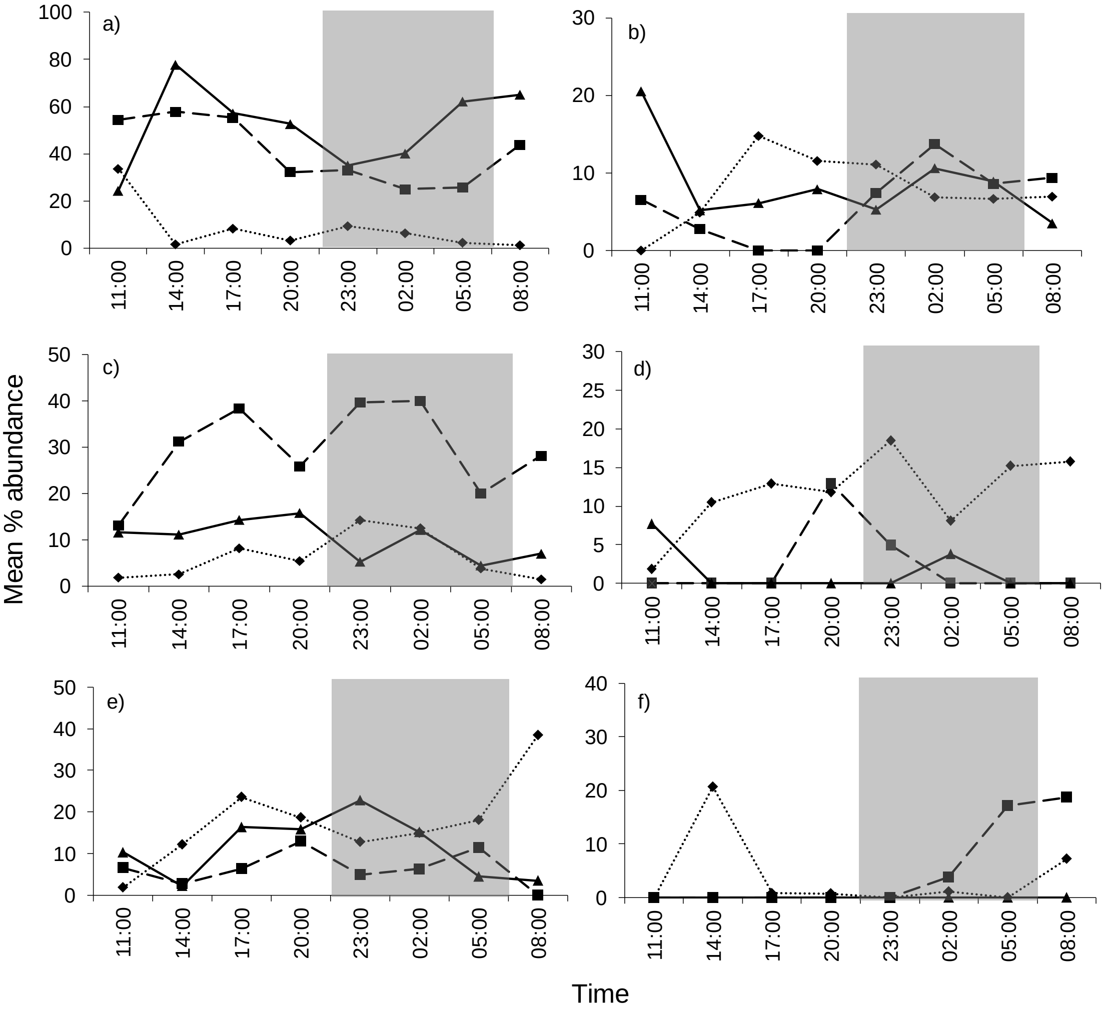


Fig. 3.2 Diel variations in the mean % abundance of a) Rotifera, b) Cyclopoida, c) copepod nauplii, d) *Eurycercus lamellatus*, e) *Simocephalus* spp. and f) *Daphnia* spp. in the zooplankton in Colwick Marina over three 24-h periods (3/4 June ♦; 17/18 June ■; 1/2 July ▲ 2009. Shaded area = darkness).

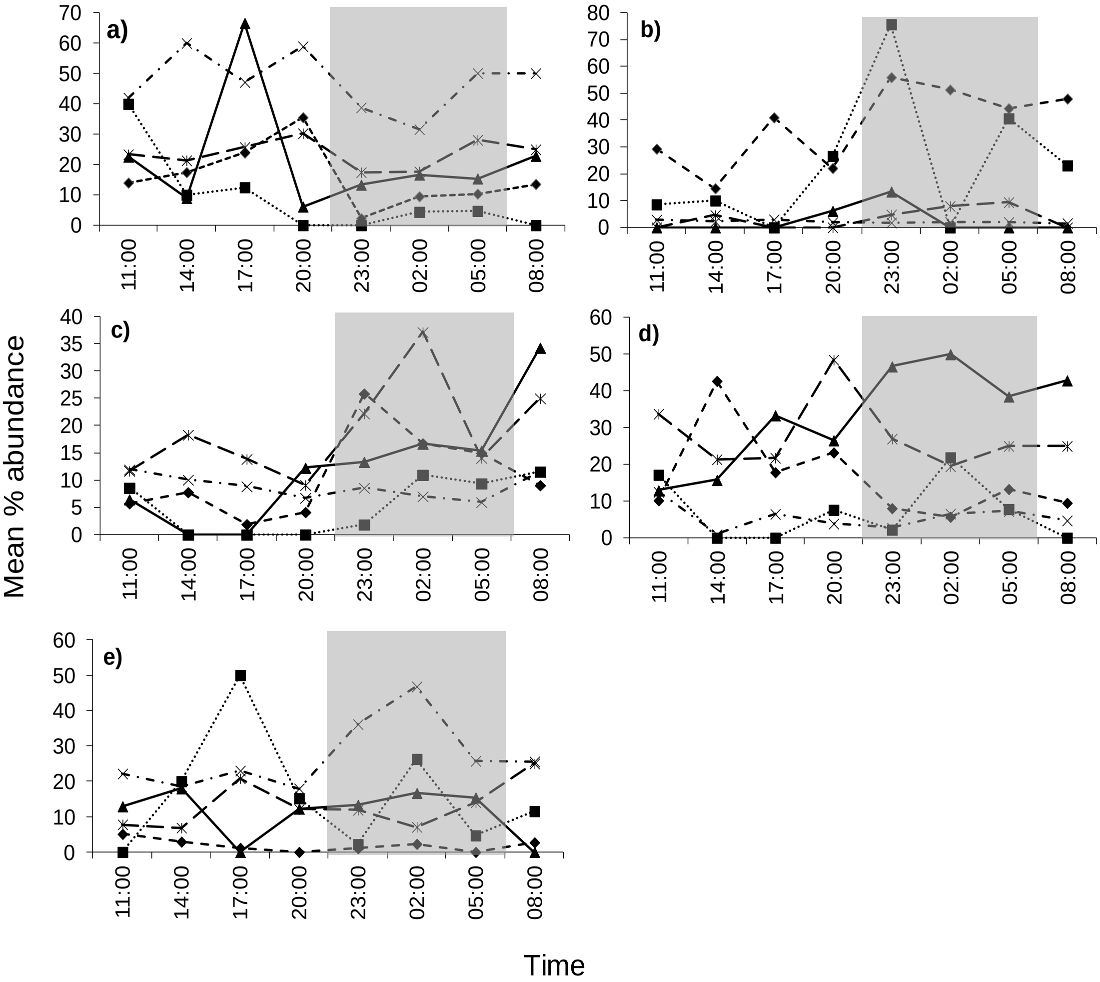


Fig. 3.3. Diel variations in the mean % abundance of a) Rotifera, b) *Daphnia* spp., c) Cyclopoida, d) copepod nauplii and e) *Chydorus* spp. in the zooplankton in Colwick Marina over five 24-h periods (19/20 May ◆; 2/3 June ■; 16/17 June ▲; 30/1 July x; 14/15 July ✳ 2010. Shaded area = darkness).

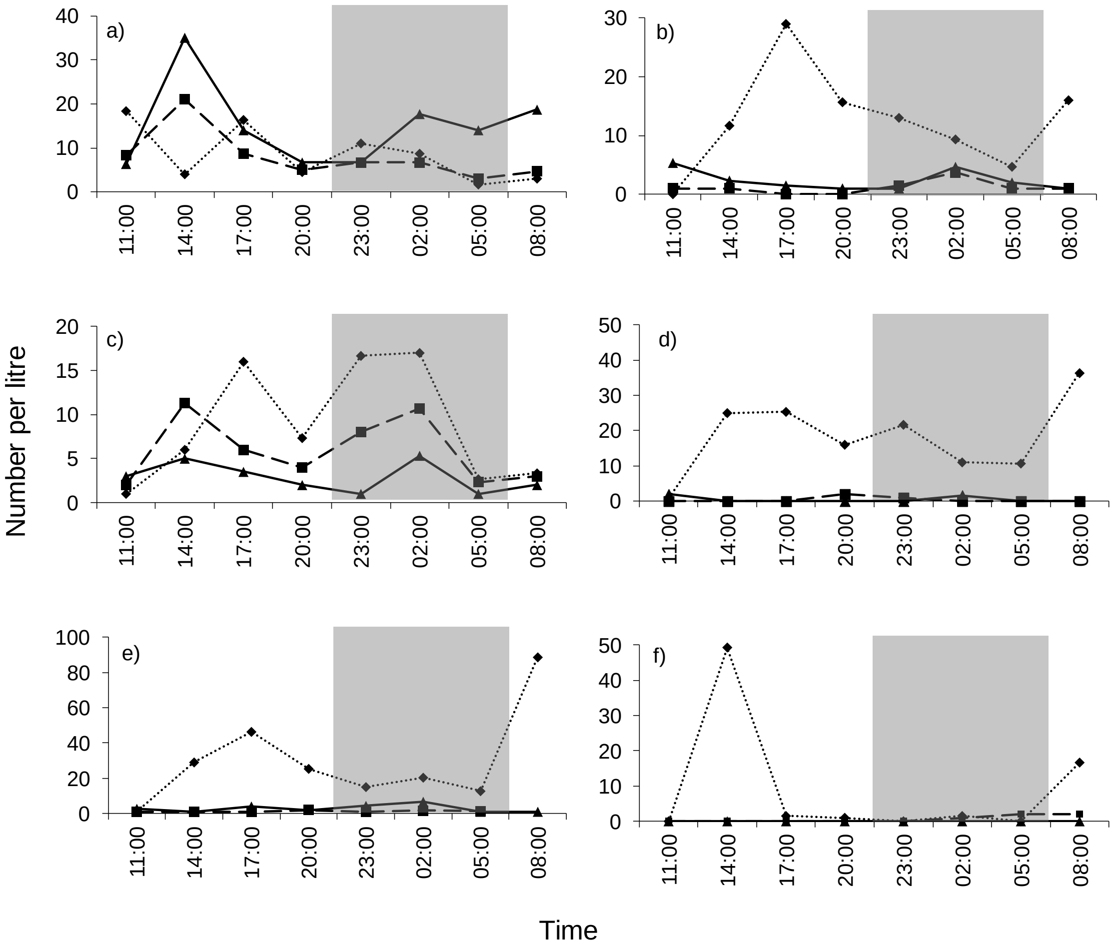


Fig. 3.4 Diel variations in the numbers of a) Rotifera, b) Cyclopoida, c) copepod nauplii, d) *Eurycercus lamellatus*, e) *Simocephalus* spp. and f) *Daphnia* spp. per litre of water in Colwick Marina over three 24-h periods (3/4 June ♦; 17/18 June ■; 1/2 July ▲ 2009. Shaded area = darkness).

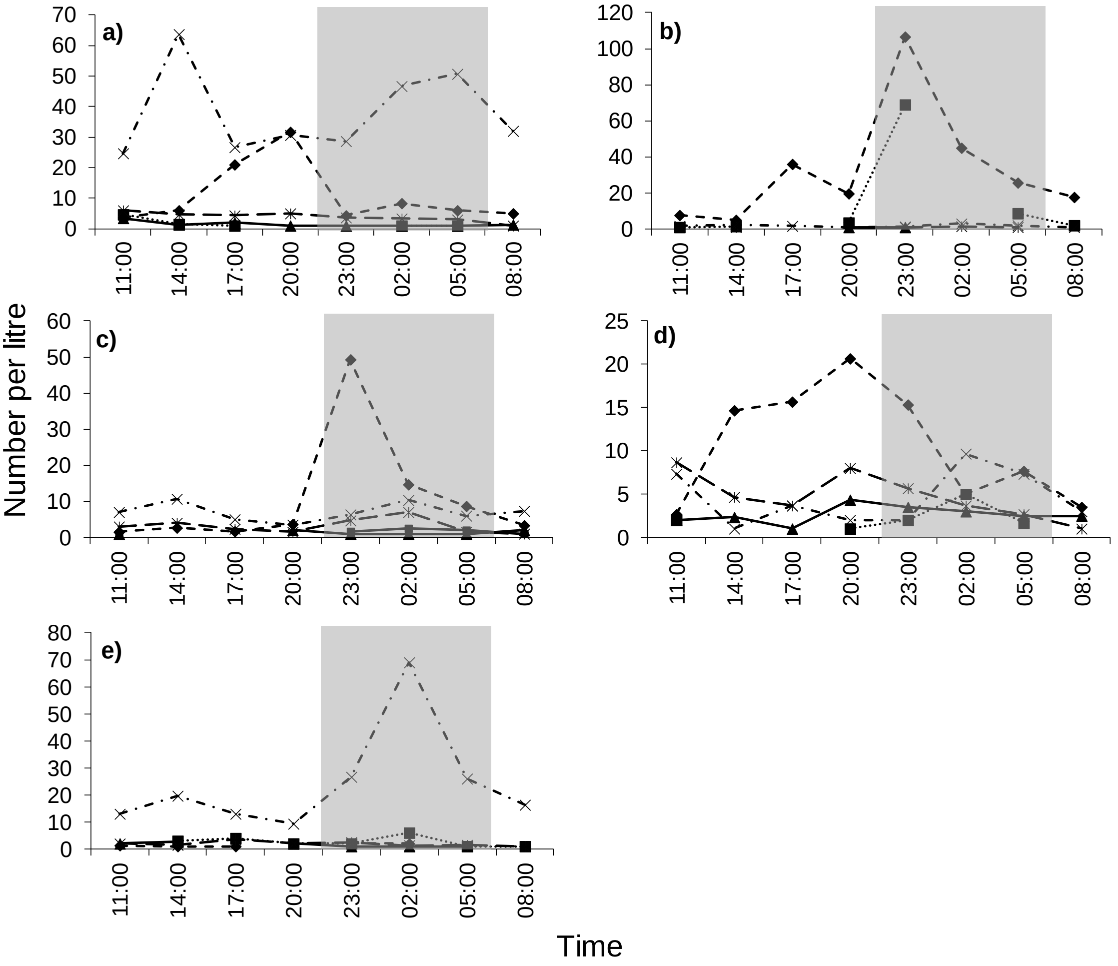


Fig. 3.5. Diel variations in the numbers of a) Rotifera, b) *Daphnia* spp., c) Cyclopoida, d) copepod nauplii and e) *Chydorus* spp. per litre of water in Colwick Marina over five 24-h periods (19/20 May ◆; 2/3 June ■; 16/17 June ▲; 30/1 July x; 14/15 July ✳ 2010. Shaded area = darkness).

3.3.1.2 SPECIES COMPOSITION

In 2010, a total of 25,232 specimens of 15 fish species was captured over five 24-h periods. Roach and perch were the most abundant species, accounting for 59% and 21% of the total catch, respectively. Dace, Spined loach (*Cobitis taenia* L.), bleak, gudgeon, bullhead (*Cottus gobio* (L.)), ruffe, pike, chub, barbel, nine-spined stickleback (*Pungitius pungitius* (L.)), three-spined stickleback, minnow (*Phoxinus phoxinus* (L.)), bream, stone loach (*Barbatula barbatula* (L.)) and tench were captured in smaller numbers.

Perch was the most abundant species in late May, but there was no clear difference in its relative abundance during daylight and at night (Fig. 3.6a). By contrast, the relative abundance of pike was higher in daylight than at night, which could have been because very few individuals of other species were captured during daylight. The relative abundance of spined loach was higher at night than during daylight (Fig. 3.6a). Roach was the most abundant species throughout the 24-h survey in early June, but there was an increase in the relative abundance of pike, bullhead and spined loach at night compared with during daylight hours (Fig. 3.6b). In mid-June, the relative abundance of dace and roach was higher in daylight than at night, and again there was a substantial increase in the relative abundance of spined loach and bullhead at night (Fig. 3.6c). A mixture of species was caught from late June to early July, with chub, perch, roach and dace dominating the samples. Generally, the relative abundance of roach and perch was higher in daylight hours than at night, whereas the opposite occurred for chub and dace in late June (Fig. 3.6d). By comparison, the relative abundance of perch was higher in daylight than at night in July, whereas the opposite occurred in roach (Fig. 3.6e).

3.3.1.3 FEEDING ACTIVITY

The mean gut fullness of finformed larvae and 0+ juvenile roach (no finfold larvae were caught) was relatively low throughout the 24-h periods, but there was some evidence of diel variations in feeding activity in 2009 and 2010, with a reduction in the gut fullness of finformed larvae and an increase in the gut fullness of 0+ juveniles at night (Fig. 3.7a). Notwithstanding, there were no statistically significant differences in gut fullness between day and night for finformed roach larvae in both years, (Mann-Whitney *U*-test, $P>0.05$), whereas the gut fullness of 0+ juvenile roach was significantly higher at night than during daylight in 2009 (independent samples *t*-test, $P<0.05$) but not in 2010 (Fig. 3.7b; independent samples *t*-test, $P>0.05$). No perch larvae were captured in 2009, but the mean gut fullness of 0+ juvenile perch was high throughout the 24-h periods, with little evidence of diel variations in feeding activity; although there was a notable reduction in gut fullness at night in early June 2009, there was no significant difference between day and night overall (Fig. 3.7c; independent samples *t*-test, $P>0.05$). In 2010, the mean gut fullness of finformed perch larvae was generally high but declined at night, although the difference between day and night was not statistically significant (Fig. 3.7d; independent samples *t*-test, $P>0.05$). The mean gut fullness of 0+ juvenile perch in 2010 was high, but did not show any significant diel variation (Fig. 3.7d; independent samples *t*-test, $P>0.05$), however, gut fullness was higher at night for 0+ juvenile perch than finformed perch in 2010.

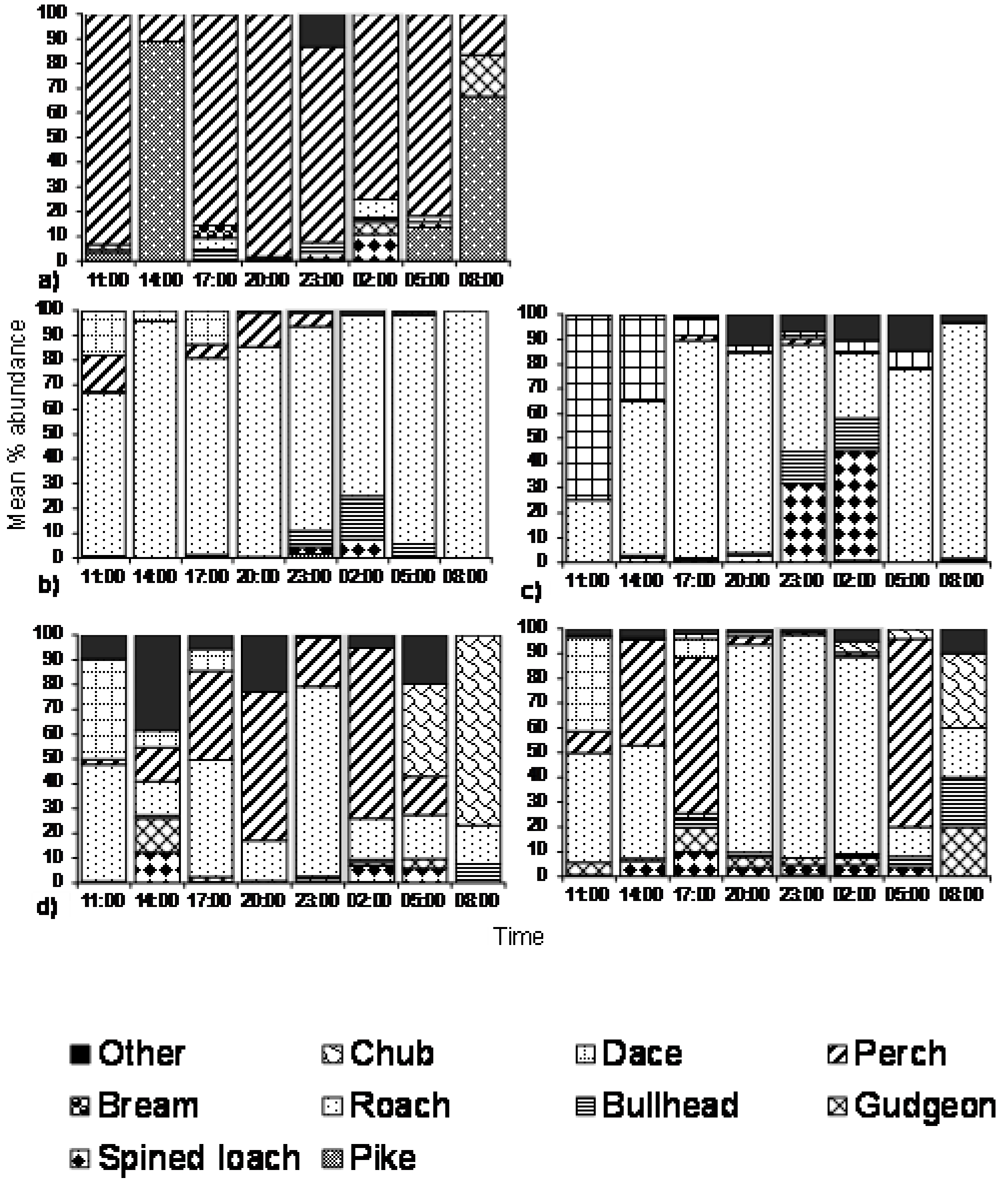


Fig. 3.6. Fish species composition of all ages, over five 24-h periods at Colwick Marina on a) 19-20 May, b) 2-3 June, c) 16-17 June, d) 30 June-1 July and e) 13-14 July 2010. Shaded area = darkness.

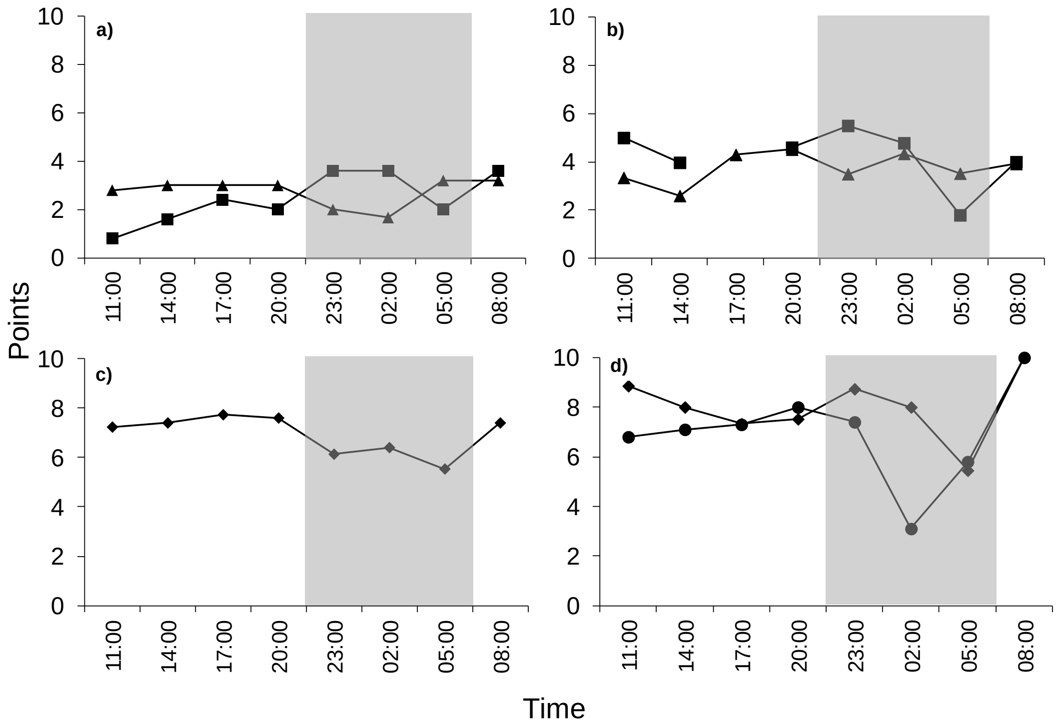


Fig. 3.7 Diel variations in the mean feeding activity (points) of a) finformed larvae (▲) and 0+ juvenile (■) roach in 2009, b) finformed larvae (▲) and 0+ juvenile (■) roach in 2010, c) 0+ juvenile perch (♦) in 2009 and d) finformed larvae (●) and 0+ juvenile (♦) perch in 2010 in Colwick Marina. Shaded area = darkness.

3.3.1.4 DIET COMPOSITION

In 2009, the mean percent abundance of Rotifera in the diet of finformed roach larvae was higher than other taxa at all times, with a peak at 23:00 (Fig. 3.8a). Consumption of *E. lamellatus* was low and consumption of *Chydorus* spp. Was negligible w throughout the 24-h periods, but there was a general increase in consumption of *E. lamellatus* at night and *Chydorus* spp. were consumed in higher numbers in daylight (Figs 3.8b & c). The mean percent abundance of chironomid larvae in the diet of finformed roach larvae was low compared with zooplankton, and no consistent diel pattern in their consumption was observed, although in 2009 consumption was highest during daylight (Fig. 3.8d). Aufwuchs consumption was negligible and exhibited no diel pattern (Fig. 3.8e).

In comparison with 2009, few Rotifera were consumed in 2010. *Bosmina* sp. was the main prey in early June and numbers generally increased at night (Fig. 3.9a). Aufwuchs consumption was higher in 2010 than in 2009, with generally less consumed at night than during daylight (Fig. 3.9b). Consumption of *E. lamellatus* and *Chydorus* spp. showed no diel variations (Figs 5.9c & d). Relatively few cyclopoid copepods were consumed, but more were consumed in daylight than at night (Fig. 3.9e). Similarly, the numbers of chironomid larvae consumed were low, but showed no diel variation (Fig. 3.9f).

In 2009, the mean percent abundance of Rotifera in the diets of 0+ juvenile roach was highest from late morning to the evening, with a peak at 23:00 but then numbers declining throughout the night and early morning (Fig. 3.10a). The mean percent abundance of *E. lamellatus* fluctuated greatly over the 24-h period, although there was a peak at 20:00 abundance then declined until dawn (Fig. 3.10b). Cyclopoid copepod and *Simocephalus* spp. numbers in the diets of 0+ juvenile roach were generally low, but there was a slight increase during the night to a peak at 05:00 (Figs 3.10c & d). No consistent diel patterns in the consumption of chironomid larvae and aufwuchs were observed (Figs 3.10e & f). Similarly, in 2010, the mean percent abundance of *E. lamellatus* in the diets of 0+ juvenile roach generally higher in hours of darkness apart from one survey (Fig. 3.11a). Consumption of *Chydorus* spp. by 0+ juvenile roach showed no diel variation, although mean abundance in the diet gradually increased from 23:00 until 08:00 (Fig. 3.11b). Chironomid larvae were highest at 14:00 and generally lower during the night. Aufwuchs peaked at 20:00 but decreased thereafter (Figs 3.11c & d).

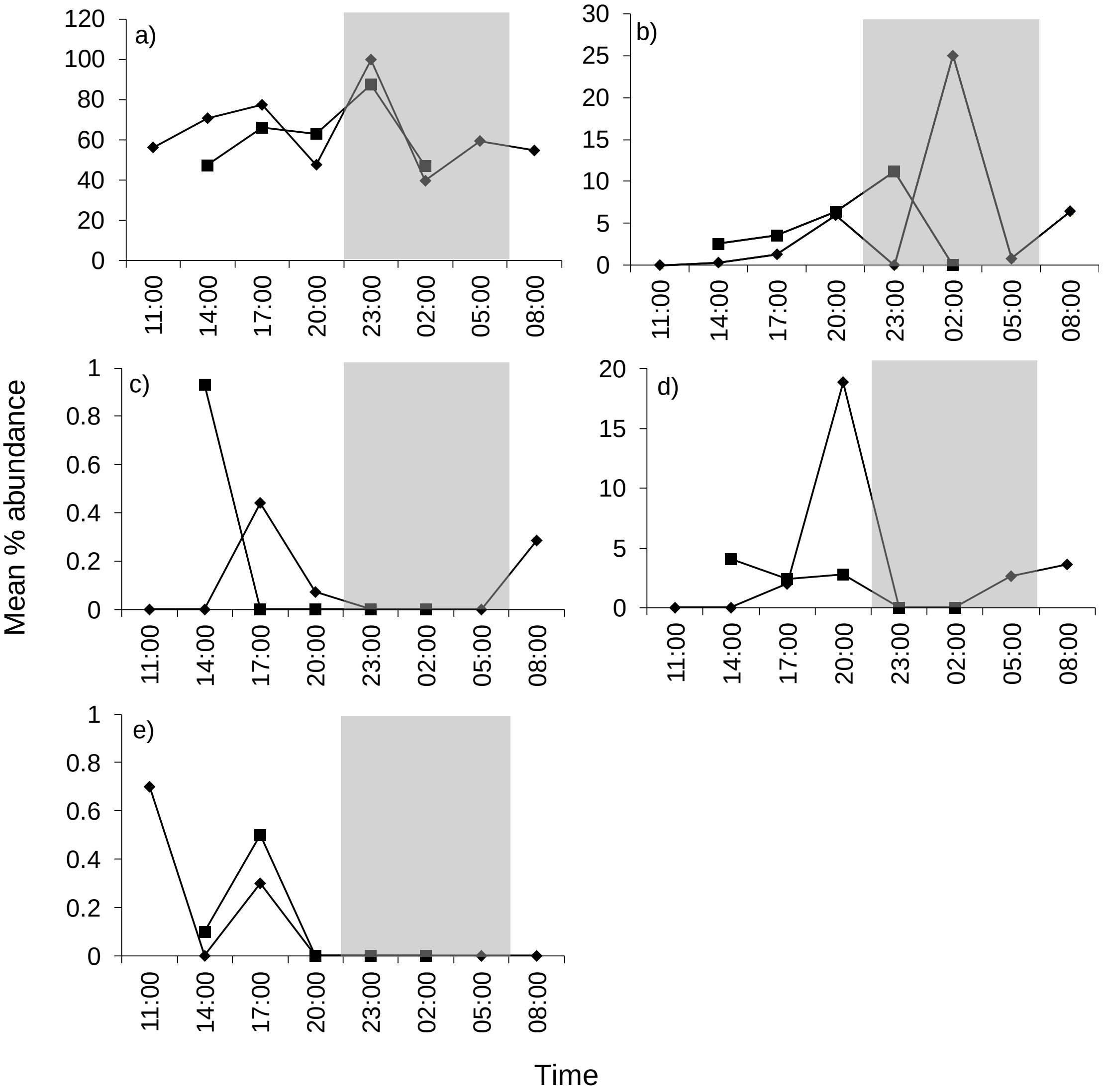


Fig. 3.8. Diel variations in the mean % abundance of a) Rotifera, b) *Eurycercus lamellatus*, c) *Chydorus* spp., d) Chironomidae (larvae) and e) aufwuchs in the diets of finformed roach larvae in Colwick Marina over two 24-h periods in 2009 (3/4 June ◆; 17/18 June ■. Shaded area = darkness.

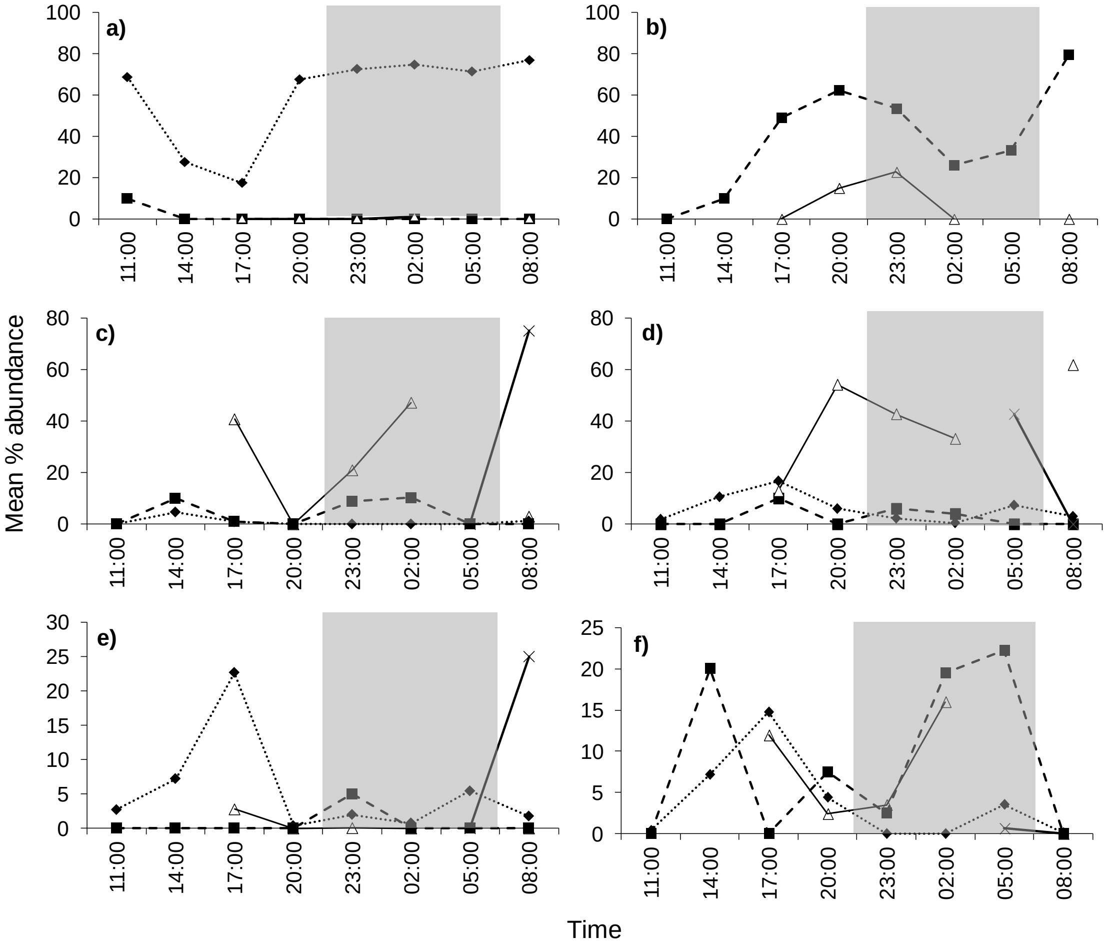


Fig. 3.9. Diel variations in the mean % abundance of a) *Bosmina* sp., b) aufwuchs, c) *Eurycercus lamellatus*, d) *Chydorus* spp., e) Cyclopoida and f) Chironomidae (larvae) in the diet of finformed roach in Colwick Marina over four 24-h periods (2&3 June ◆ 16&17 June ■ 30/1 July Δ and 14/15 July x 2010). Shaded area = darkness. NB: no 0+ juvenile roach were caught at 05:00.

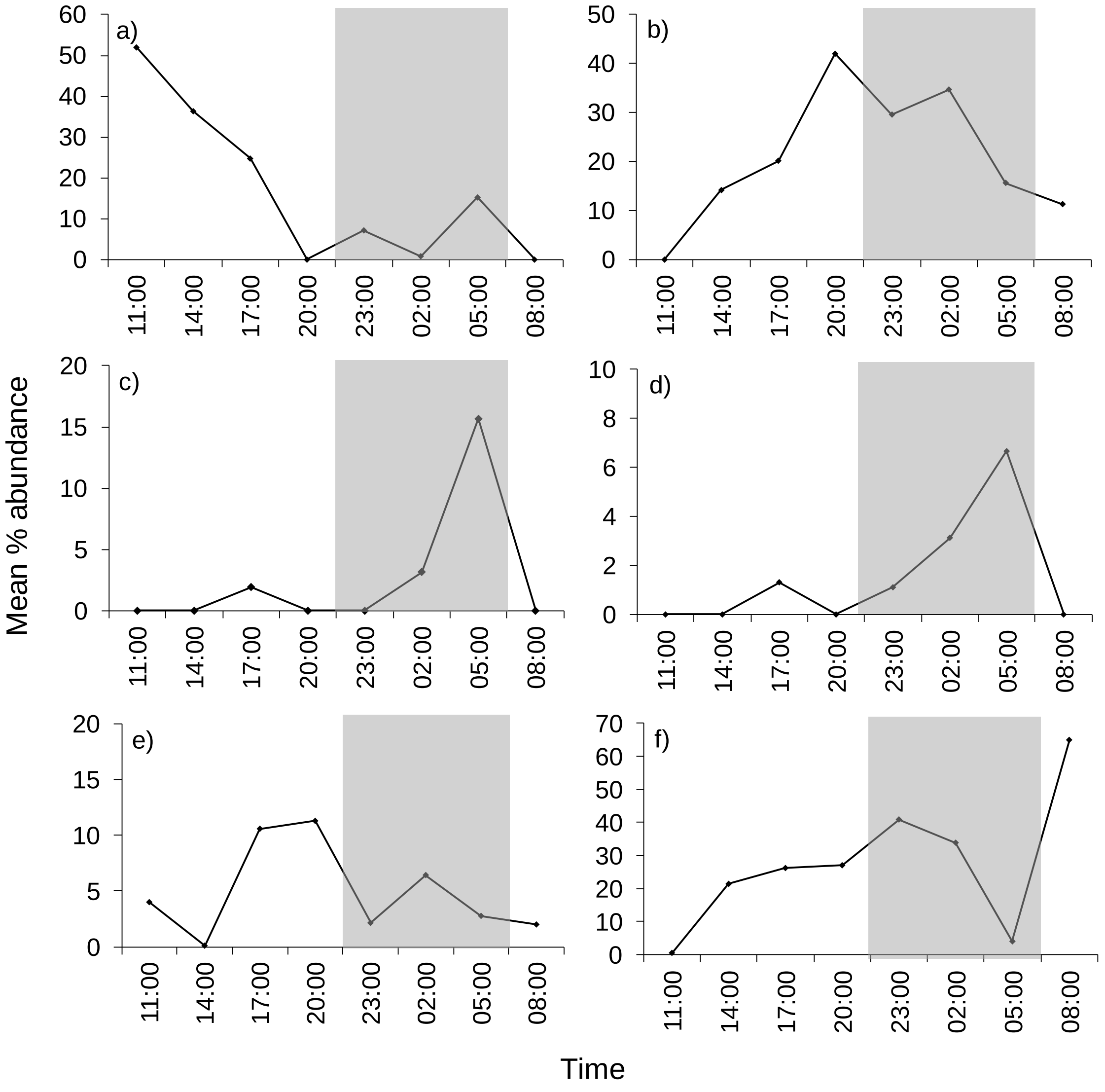


Fig. 3.10. Diel variations in the mean % abundance of a) Rotifera, b) *Eurycercus lamellatus*, c) Cyclopoida, d) *Simocephalus* spp., e) Chironomidae (larvae) and f) aufwuchs in the diet of 0+ juvenile roach in Colwick Marina on 1/2 July ◆ 2009. Shaded area = darkness.

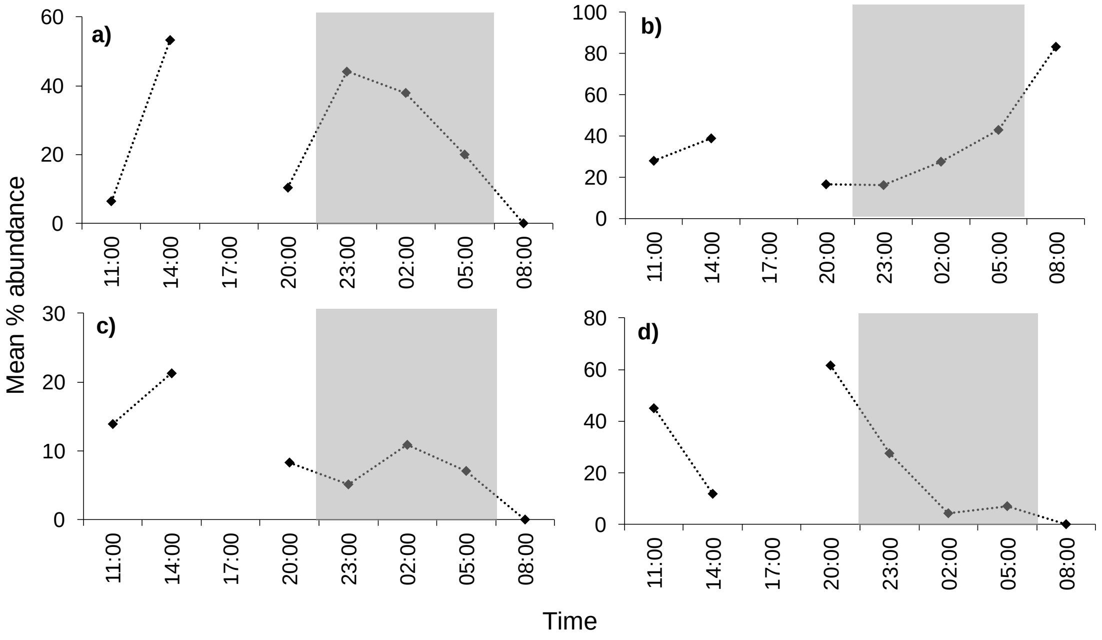


Fig. 3.11. Diel variations in the mean % abundance of key taxa in the diet of 0+ juvenile roach preying upon a) *Eurycercus lamellatus,* b) *Chydorus* spp., c) Chironomidae (larvae) and d) aufwuchs in Colwick Marina (30/1 July and 14/15 July 2010 combined). Shaded area = darkness. NB: No 0+ fishes were caught at 05:00.

In 2010, the mean percent abundance of cyclopoid copepods in the diets of finformed perch larvae were highest at 14:00 and decreased to 02:00 before increasing at 05:00. By contrast, consumption of *Bosmina* sp. and *Daphnia* spp. was low throughout the 24-h periods, with no consistent diel patterns (Figs 3.12a-c).

The mean percent abundance of *Daphnia* spp. in the diets of 0+ juvenile perch was low in 2009 and showed no diel pattern (Fig. 3.13a). Similarly, in 2010, few or no *Daphnia* spp. were consumed. The mean percent abundance of *E. lamellatus* was high during most of the 24-h periods in 2009, but no consistent diel pattern was observed (Fig. 3.13b). The mean percent abundance of cyclopoid copepods in the diets of 0+ juvenile perch was low compared with other zooplankton, but numbers generally increased at night (Fig. 3.13c). By comparison, consumption of *Simocephalus* spp. by 0+ juvenile perch decreased at night from a peak in daylight hours (Fig. 3.13d). Chironomid larvae numbers fluctuated greatly over the 24-h periods and showed no consistent diel pattern (Fig. 3.13e). In 2010, *E. lamellatus,* cyclopoid copepods*, Simocephalus* spp. and chironomid larvae followed the same patterns as 2009 (Figs 3.14a-e). Consumption of *Chydorus* spp. was low and showed no diel pattern, by comparison, chironomid pupae numbers were low but increased at night in two of the surveys (Fig. 3.14f).

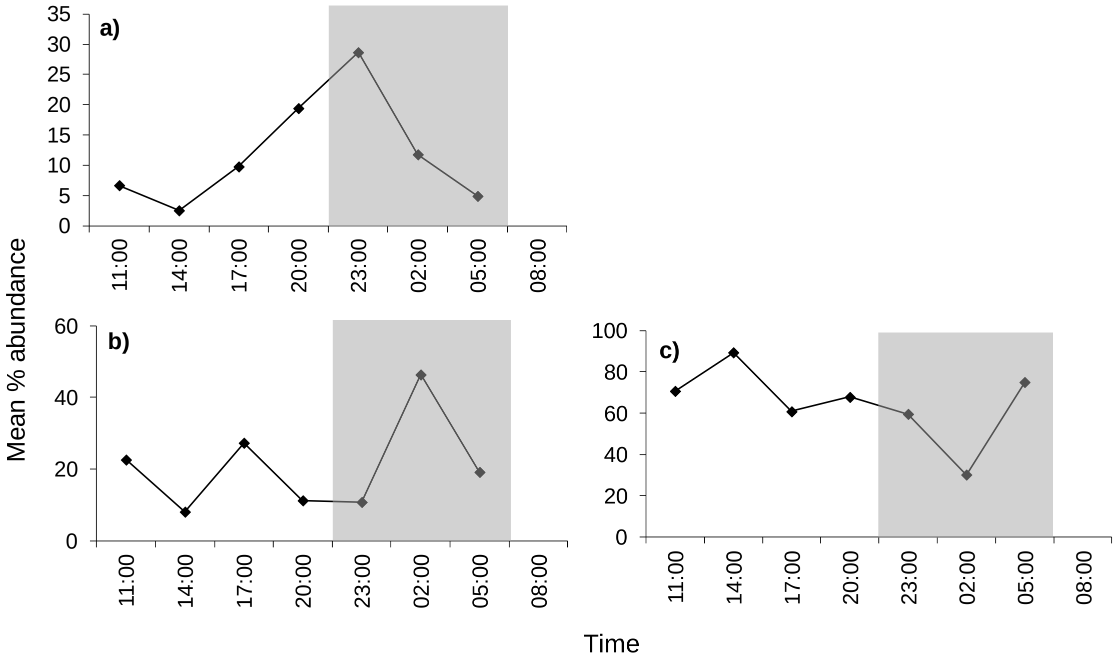


Fig. 3.12. Diel variations in the mean % abundance of key taxa in the diet of finformed perch preying upon a) *Bosmina* sp., b) *Daphnia* spp. and c) Cyclopoida in Colwick Marina (19/20 May 2010). Shaded area = darkness.

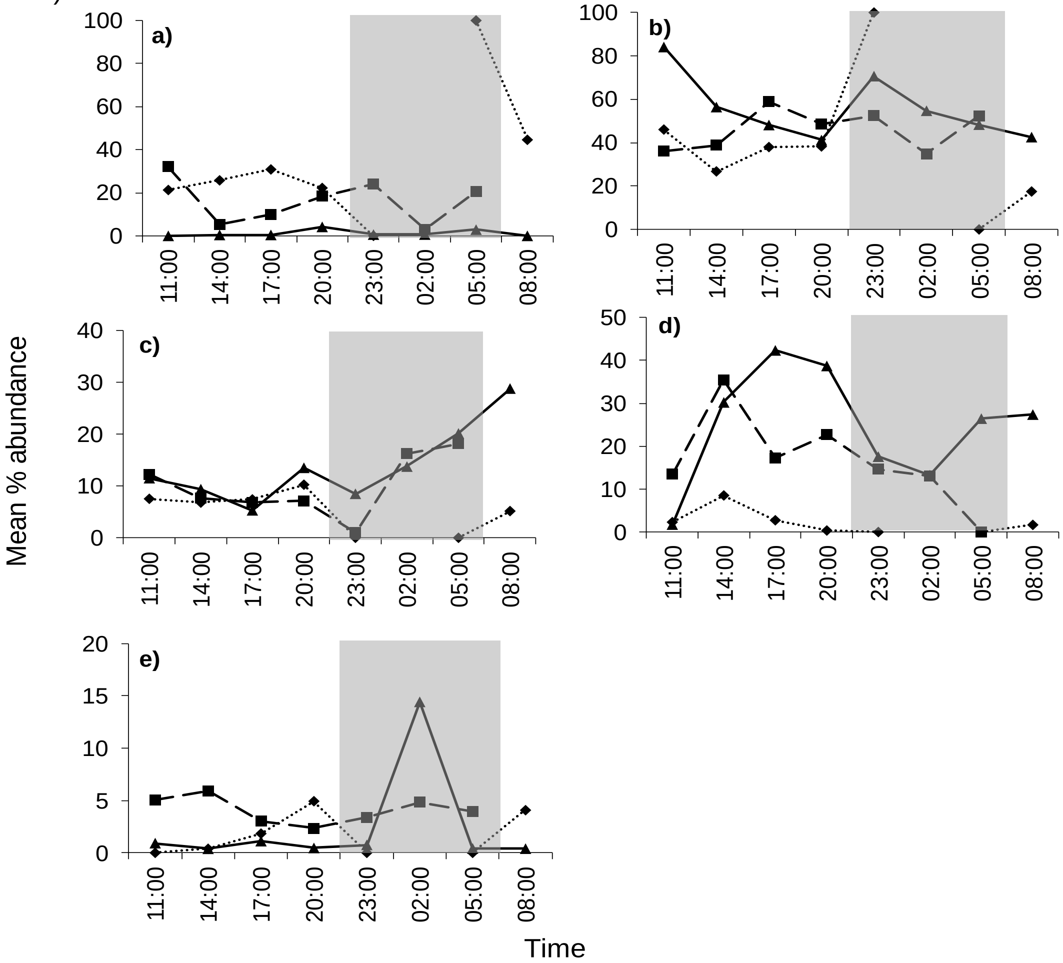


Fig. 3.13. Diel variations in the mean % abundance of key taxa in the diet of 0+ juvenile perch preying upon a) *Daphnia* spp., b) *Eurycercus lamellatus*, c) Cyclopoida, d) *Simocephalus* spp., and e) Chironomidae (larvae) in Colwick Marina (3/4 June ◆, 17/18 June ■ and 1/2 July ▲ 2009). Shaded area = darkness.

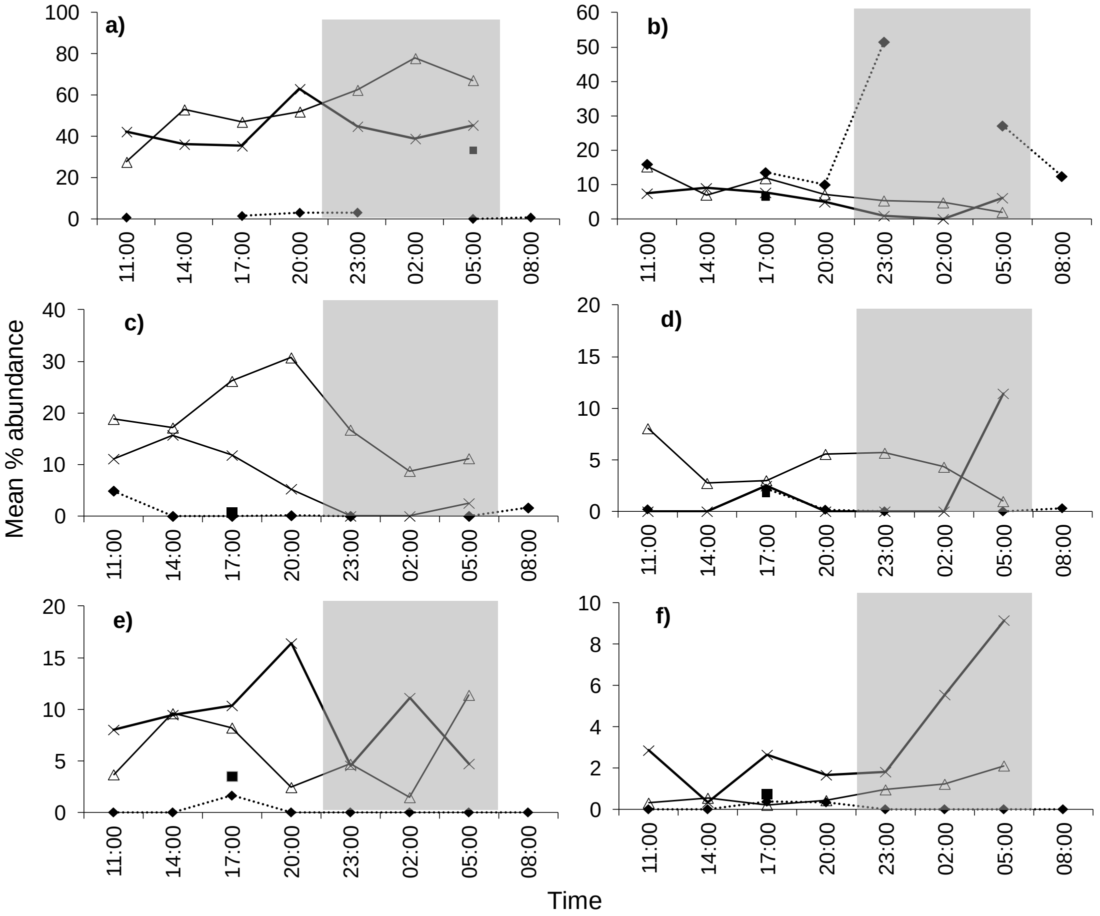


Fig. 3.14. Diel variations in the mean % abundance of key taxa in the diet of 0+ juvenile perch preying upon a) *Eurycercus lamellatus*, b) Cyclopoida, c) *Simocephalus* Spp. d) *Chydorus* spp., e) Chironomidae (larvae) and f) Chironomidae (pupae) in Colwick Marina (2/3 June ◆ 16/17 June ■ 30/1 July Δ and 14/15 July x 2010). Shaded area = darkness.

3.3.1.5 PREY SELECTION

Finformed roach larvae generally selected Rotifera throughout the 24-h period in 2009, although there was a reduction in *E** at 02:00 (Fig. 3.15a). By contrast, *E. lamellatus* was avoided, with no diel pattern (Fig. 3.15b). *Daphnia* spp. were either consumed in proportion to their abundance or avoided, with no obvious diel pattern (Fig. 3.15c). In contrast to 2009, in 2010, Rotifera were consistently avoided throughout the 24-h period (Fig. 3.16a). *Chydorus* spp. and cyclopoid copepods were generally avoided or consumed in proportion to their abundance by finformed roach larvae (Figs 3.16b & c). Conversely, *Bosmina* sp. and *E. lamellatus* were strongly selected or consumed in proportion to their abundance, although no diel patterns were observed (Figs 3.16 d &e). Selection for *Alona* spp. and *Daphnia* spp. in 2010 was highly variable, but both taxa were generally avoided especially at night (Figs 3.16f & g).

Eurycercus lamellatus was strongly selected by 0+ juvenile roach throughout the 24-h period, with no diel pattern evident in 2009 (Fig. 3.17a). Rotifera were typically avoided, especially at night (Fig. 3.17b). Juvenile roach tended to avoid *Simocephalus* spp. and cyclopoid copepods, but there was a general increase in *E** at night and around dawn (Figs 3.17c & d). In 2010, a similar pattern was followed, with Rotifera copepod nauplii and *Daphnia* spp. being consistently avoided (Figs 3.18a, b & c). *E** values for *Chydorus* spp. were highly variable, with no consistent diel pattern observed (Fig. 3.18 d). As in 2009, *E. lamellatus* was strongly selected over the whole 24-h period in 2010 (Fig. 3.18e).

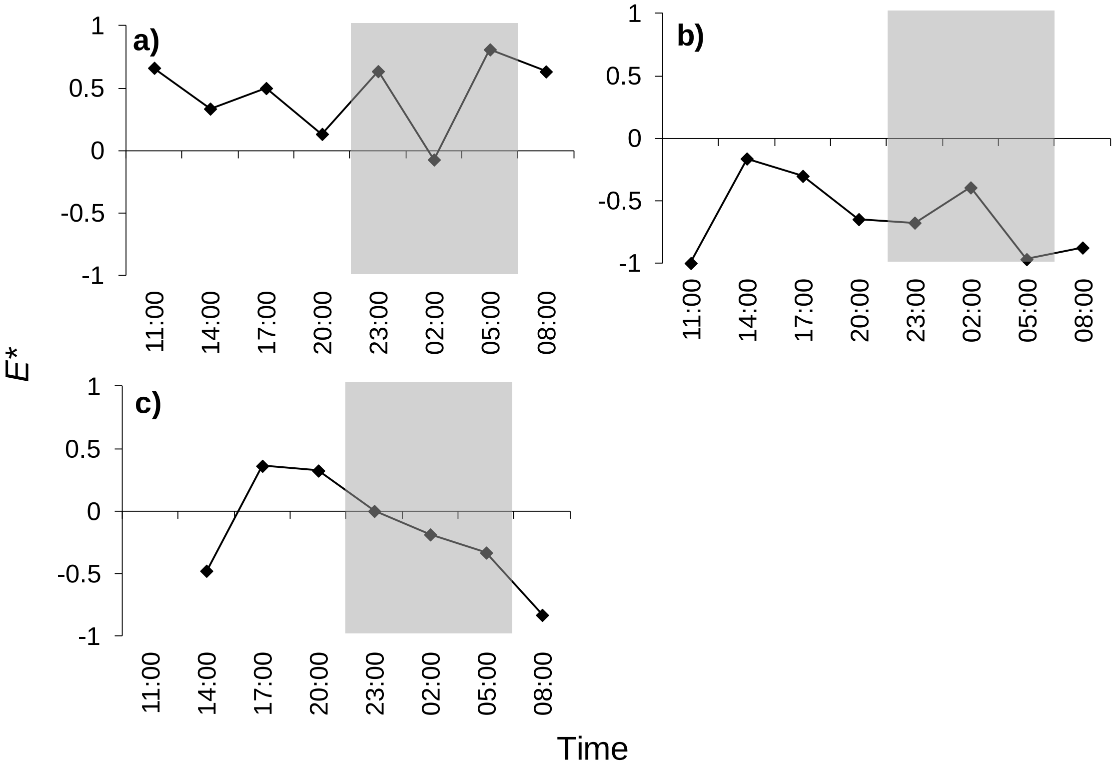


Fig. 3.15. Diel variations in mean electivity indices (*E**) for finformed roach larvae a) Rotifera, b) *Eurycercus lamellatus* and c) *Daphnia* spp. over two 24-h periods in Colwick Marina (3/4 June and 17/18 June 2009). Shaded area = darkness.

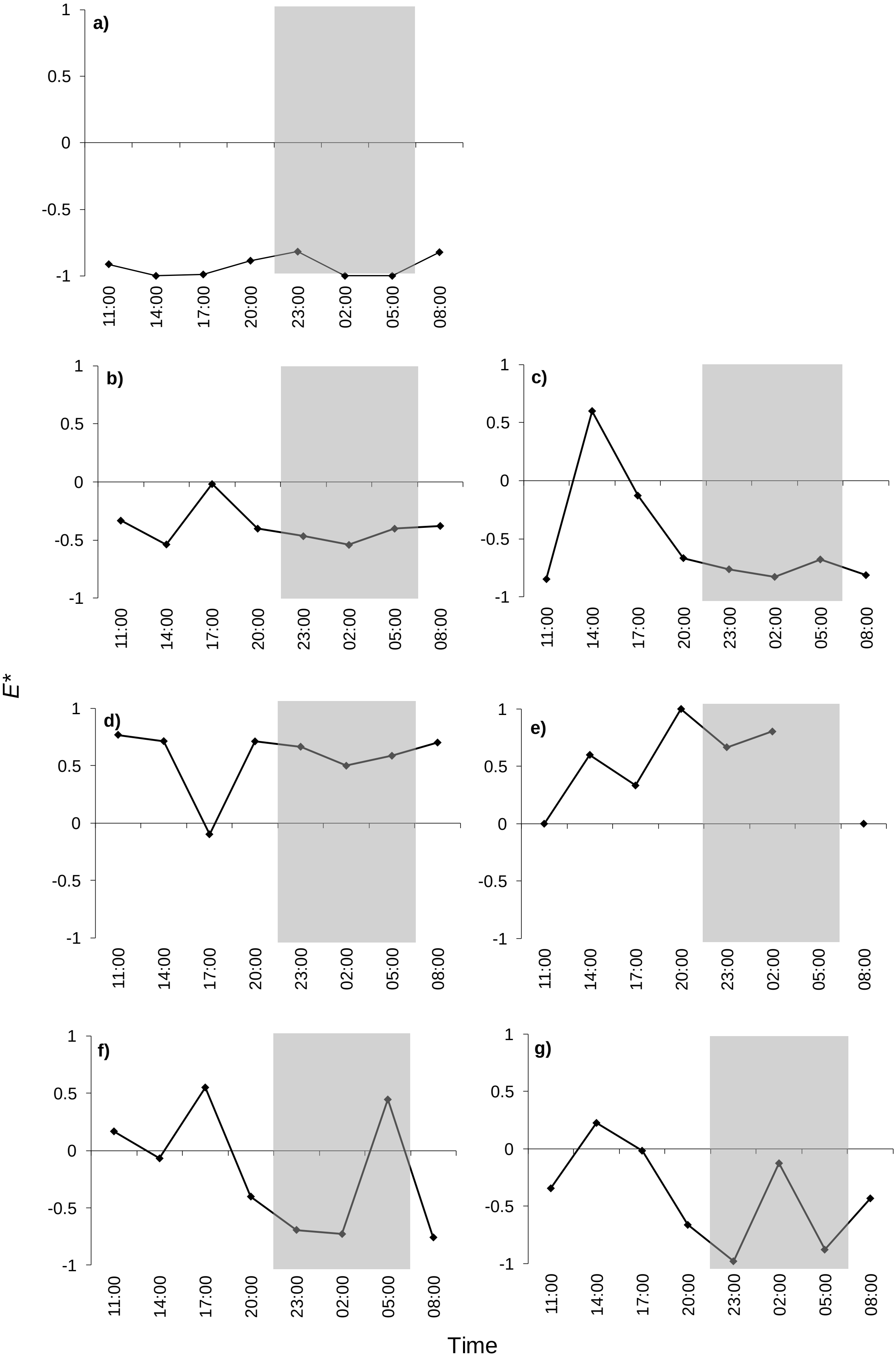


Fig. 3.16. Diel variations in mean electivity indices (*E**) for finformed roach larvae a) Rotifera, b) *Chydorus* spp., c) Cyclopoida, d) *Bosmina* sp., e) *Eurycercus lamellatus*, f) *Alona* spp. and g) *Daphnia* spp. over three 24-h periods combined in Colwick Marina (2/3 June,16/17 June and 30/1 July 2010). Shaded area = darkness.

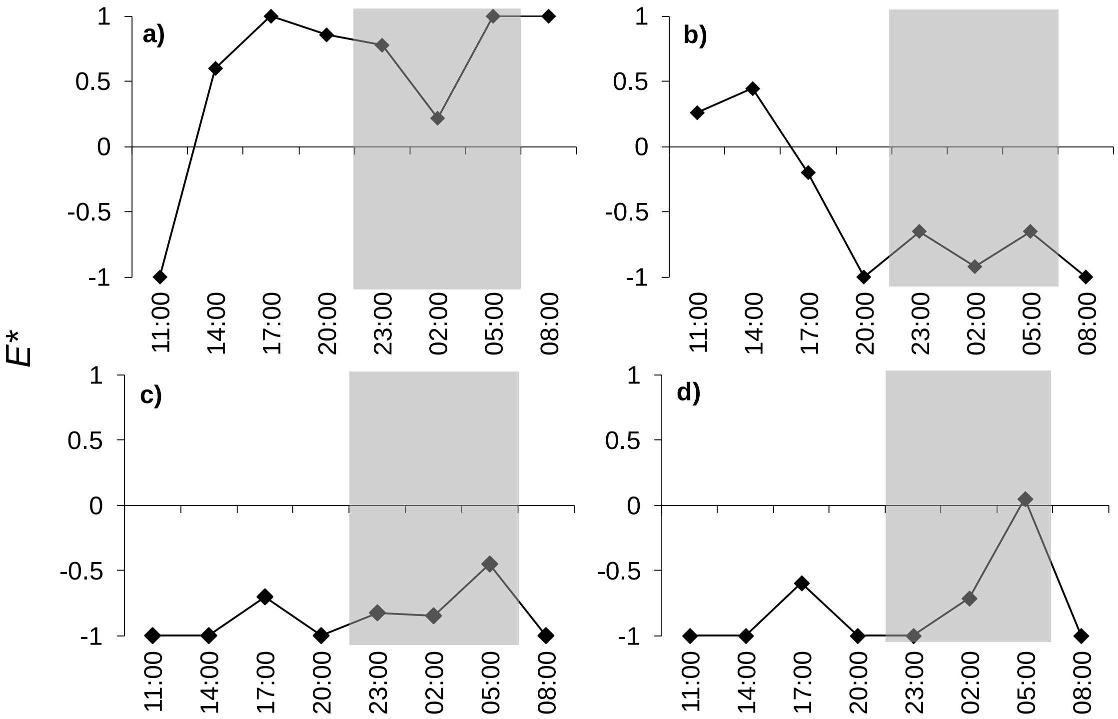


Fig. 3.17. Diel variations in mean electivity indices (*E**) for 0+ juvenile roach a) *Eurycercus lamellatus,* b) Rotifera, c) *Simocephalus* spp. and d) Cyclopoida over three 24-h periods in Colwick Marina (3/4 June, 17/18 June and 1/2 July 2009). Shaded area = darkness.

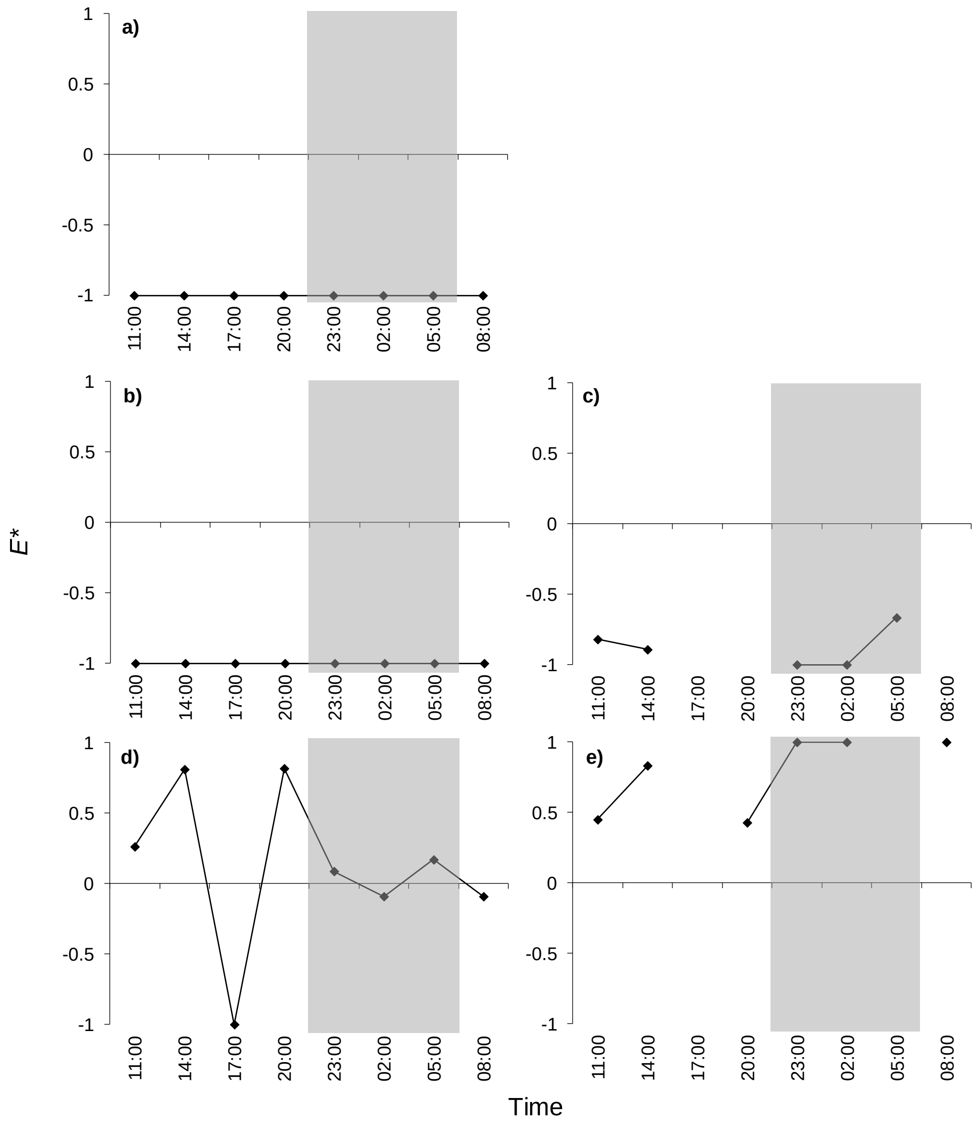


Fig. 3.18. Diel variations in mean electivity indices (*E**) for 0+ juvenile roach a) Rotifera, b) copepod nauplii, c) *Daphnia* spp., d) *Chydorus* spp. and e) *Eurycercus lamellatus* over two 24-h periods in Colwick Marina (30/1 July and 14/15 July 2010). Shaded area = darkness.

In 2010, finformed perch larvae consistently avoided Rotifera, although *E** values increased negligibly at night (Fig. 3.19a). Electivity indices for *Bosmina* sp. remained consistently low throughout the day but peaked at 23:00 when they were selected before declining until dawn (Fig. 3.19b). Cyclopoid copepods were consistently selected, but *E** values declined at night before increasing at 05:00 (Fig. 3.19c). *Daphnia* spp. were consistently avoided by finformed perch larvae, but electivity indices increased at night (Fig. 3.19d).

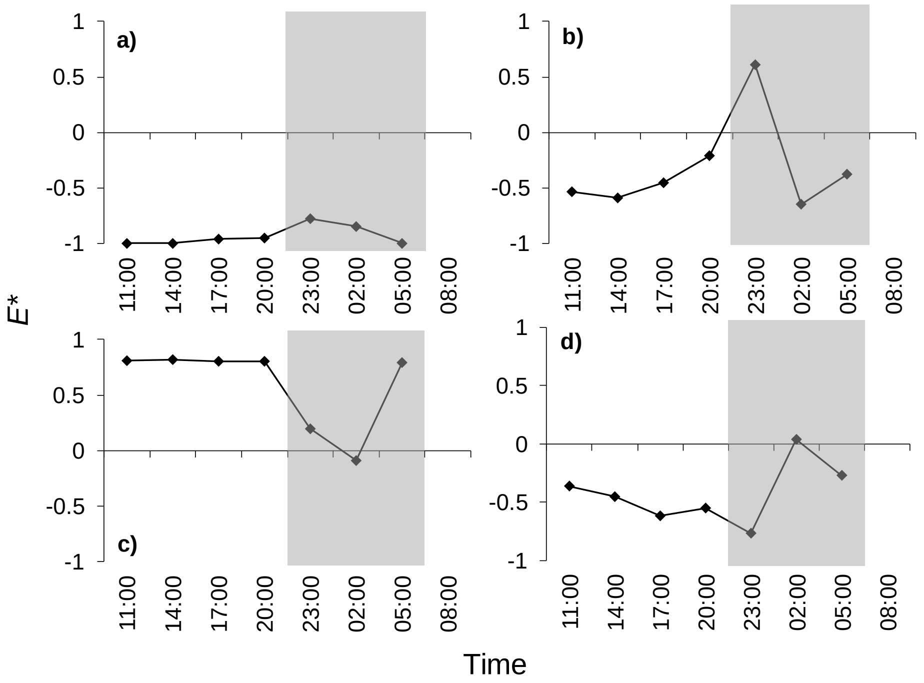


Fig. 3.19. Diel variations in mean electivity indices (*E**) for finformed perch a) Rotifera, b) *Bosmina* sp., c) Cyclopoida and d) *Daphnia* spp. in Colwick Marina on 19/20 May 2010. Shaded area = darkness.

In 2009, juvenile perch consistently selected *E. lamellatus* and *Daphnia* spp., with no diel patterns in the *E** values observed (Figs 3.20a & b). *Simocephalus* spp. were consumed in proportion to their abundance, with no diel variation (Fig. 3.20c). Cyclopoid copepods were avoided or consumed in proportion to their abundance, although *E** values generally increased at night (Fig. 3.20d). By comparison, although *Pleuroxus* spp. and *Chydorus* spp. were also avoided or consumed in proportion to their abundance, their *E** values generally declined at night (Figs 3.20e & f). The majority of the results for 0+ juvenile perch in 2010 were similar to those in 2009 (Fig. 3.21). The exceptions were that *Daphnia* spp., *Simocephalus* spp. and cyclopoid copepods were generally avoided at night in 2010 (Figs 3.21b, c & e). Other species consumed included *Bosmina* sp., although there was no diel pattern in the electivity values (Fig. 3.21). Rotifera were avoided during daylight, but *E** values increased at night, even though they were still avoided (Fig. 3.21f). *Alona* spp. and Ostracoda were typically avoided by juvenile perch, with no diel patterns observed (Figs 3.21g & i).

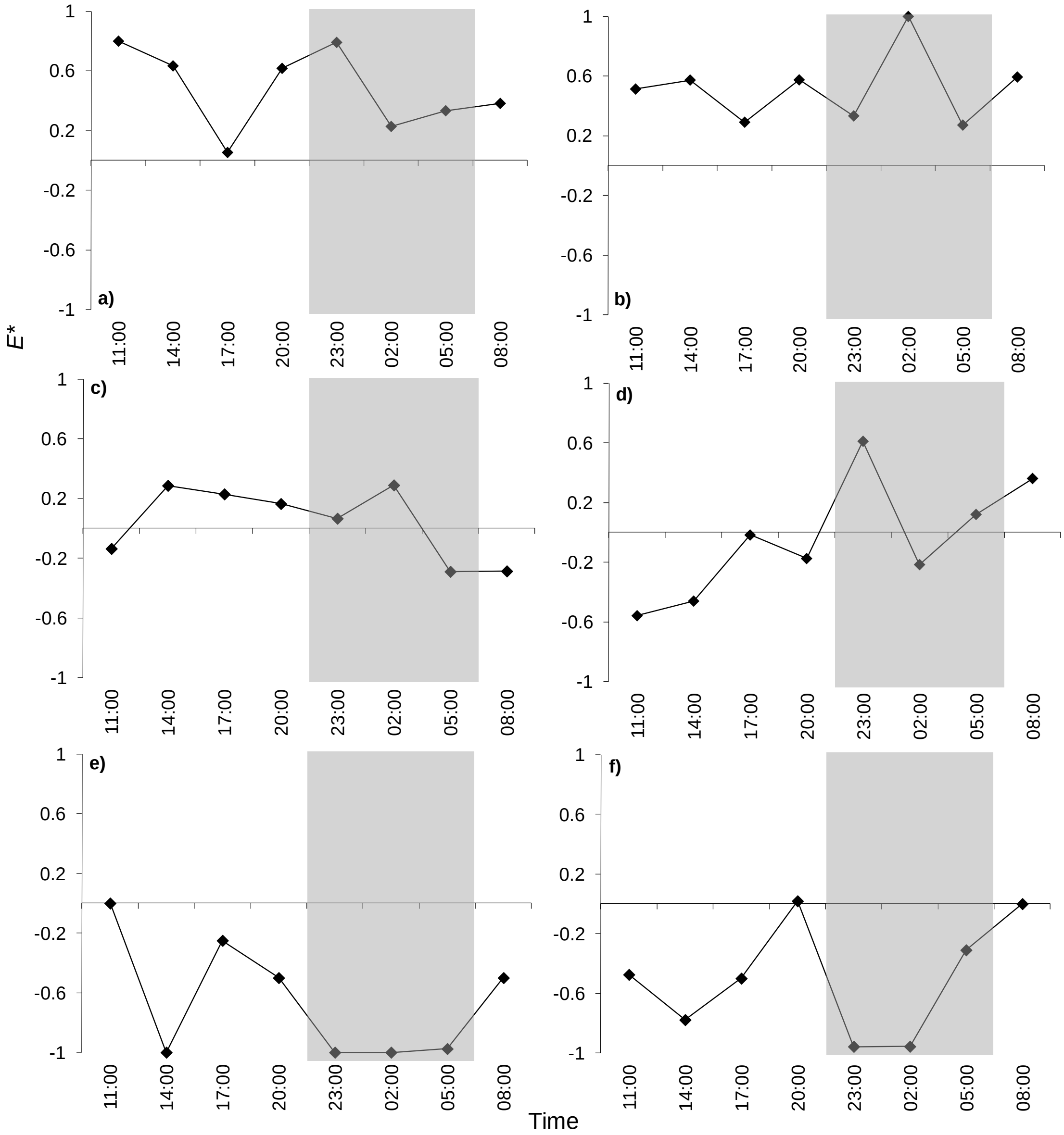


Fig. 3.20. Diel variations in mean electivity indices (*E**) for 0+ juvenile perch a) *Eurycercus lamellatus,* b) *Daphnia* spp., c) *Simocephalus* spp., d) Cyclopoida, e) *Pleuroxus* spp. and f) *Chydorus* spp. over three 24-h periods in Colwick Marina (3/4 June, 17/18 June and 1/2 July 2009). Shaded area = darkness.

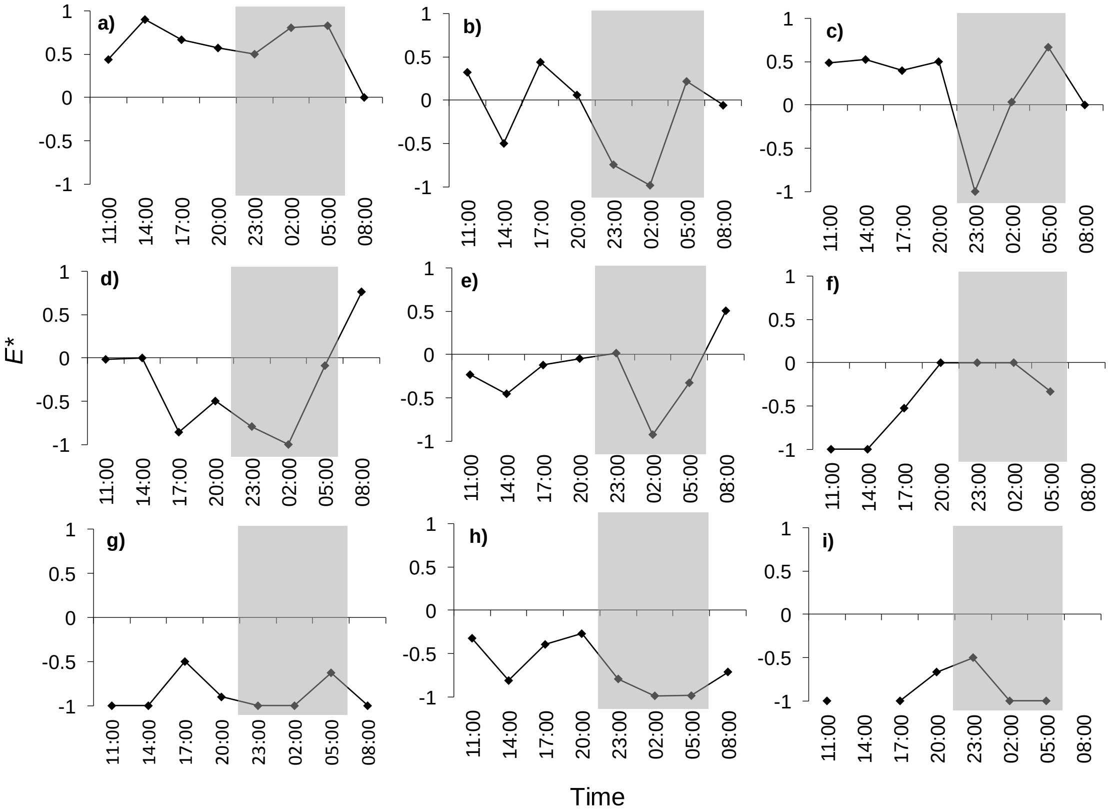


Fig. 3.21. Diel variations in mean electivity indices (*E**) for 0+ juvenile perch a) *Eurycercus lamellatus*, b) *Daphnia* spp., c) *Simocephalus* spp., d) *Bosmina* sp., e) Cyclopoida, f) Rotifera, g) *Alona* spp., h) *Chydorus* spp. and i) Ostracoda in Colwick Marina over five 24-h periods combined (19/20 May, 2/3 June,16/17 June, 30/1 July and 14/15 July 2010). Shaded area = darkness.

3.3.1.6 DENSITY

There were no consistent diel patterns in the density of fishes (all species and ages combined). In May, most of the fishes caught were perch larvae and densities were generally higher at night than during daylight, with the highest densities at 20:00 and 23:00 (Fig. 3.22a). In early and mid-June, most of the fishes caught were cyprinid larvae and densities were high during the day and lower at night and dawn (Figs 3.22b & c). In late June and mid-July, when most of the fishes were 0+ juvenile cyprinids, densities were generally peaked at 23:00 and were lower during daylight (Figs 3.22d & e). There was a gradual increase in fish density from May (max. 1.25 fish m^{-2}) until the end of June (max. 72 fish m^{-2}), followed by a decline in mid-July (max. 20 fish m^{-2}) (Fig. 3.22). The mean percent abundance of 0+ pike was marginally higher in daylight than at night (Fig. 3.23). There was also a significant increase in the abundance of >0+ pike at night compared with during daylight (ANOVA, $P<0.05$).

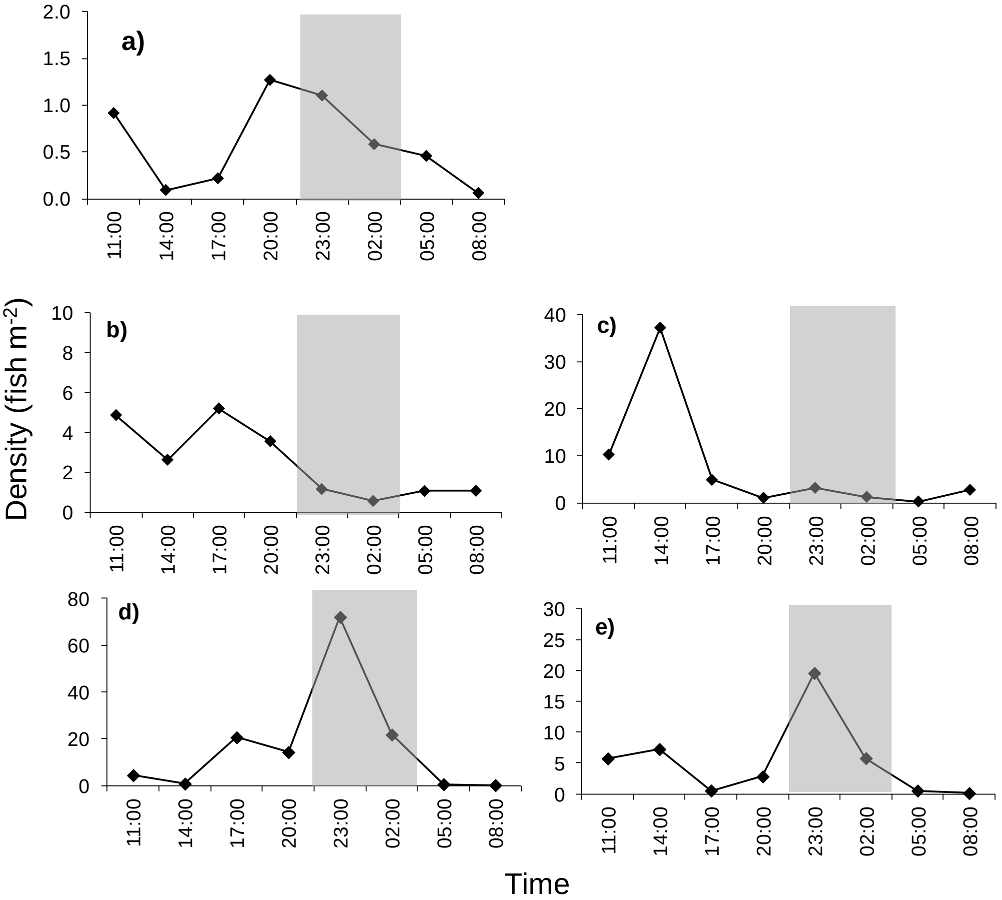


Fig. 3.22. Density of all fish at Colwick Marina over five 24-h periods on a) 19/20 May, b) 2/3 June, c) 16/17 June, d) 30 June–1 July and e) 13/14 July 2010. Shaded area = darkness.

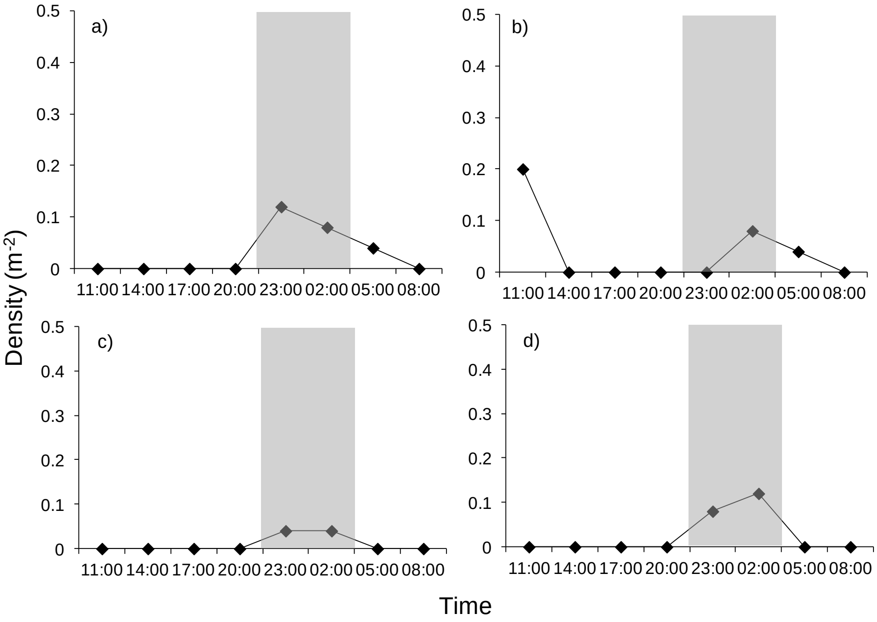


Fig. 3.23. Density of >0+ pike captured in Colwick Marina on a) 19/20 May, b) 2/3 June, c) 30 June–1 July and d) 13/14 July 2010. Shaded area = darkness. NB: No >0+ pike were caught on 16/17 June.

3.3.1.7 SIZE STRUCTURE

There was a significant difference in the length distributions of perch between day and night in late May and mid-June, which was caused mainly by an increase in the number of >0+ perch at night (two-sample Kolmogorov-Smirnov tests, *P* >0.05; Figs 3.24a & c). More >0+ perch were captured at night than in daylight across all surveys. Similar sizes of roach were caught during the day and night in late June and mid-July. No significant diel variations in the size structure of roach catches were observed in any of the surveys (two-sample Kolmogorov-Smirnov tests, *P*>0.05; Figs 3.25a-d). The main piscivores captured in all surveys was pike. There was a significant increase in the mean length of pike at night compared with during daylight (independent samples *t*-test, *P*<0.05).

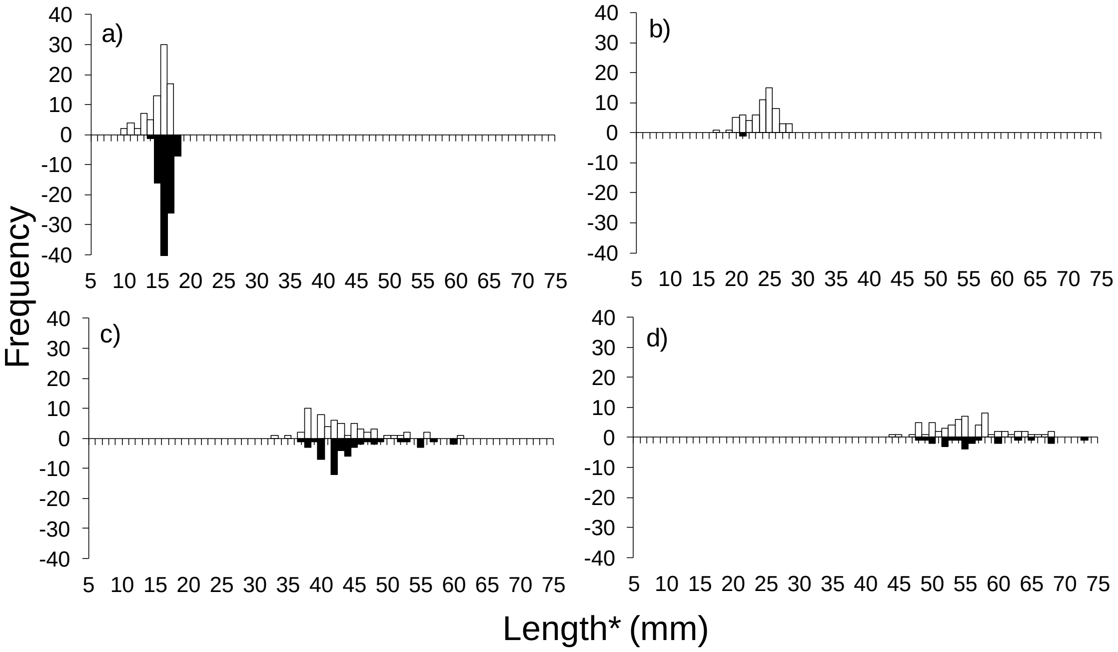


Fig. 3.24. Length frequency histograms for perch captured in Colwick Marina during the day (white bars) and night (black bars) on a) 19-20 May, b) 2-3 June, c) 30 June-1 July and d) 13-14 July 2010. *Larval fish were measured in total length and juvenile fish were measured in fork length.

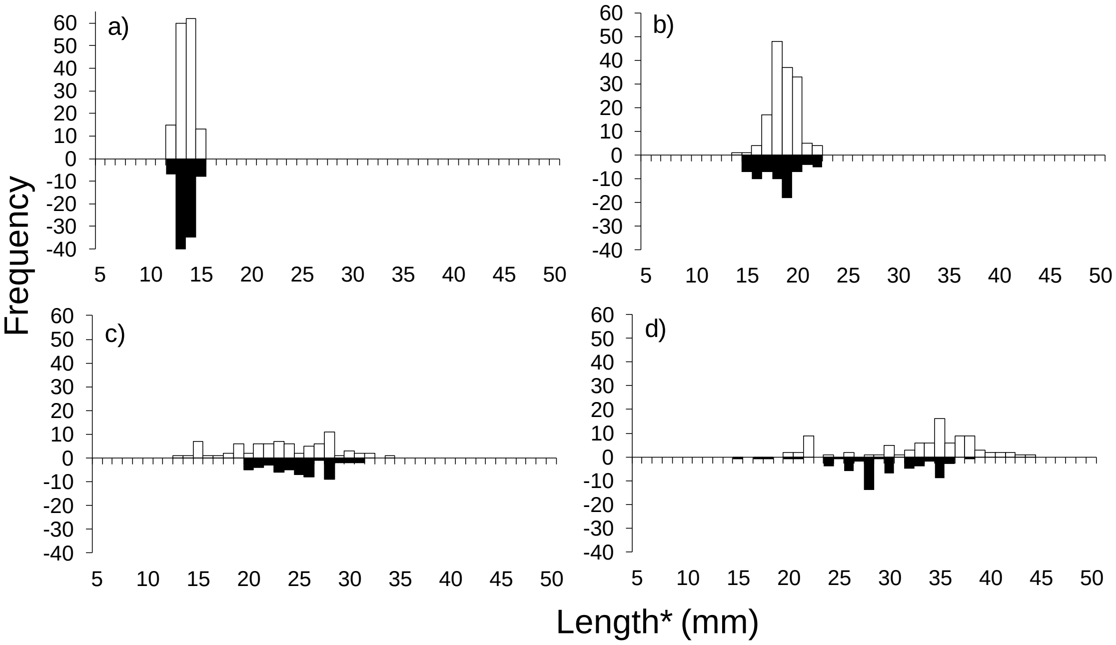


Fig. 3.25. Length frequency histograms for roach captured in Colwick Marina during the day (white bars) and night (black bars) on a) 2-3 June b) 16-17 June c) 30 June – 1 July 2010 and d) 13-14 July 2010.*Larval fish were measured in total length and juvenile fish were measured in fork length.

3.3.3 SEASONAL VARIATIONS IN THE FORAGING ECOLOGY OF 0+ JUVENILE FISHES

3.3.3.1 FEEDING ACTIVITY

The mean feeding activity of 0+ juvenile roach was high throughout the summer, but significantly lower in the autumn (Mann-Whitney *U*-test, $P<0.05$) and winter (Mann-Whitney *U*-test, $P<0.05$) (Fig. 3.26a). The mean feeding activity of 0+ juvenile bream followed a similar pattern to roach, being high throughout the summer and significantly lower throughout the winter (ANOVA, $P<0.05$) (Fig. 3.26b).

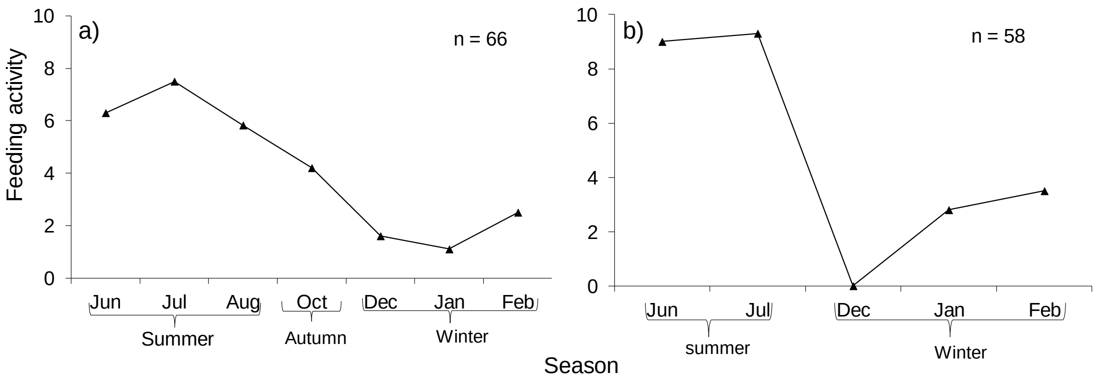


Fig. 3.26. Monthly variations in the mean feeding activity (gut fullness) of a) 0+ juvenile roach and b) 0+ juvenile bream in summer autumn and winter 2010, River Trent.

3.3.3.2 DIET COMPOSITION

The summer diet of 0+ juvenile roach was characterised by cyclopoid copepods and aufwuchs, with the former dominating the diet in over 50% of fish (Figs 3.27 & 3.28). In the autumn, the diet was dominated by *Bosmina* sp. and aufwuchs, with cyclopoid copepods contributing substantially less than in the summer (Figs 3.27 & 3.28). The winter diet was also characterised by cyclopoid copepods and aufwuchs, although *Bosmina* sp. was also important in early winter (Figs 3.27 & 3.28). More individual specialism was recorded in autumn and winter for 0+ juvenile roach compared with in the summer (Fig. 3.28). Notwithstanding, none of the differences in the diets of 0+ juvenile roach were statistically significant between seasons (ANOSIM, global R = 0.152, *P* >0.05). The summer diet of bream was dominated by cyclopoid copepods, comprising almost 100% of the diet in all fish (Figs 3.29 & 3.30). The winter diet of bream also consisted of a large amount of cyclopoid copepods, with aufwuchs and *Alona* spp. consumed in lesser amounts, although aufwuchs became more important as the winter progressed (Figs 3.29 & 3.30). By comparison, there was a statistical significance in the diets of bream between summer and winter (ANOSIM, global R = 0.499, *P* <0.05). Insufficient bream were caught in the autumn for diet analysis.

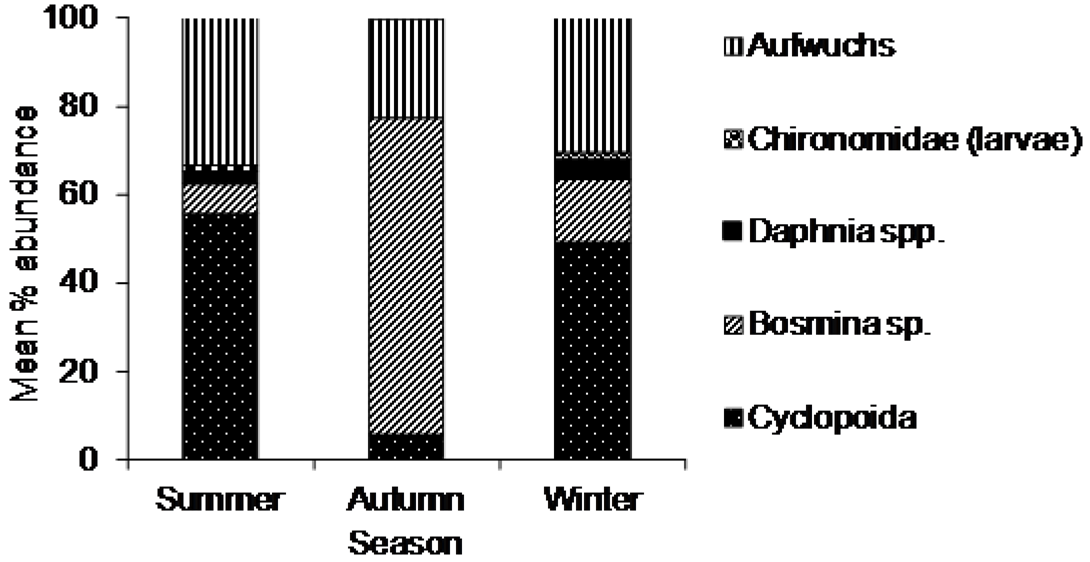
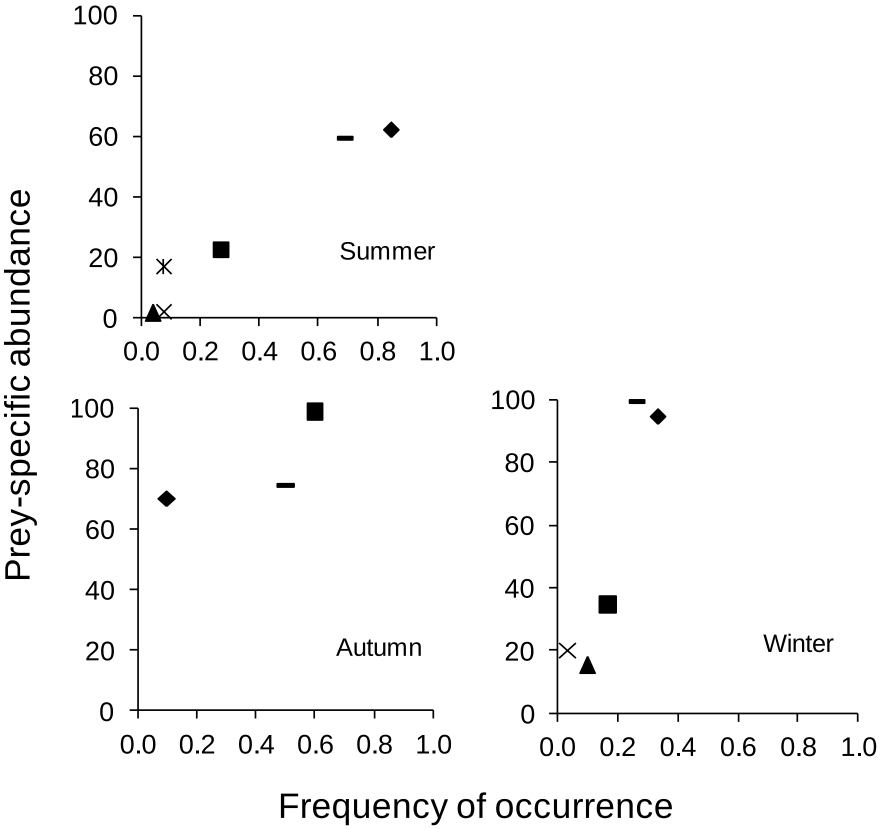


Fig. 3.27. Diet composition of 0+ juvenile roach in the summer, autumn and winter at Attenborough on the River Trent, 2010.



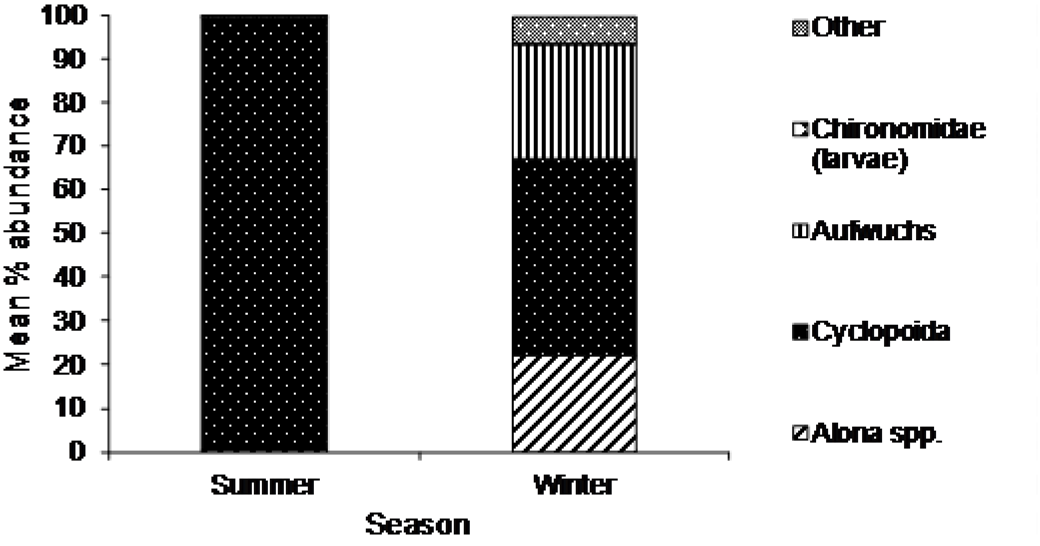


Fig. 3.28. Diet composition and feeding strategy of 0+ juvenile roach in the a) summer, b) autumn and c) winter at Attenborough on the River Trent, 2010. Each point represents a separate prey category. Prey category symbols are: aufwuchs (-); copepod nauplii (✻); *Daphnia* spp. (▲); *Bosmina* sp. (■); chironomid larvae (x); cyclopoid copepods (♦).

Fig. 3.29. Diet composition of 0+ juvenile bream in the summer and winter at Attenborough on the River Trent.

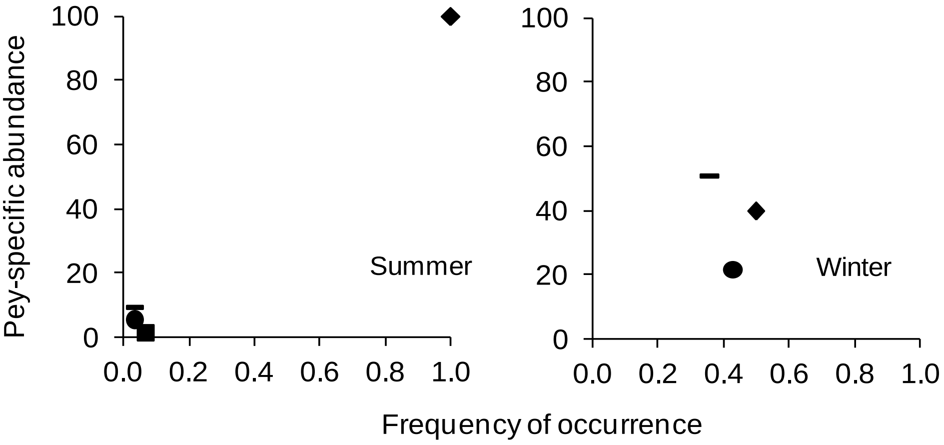


Fig. 3.30. Diet composition and feeding strategy of 0+ juvenile bream in the summer and winter at Attenborough on the River Trent, 2010. Each point represents a separate prey category. Prey category symbols are: aufwuchs (-); *Alona* spp. (●); cyclopoid copepods (♦) *Bosmina* sp. (■).

The diversity in the diets of 0+ juvenile roach were generally lower in winter months compared with summer and autumn months. Diversity was highest in summer and lowest in winter, while evenness was highest in winter, but lowest in autumn (Fig. 3.31). The diversity and evenness of the diets of 0+ juvenile bream were substantially higher in winter than summer (Fig. 3.32).

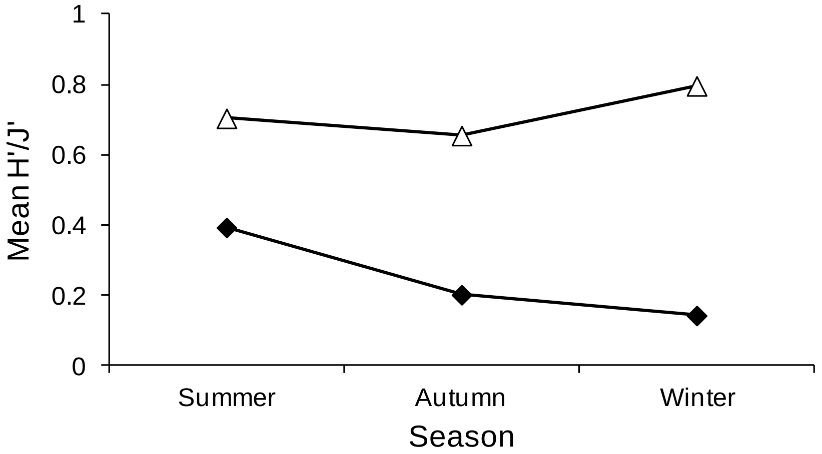


Fig. 3.31. Seasonal variations in the diversity (*H’*, ♦) and evenness (*J’*, Δ) of the diets of 0+ juvenile roach from Attenborough on the River Trent.

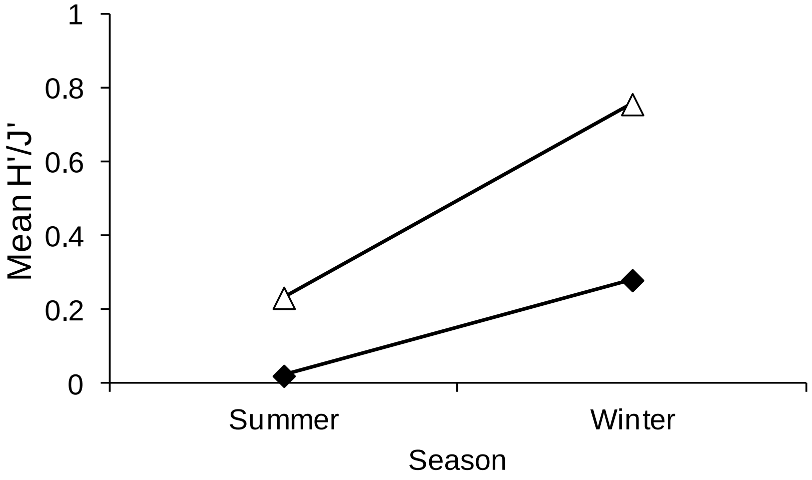


Fig. 3.32. Seasonal variations in the diversity (*H’*, ♦) and evenness (*J’*, ∆) of the diets of 0+ juvenile bream from Attenborough on the River Trent.

3.3.3.3 CONDITION

The condition of 0+ juvenile roach and bream was not affected by season and remained constant at *K* = 1 (Table 3.1).

Table 3.1 Mean (± SD) condition of 0+ juvenile roach and bream from Attenborough on the River Trent in summer, autumn and winter 2010.

	Summer	Autumn	Winter
Roach	1 (± 0.06)	1 (± 0.23)	1 (± 0.29)
Bream	1 (± 0.07)	–	1 (± 0.39)

– catches insufficient for calculation of condition

3.4 DISCUSSION

A number of studies have investigated diel variations in fish densities and distributions, predator and prey activity and their interactions, and habitat use (Gehrke, 1992; Gliwicz & Jachner, 1992; Copp & Jurajda, 1999; Copp, 2004, 2008; Hansen & Closs, 2005; Nunn *et al.*, 2010; Janáč & Jurajda, 2011). Copp & Jurajda (1999), for example, found that greater numbers of small fishes were captured at night along river banks than during the day, suggesting that shallow river shorelines represent important night-time refuges from predation for smaller size classes of fishes, and other studies have corroborated these findings (Copp & Jurajda, 1993; Baras & Nindaba, 1999; Copp, 2004). This is crucial as predation is an important factor in determining fish recruitment success in rivers (Myers *et al.*, 1997). Additionally, Gehrke (1992) demonstrated that the modal length of fish larvae in a backwater was 5–6 mm at night, compared with 3–4 mm during the day. Diel patterns in the diets of larval and juvenile fishes are an important part of their ecology (Johnson & Dropkin, 1993; Garner, 1996b; Horppila, 1999; Copp *et al.*, 2005). However, since the vast majority of studies have only examined the diets of fishes caught during daylight hours, knowledge of the foraging ecology of fishes at night is generally poor. In the present study, higher densities of fishes were found in the margins at night in July (when most of the fishes were juveniles) than during the day. By contrast, densities of larvae fishes were higher in daylight hours than at night in two of the five surveys. This can, in part, be linked to ontogenetic shifts in diel feeding behaviour. Gut fullness can be used to examine diel variations in feeding activity (Becker & Laurenson, 2007). Shepherd & Mills (1996), for example, found that gut fullness declined at night in gizzard shad. In the current study, gut fullness of 0+ juvenile perch and roach was always higher than that of larval perch and roach, but especially at night, supporting the theory that foraging behaviour changes during ontogeny (Reyesmarchant *et al.*, 1992; Nunn *et al.*, 2007a). Larvae feed mainly during the day, whereas there appears to be an increase in nocturnal feeding activity in the juvenile period as the fishes develop and have improved swimming ability and vision. This corroborates the observation of Mills *et al.* (1985), who found that the gut contents of dace larvae in daylight averaged 3-4 times the volume present during hours of darkness.

Predation may also explain the shifts in habitat use of fishes in this study. For example, there was an increase in the densities of >0+ pike and perch in the sampling area at night compared with daylight hours. Jacobsen *et al*. (1997) showed that roach changed their habitat in response to threats from predatory fishes such as pike or perch. Pike are generally not very mobile but are able to strike at prey that pass them in close proximity (Savino & Stein 1989). This emphasises why 0+ fishes were infrequent in the vegetated marginal areas at night, to avoid spatial overlap with pike (Jacobson & Perrow, 1998). Contrary to the results in this study, Copp *et al*. (2005) found relatively consistent diel patterns in fish density over three 24-h periods with the density of most species/age classes increasing at night and Garner (1996b) found that the habitat use of 0+ juvenile roach remained near constant over a 24-h period. Other species that exhibited substantial diel variations in spatial distribution were spined loach and bullhead, both of which were found more frequently in the shallow marginal areas at night than during daylight hours. This corroborates the findings of Copp *et al*. (2005), and emphasises the need to survey riverine fish populations over the full 24-h period before any conservation measures can be put in place (such as the conservation status of spined-loach and bullhead), as day-time only surveys may produce unreliable estimates of fish population demographics.

Fish forage during daylight or at night depending upon which is more advantageous. This is influenced by many factors, including predator avoidance and prey migration and availability (Beauchamp, 1990; Angeli *et al*., 1995; Masson *et al.*, 2001; Burks *et al.*, 2002; Alajarvi & Horppila, 2004; Olsson *et al*., 2007). Railsback *et al*. (2005) stated that habitat that is safe and productive during daylight may be unsafe or unproductive at night and *vice versa*. For example, in deep lakes, many zooplankton species exhibit diel vertical migrations between the hypolimnion and epilimnion, seeking refuge in deep water from fish predation during daylight and grazing on phytoplankton in the surface layers at night (Lampert, 1993). By contrast, zooplankton sometimes exhibit horizontal migrations in shallow lakes (Lauridsen *et al.*, 1996; Scheffer, 1998; Wojtal *et al.*, 2003), which can also affect the prey availability to, and predation efficiency of, fishes. In the current study Colwick Marina acts like a lake system because of its negligible flow. In this study there was circumstantial evidence of zooplankton migration, with densities of rotifers in the margins declining at night, perhaps suggesting they moved into open water. By contrast, densities of copepod nauplii increased at night, perhaps suggesting migration into the margins, although this pattern was only apparent in 2009 and in one survey in 2010. There were no consistent diel patterns in the abundance of *Daphnia* spp., possibly because of the low numbers present, although densities in early June 2009 were generally highest in daylight hours; by comparison, there was an increase in densities in the hours of darkness in May 2010.

In shallow waterbodies, macrophytes provide refuge for zooplankton, reducing mortality from fishes (Burks *et al.*, 2002) as fish predation efficiency is reduced (Winfield, 1986). Such changes in spatial distribution may consequently affect the diet composition of fishes. A number of studies have shown how the diet composition of fishes may vary on a diel basis (Johnson & Dropkin, 1993). Bohl (1980), for example, observed diel changes in the diets of a number of cyprinid species, which were linked to migrations between the littoral and pelagic zones. Similarly, Haertel & Eckmann (2002) noted that adult roach performed diel habitat shifts that influenced their diet. During the day, adult roach inhabited the littoral zone whereas at night they occupied open water, with littoral organisms consumed during daylight and pelagic organisms consumed at night. Similarly, in the current study, the percentage contribution of rotifers in the diets of larval roach was substantially higher than all other taxa at all times in 2009, but fewer were eaten at night than daylight. This might be expected because of the dominance of rotifers in the zooplankton, but the lesser importance of rotifers in the diet at night possibly linked to a reduction in density of rotifers in zooplankton samples at night. However, the electivity values for rotifers also declined at night, suggesting that the change in diet composition at night was caused by a diel shift in fish behaviour, rather than prey abundance. Similarly, 0+ juvenile roach selected rotifers only during daylight, suggesting a switch in feeding behaviour at night. However, caution must be taken when interpreting these data because larval and 0+ juvenile roach and perch consumed few rotifers in 2010, and they appear to have been avoided as a food source. Despite a high relative abundance of rotifers in the water column, density was very low, which may have influenced feeding behaviour. In 2010, larval roach selected and consumed large numbers of *Bosmina* sp., even though few were recorded in the zooplankton. The abundance of *E. lamellatus* in the zooplankton and the diet of finformed roach larvae was comparatively low in both years, but a diel switch in prey selection was nonetheless observed; electivity values of *E. lamellatus* for roach larvae generally increased at night. By contrast, electivity values for *E. lamellatus* declined at night for 0+ juvenile roach in 2009*,* indicating a switch in diel feeding behaviour and feeding activity with ontogeny. However, this pattern was not followed by 0+ juvenile roach in 2010, when selection for *E. lamellatus* increased at night even though its abundance in the zooplankton was low.

Some fish species are nocturnal and largely inactive during the day, whereas visual hunters forage mainly during daylight. There were no significant differences in the feeding activity of juvenile perch in daylight or at night in the present study, although some changes in behaviour were observed. For example, electivity values for *E. lamellatus* were positive throughout the 24-h cycle, but there was an increase at night in 2009, which was reflected by an increased mean percent abundance of *E. lamellatus* in the diet at night. By contrast, the mean percent abundance of *Daphnia* spp. showed the opposite pattern, with higher numbers recorded in the diet in daylight, although electivity values were still positive at night. This change in behaviour may have been a result of predator avoidance as there was an increase in the abundance and size of pike in the sampling area in the hours of darkness and therefore perch may have changed their habitat use, which will have influence their diet composition. Jacobson & Berg (1998) found that under predation risk there was significant diel variation in habitat use by 0+ perch, suggesting a migration from open-water habitats at night into macrophytes in the morning (the opposite of roach), these results were only supported in one of the surveys in the current study.

Seasonal variations in the diet composition and feeding activity of 0+ juvenile fishes have also been shown to influence their growth, condition and survival (Welker *et al*., 1994; Aarnio *et al*., 1996; DeVries *et al*., 1998; Garcıa-Berthou & Moreno-Amich, 2000; Hoxmeier *et al*., 2004; Nunn *et al.*, 2012). In general, 0+ fishes are more susceptible to overwinter mortality than older (larger) fishes (Hurst, 2007), which in turn will affect year-class strength. Seasonal variations in prey abundance can influence diet composition of 0+ fishes (van Dijk & van Zanten, 1995; Bass *et al.*, 1997; Kobayashi *et* *al.*, 1998; Viroux, 2002; Nunn *et al.,* 2012). It is therefore important that peaks in the availability of specific sizes and types of prey coincide with the suitable stages of fish development. The availability of zooplankton for consumption by 0+ fishes is widely known as the 'Match-mismatch hypothesis' (Chapter 1). Factors that can influence this scenario include climate, which influences water temperatures and in turn the timing of zooplankton blooms and fish spawning (Durant *et al*., 2007). Temperature can influence invertebrate distribution seasonally, for example, Rooney & Kalff (2000) found that early season warm temperatures allowed for much deeper macrophyte colonization, which in turn will affect associated fauna populations. Similarly, May (1983) found that rotifer species in Loch Leven occur seasonally, which appears to be primarily an effect of temperature.

Although fishes in this study were 0+ juveniles, seasonal variations in temperatures may have influenced the availability of zooplankton earlier in their ontogeny. Significant seasonal differences were found in the diet composition of 0+ juvenile bream, but not for 0+ juvenile roach. The diversity and evenness of the diets of 0+ juvenile bream were higher in winter than in the summer, which could have been linked to a reduction in the availability of zooplankton, such as cyclopoid copepods, in the winter, which consequently led to a more varied winter diet. By contrast, the diversity of 0+ juvenile roach diets was lowest in winter, although there was a greater evenness in taxa consumed. There was also more individual specialism in autumn and winter by 0+ juvenile roach compared with the summer. The diets of 0+ juvenile bream consisted almost entirely of cyclopoid copepods in the summer, whereas a more diverse range of taxa, including copepods, cladocerans and aufwuchs, were consumed in the winter, suggesting that the diversity of 0+ juvenile bream diets changed in response to what was available, as many copepod species experience population crashes in the winter (Nunn *et al*., 2007a). This suggests that bream are more specialised feeders than roach in their early life stages. The diets of 0+ juvenile roach mainly comprised cyclopoid copepods in the summer and winter, compared with mainly *Bosmina* sp. in the autumn. Aufwuchs was consumed in similar amounts in all surveys, which corroborates other studies on the diet of this fish species that found aufwuchs to be important in the diet of roach (Garner, 1996b; Nunn *et al*., 2007a, 2008). Aufwuchs can be abundant after plankton populations have declined (Mann *et al*., 1997; Marker & Collett, 1997). Weatherley (1987) found that the proportion of aufwuchs in the diets of 0+ juvenile roach typically increased through the summer, which often coincides with reduced densities of animal prey, particularly planktonic cladocerans (Persson, 1983). By contrast, the switch to aufwuchs may be delayed or not occur where sufficient animal prey is available (Mann *et al*., 1997; Nunn *et al*., 2007a). Even though aufwuchs was present in the diets of 0+ juvenile roach and bream in autumn and winter, it did not dominate the diets, indicating that there may have been sufficient animal prey available, despite it being widely understood that zooplankton populations in temperate fresh waters are low throughout the autumn and winter (Sommer *et al*., 1986; van Dijk & van Zanten, 1995; Nunn *et al*., 2007c).

Numerous studies have reported a reduction in condition over the winter due to the utilisation of lipid reserves (e.g. Griffiths & Kirkwood, 1995; Kirjasniemi & Valtonen, 1997). In addition, Kirjasniemi & Valtonen (1997) and Pangle *et al*. (2004) reported that food ration has an influence on survival, with fed fish more likely to survive than starved individuals. However, growth rates of fish feeding on aufwuchs are typically lower than of those feeding on animal prey (Garner *et al*., 1996; Lemke & Bowen, 1998), thus, aufwuchs is considered a poor food resource due to its low digestibility and nutritional value (Persson, 1983; Mann, 1997). The combination of reduced feeding activity during the winter and poor food quality could have implications for the survival of 0+ fishes. Seasonal variations in the feeding activity of 0+ juvenile roach and bream was found in the current study, with a significant reduction in feeding activity in winter compared to summer. Notwithstanding, the condition of 0+ juvenile roach and bream remained constant across all seasons and was not affected by the seasonal variations in feeding activity. Similarly, Nunn *et al*. (2008) reported no significant changes in the condition of 0+ juvenile dace and roach between October and February in the lower River Trent. It is possible, therefore, that the duration of this study and the study by Nunn *et al*. (2008) was inadequate to detect reductions in condition. Alternatively, winters in the UK may rarely be sufficiently long or severe to have a major size-selective influence on 0+ fish survival (Nunn *et al*., 2008).

CHAPTER FOUR

THE INFLUENCE OF HABITAT STRUCTURE ON THE FORAGING ECOLOGY OF 0+ FISHES

4.1 Introduction

Spatial variations in prey availability can have important implications for the feeding ecology, growth, development, survival and recruitment success of fishes. This is particularly the case for larval and 0+ juvenile fishes, which require a continuous and abundant food supply to avoid starvation (Graeb *et al.*, 2004; Hoxmeier *et al.*, 2004). Spatial variations in prey availability may occur for a variety of reasons. Many zooplankton species, for example, undertake diel vertical or horizontal migrations, which are believed to be a response to predation risk or spatial variations in resources. Indeed, Gliwicz (1986) demonstrated that diel vertical migrations of copepods were only apparent in lakes with predatory fishes, while Wojtal *et al*. (2003) found that large-bodied zooplankton (daphnids and copepods) generally swam towards open water at dusk and towards submerged macrophytes at dawn, and concluded that this was in response to predatory pressure. Environmental conditions, such as water temperature and hydrological regime, can also influence the spatial distribution of potential prey. For example, areas of reduced water velocity increase water-residence times, which encourages plankton development, therefore plankton densities are generally higher in river margins than in the mid-channel (Reckendorfer *et al.,* 1999; Schiemer *et al.,* 2001; Nunn *et al.*, 2012). Nunn *et al.* (2007c) found a greater availability of zooplankton in connected waterbodies (marinas and ponds) compared with a main river channel, with connected waterbodies providing abundant prey for a wide range of fish species, which may enhance their survival and recruitment success. Spatial variations in invertebrate densities inevitably influence the diet composition of fishes. Differences in diet composition have also been observed at smaller spatial scales, for example, Garner (1998) found significant differences in the diets of 0+ roach, chub, bleak, common bream and gudgeon between mesohabitats in a lowland river.

Habitat structure and complexity are two of the fundamental factors determining the distribution of organisms at all spatial scales (micro, meso, macro and catchment). Vegetation is of primary importance in shaping the structural environment for associated fauna in many systems (Cowx & Welcomme, 1998; McAbendroth *et al.*, 2005; Thomaz & Cunha, 2010), providing habitats for a diversity of benthic and planktonic organisms (Garner *et al.*, 1996; Bass *et al.*, 1997; Stansfield *et al.*, 1997; Grenouillet & Pont, 2001; Grenouillet *et al.*, 2002). Allelopathy (i.e. the release of chemicals by macrophytes) may also play a role in zooplankton distribution. For example, Pennak (1973) demonstrated that biochemicals were released from macrophytes such as *Elodea* spp. to repel limnetic species of *Daphnia* (other examples are described in Burns & Dodds, 1999 and Burks *et al.*, 2000). Indeed, complex habitats invariably support higher densities, and greater diversities and ranges of body size of invertebrates than do areas of open water (Northcott, 1979; Whiteside *et al.*, 1985; Jeffries, 1993; McAbendroth *et al.*, 2005; Thomaz & Cunha, 2010), making aquatic macrophytes ideal foraging areas for many 0+ fishes (Cowx & Welcomme, 1998; Nunn *et al*., 2007a, b). However, macrophyte structure (e.g. emergent, submerged and floating-leaved species) may also have an important influence on the density, diversity and body sizes of zooplankton, which could in turn influence the foraging ecology of 0+ fishes. The aim of this chapter was to investigate the influence of habitat complexity on the foraging ecology of 0+ fishes. The specific objectives were to examine how macrophyte structure affects food availability and how this influences the diet composition, prey selection and condition of 0+ fishes. It was predicted that there will be differences in the species composition, abundance and diversity of zooplankton associated with macrophytes of contrasting structure and, moreover, that this will be reflected in the diet composition, prey selection and condition of 0+ fishes. This information is crucial to understanding the feeding behaviour and ecology of fish during early development, as well as the management and rehabilitation of fish populations and habitats.

4.2 MATERIALS AND METHODS

Experimental procedure

The River Ancholme was used to investigate the influence of macrophyte structure on the feeding ecology of 0+ fishes. The study was conducted over a 0.5 km stretch of the River Ancholme near Hibaldstow (Plate 4.1), this is a highly regulated river, which was chosen for its high biomass and diversity of aquatic macrophytes that represent habitats of varying structural complexity. This river is situated in north Lincolnshire, England, and is a tributary of the Humber Estuary (Fig. 4.1). It runs from Bishopbridge (west of Market Rasen), passes through Brigg and flows into the Humber at South Ferriby. It is a highly regulated river that is navigable for 27 km, from its confluence with the Humber at South Ferriby to Bishopbridge, with over 250 boats registered (Cowx *et al*., 2007).

The Ancholme Valley catchment covers an area of 573 km² and is mainly rural with agriculture as the major land use. Water quality on the Ancholme is generally satisfactory for fish populations even though the pH is slightly above average at ≈8.1. Dissolved oxygen is relatively stable and never falls below approximately 70%

saturation (7.9 mg L^{-1}) but rises to about 140% (14.8 mg L^{-1}) at times (Cowx *et al*., 2007). The high oxygen content and vulnerability to increased nitrate loading from agricultural run-off may promote excessive plant growth during the summer months (Defra, 2005; Cowx *et al.,* 2007). Water velocity of the River Ancholme is generally slow and stable as it is regulated, creating a very uniform environment with lacustrine characteristics.

Sampling was conducted in the margins of the river as that is where 0+ fishes tend to aggregate and aquatic macrophytes are usually most abundant. *Potamogeton* spp., reed sweet-grass (*Glyceria maxima* (Hartm.)), greater reedmace (*Typha latifolia* (L.)), common reed (*Phragmites australis* (Cav.)) and yellow water-lily (*Nuphar lutea* (L.)) were the most abundant macrophyte species. Flow was negligible and water depths ranged from 28 to 160 cm. The substratum consisted mainly of silt and gravel in all vegetation categories. There was abundant riparian vegetation, which was dominated by common butterbur (*Petasites hybridus* (L.)) and cow parsley (*Anthriscus sylvestris* (L.)), but it provided little or no cover for fishes, making them reliant on instream vegetation.

Larval and 0+ juvenile fishes were captured from four contrasting vegetation categories on five dates (17 and 27 May, 7 and 16 June, 1 July 2011). The vegetation categories were: (1) "submerged macro", consisting of horned pondweed (*Zannichellia palustris* L.), fennel pondweed (*Potamogeton pectinatus* L.), shining pondweed (*Potamogeton lucens* L.) and perfoliate pondweed (*Potamogeton perfoliatus* L.); (2) "emergent macro", consisting of common reed, reed sweet-grass**,** lesser pond-sedge (*Carex acutiformis* (Ehrh.)), greater reedmace and yellow iris (*Iris pseudacorus* (L.)); (3) "floating-leaved macro", dominated by yellow water-lily; and (4) “filamentous algae”. Vegetation was categorised as “mixed” for sampling points where no one category was dominant according to the DAFOR scale; Dominant >75%, Abundant 51-75%, Frequent 26-50%, Occasional 11-25%, Rare <11% (Palmer *et al.*, 1992; Bennion *et al.*, 2000; Duigan *et al.*, 2007).

For the purpose of this study, the vegetation categories were ranked as floating-leaved macro < emergent macro < submerged macro < filamentous algae in terms of structural complexity. The floating-leaved macro category was classed as the least complex habitat due to its low stem density and the low surface area to volume ratio of

Fig. 4.1 Location and site map of the River Ancholme where the habitat structure surveys were carried out.

Plate 4.1. Survey site and sampling at Hibaldstow on the River Ancholme.

its leaves (i.e. sparse stems and broad floating leaves). The emergent macro and submerged macro categories were classed as moderate complexity because of their higher stem densities and, in the case of the submerged macro category, the higher surface area to volume ratio of its leaves. The filamentous algae category was classed as the most complex habitat because of its very high density and surface area to volume ratio.

A random stratified sampling strategy was employed, with point sampling by electric fishing (PSE) conducted in each of the vegetation categories (481 points in total) as it has been used successfully in other studies (Copp & Peňáz, 1988; Copp, 1989; Persat & Copp, 1989; Janáč & Jurajda, 2007). PSE was chosen as it is more useful than other techniques for investigating habitat use by 0+ fishes as well as being cost efficient in terms of time, effort and expense. In addition, point data can be analysed using conventional and multivariate statistical techniques (Copp, 1989; Garner, 1997). Fish hidden by cover are also captured more efficiently using this method than other methods described below (Perrow *et al.*, 1996). Seine nets were not suitable, as they cover too large an area and are inefficient in dense vegetation, in addition to damaging the habitat. Direct observations were also not suitable for this study because the smallest larvae could only be identified under a microscope and because fishes had to be collected for diet analysis. PSE has also been used successfully in a number of other studies examining habitat use in larval and 0+ juvenile fishes (Copp, 1990b; Copp & Jurajda, 1993; Garner, 1995, 1996a, 1998; Penaz *et al.*, 1995; Jurajda, 1999; Jurajda *et al.*, 2001). Notwithstanding, Cowx *et al.*, (2001) concluded that PSE is likely to underestimate 0-group fish density in late summer due to the small sample size. Copp, (2010) has also stated that sampling accuracy and precision decrease as fishes enter the juvenile period of development. In this study, fish were only analysed up to larval step 6. A 2 kVA generator powering a control box with a 220 V 100 Hz Pulsed

DC output was employed and moved upstream through the sampling site in a small boat. The anode operator waded ahead of the boat and randomly selected sampling points by walking forward and putting the anode in the water at a random point. At each point the anode, which had a 15 cm diameter ring, was energised before it was submersed for a few seconds approximately half way down the water column; at deep sites the anode was only submersed to a safe distance (i.e. before the hand of the operator touched the water). All immobilised fishes were collected in a dip-net by a nets man positioned alongside the anode operator. There were two other members of the team, one that was in charge of the equipment (generator, control box and pushing the boat) whilst the fourth member stayed on the bank and was a scribe for the data collection. All members of the team in the river moved stealthily through the water to minimise disturbance of the sampling points. For each point, all 0+ fishes were transferred to a small container and preserved in 4% formalin solution and the water depth (nearest cm) was measured. The percentage area of each vegetation category was measured using the DAFOR scale described previously (within 1 m^2 from the centre of the sampling point). Zooplankton was also collected to investigate differences in species composition, density and diversity between vegetation categories. Five random 10 L water samples were collected from each vegetation category after the PSE had been completed and sieved through a 100-μm-meshed net. It was not possible to collect the zooplankton simultaneously with the PSE samples due to the disturbance caused by netting the fishes.

Laboratory analysis

In the laboratory, the fishes were identified to species, measured (SL, nearest 0.5 mm) and categorised as either finfold larvae, finformed larvae or 0+ juveniles (Section 3.2.1). When available, the contents of the entire gastrointestinal tract were removed from 30 individuals of each fish species in each vegetation category (total roach n = 279, bream n = 203). Fish gut contents and zooplankton samples from each vegetation category were analysed as described in Section 3.2.1.

Data analysis

The number of each taxon in each zooplankton sub-sample was used to calculate the mean (± SD) density (plankters L^{-1}) in each vegetation category for each sampling occasion. The diversity of the zooplankton populations and the diets of finfold larvae, finformed larvae and 0+ juvenile roach and bream in each vegetation category was also calculated by applying the Shannon-Wiener diversity index (H') (Washington, 1984). Dietary and zooplankton data were used to calculate the relative abundance (percent abundance) of each taxon in the diet/zooplankton (Hynes, 1950; Hyslop, 1980). Bray-Curtis similarity matrices (Czekanowski, 1913; Bray & Curtis, 1957) were calculated in the PRIMER statistical package, using the mean percent abundance of each taxon in the diet/zooplankton in each vegetation category, and presented as non-metric multidimensional scaling (MDS) plots to test for an effect of habitat complexity on zooplankton and diet composition, as described previously (Section 3.2.1). Permutational multivariate analysis of variance (PERMANOVA; a distance-based permutational multivariate analysis of variance; Anderson 2001; McArdle & Anderson 2001; Anderson 2005) was then conducted to test for differences in the diet composition of finfold larvae, finformed larvae and 0+ juvenile roach and bream between each vegetation category using the number of each zooplankton taxon in the gastrointestinal tract of individual fish. "PERMANOVA is a computer program for testing the simultaneous response of one or more variables to one or more factors in an ANOVA experimental design on the basis of any distance measure, using permutation methods" (Anderson 2001). The analysis in this test used 9999 random permutations of appropriate units (Anderson & ter Braak 2003) and was based on log10(x+1) transformed data. The Monte Carlo P-value was used, where a value <0.05 is significant and a value ≥ 0.05 is not significant. PERMANOVA gives the permutation P-value and also the Monte Carlo asymptotic P-value for each test performed. When there is a large number of possible permutations, these two P-values should be very close to one another, however, when there are very few possible permutations, then the P-value associated with the permutation test may be quite different, because of this limitation, and so the Monte Carlo P-value should be used in preference (Anderson 2001). This method has the advantage over classical multivariate analysis of variance (MANOVA) by having no restrictive upper limit on the number of species that can be analysed simultaneously.

Mean zooplankton densities (all taxa combined) were compared between vegetation categories using either independent samples *t*-tests or Mann-Whitney *U*-tests (Dytham, 2003). Gut fullness was used as a measure of feeding activity to see if habitat structure had an influence on feeding behaviour. Feeding activity was assessed for finfold larvae, finformed larvae and 0+ juvenile roach and bream in each vegetation category using the points method (Hynes, 1950; Hyslop, 1980) as described in Section 3.2.1.

When catches were sufficient, prey selection by finfold larvae, finformed larvae and 0+ juvenile roach and bream was calculated to test for an influence of habitat complexity on feeding behaviour (see Section 3.2.1). The condition of finfold larvae, finformed larvae and 0+ juvenile roach and bream was also calculated (see Section 3.2.1) to determine if there was an effect of vegetation category using independent samples *t*-tests.

4.3 RESULTS

4.3.1 INFLUENCE OF HABITAT STRUCTURE ON ZOOPLANKTON COMPOSITION, DENSITY AND DIVERSITY

The most abundant taxa in the zooplankton across all surveys were *Polyphemus pediculus* (L.)*,* copepod nauplii, cyclopoid copepods, *Simocephalus exspinosus* (DeGeer) and *Ceriodaphnia* sp. Other taxa recorded were *E. lamellatus*, *Bosmina* sp., *Daphnia* spp., *Alona* spp., *Chydorus* spp., Harpacticoidea, Rotifera, *Simocephalus vetulus* (Müller) and *Sida crystallina* (Müller). The mean percent abundances of most zooplankton taxa (*P. pediculus*, *S. expinosus*, cyclopoid copepods and *Ceriodaphnia* sp.) were highest in floating-leaved and emergent vegetation (the least complex habitats). There were no significant differences in zooplankton densities (all taxa combined) between floating-leaved, submerged and emergent vegetation in all surveys (Kruskal-Wallis test, $P>0.05$).

In the first two surveys, *P. pediculus* dominated the zooplankton in all vegetation categories (Figs 4.2a, b). A mixture of zooplankton taxa, namely *P. pediculus,* copepod nauplii, *S. exspinosus* and *Ceriodaphnia* sp., was found in the third survey, with no single taxon dominating the samples (Fig. 4.2c). The zooplankton in the fourth and fifth surveys comprised mainly copepod nauplii, cyclopoid copepods and *Ceriodaphnia* sp., with a higher mean percent abundance of cyclopoid copepods in the latter survey (Figs 4.2d, e). The fifth was the only survey when *S. crystallina* was found (in floating-leaved vegetation; none were found in submerged or emergent vegetation).

In the first and second surveys, the highest densities of *P. pediculus* were found in emergent vegetation, with means of 23 L^{-1} and 51 L^{-1}, respectively (Fig. 4.3a). Densities were significantly higher in floating-leaved and emergent vegetation than submerged vegetation in the second survey (Kruskal-Wallis test, $P<0.05$). A similar pattern was observed for other key taxa in the second survey, with the densities of *S. exspinosus* and cyclopoid copepods being highest in emergent vegetation and lowest in submerged vegetation (Kruskal-Wallis tests, $P<0.05$). In the third survey, densities of all zooplankton taxa were generally low, but Ceriodaphnia sp. and copepod nauplii densities were generally higher than the second survey (Figs 4.3a-f). In contrast to the first two surveys, the highest densities of *Ceriodaphnia* sp. and *P. pediculus* were found in submerged vegetation, with means of 11 L^{-1} and 8 L^{-1} respectively, whereas those of *S. exspinosus* were found in emergent and floating-leaved vegetation (Fig. 4.3a, c). Similarly, the highest densities of copepod nauplii were found in floating-leaved vegetation (7 L^{-1}) (Fig. 4.3f). In the fourth survey, copepod nauplii were found in similar densities in all vegetation categories, whilst *Ceriodaphnia* sp. and cyclopoid copepods were found in low densities in submerged (2 and 3 L^{-1}) and floating-leaved (4 and 5 L^{-1}) vegetation, and higher (although still low) densities in emergent vegetation (6 and 9 L^{-1}). *Simocephalus exspinosus* was recorded in only low densities, but significantly higher densities were found in floating-leaved than in emergent and submerged vegetation (Fig. 4.3d; Kruskal-Wallis test, $P<0.05$). In the last survey, *Ceriodaphnia* sp. was found in low densities in all vegetation categories, but were most abundant (6 L^{-1}) in emergent vegetation (Fig. 4.3e). Cyclopoid copepods and copepod nauplii were also found in low densities, with densities lowest in emergent and highest in submerged vegetation but no results were significantly different (Fig. 4.3e; Kruskal-Wallis test, $P<0.05$).

There was no significant difference in mean zooplankton diversity between habitat types in the first three surveys (ANOVA, $P>0.05$; Fig. 4.4a-c). In the fourth survey there was a substantial difference in the mean zooplankton diversity in floating-leaved vegetation compared to submerged and emergent vegetation, although this was not significant (ANOVA, $P>0.05$; Fig 4.4d). By comparison, in the fifth survey the diversity of zooplankton was highest in emergent vegetation compared to submerged and floating-leaved habitats (Fig. 4.4e). There is no data from the filamentous or mixed vegetation categories as separate zooplankton samples could not be collected on every survey.

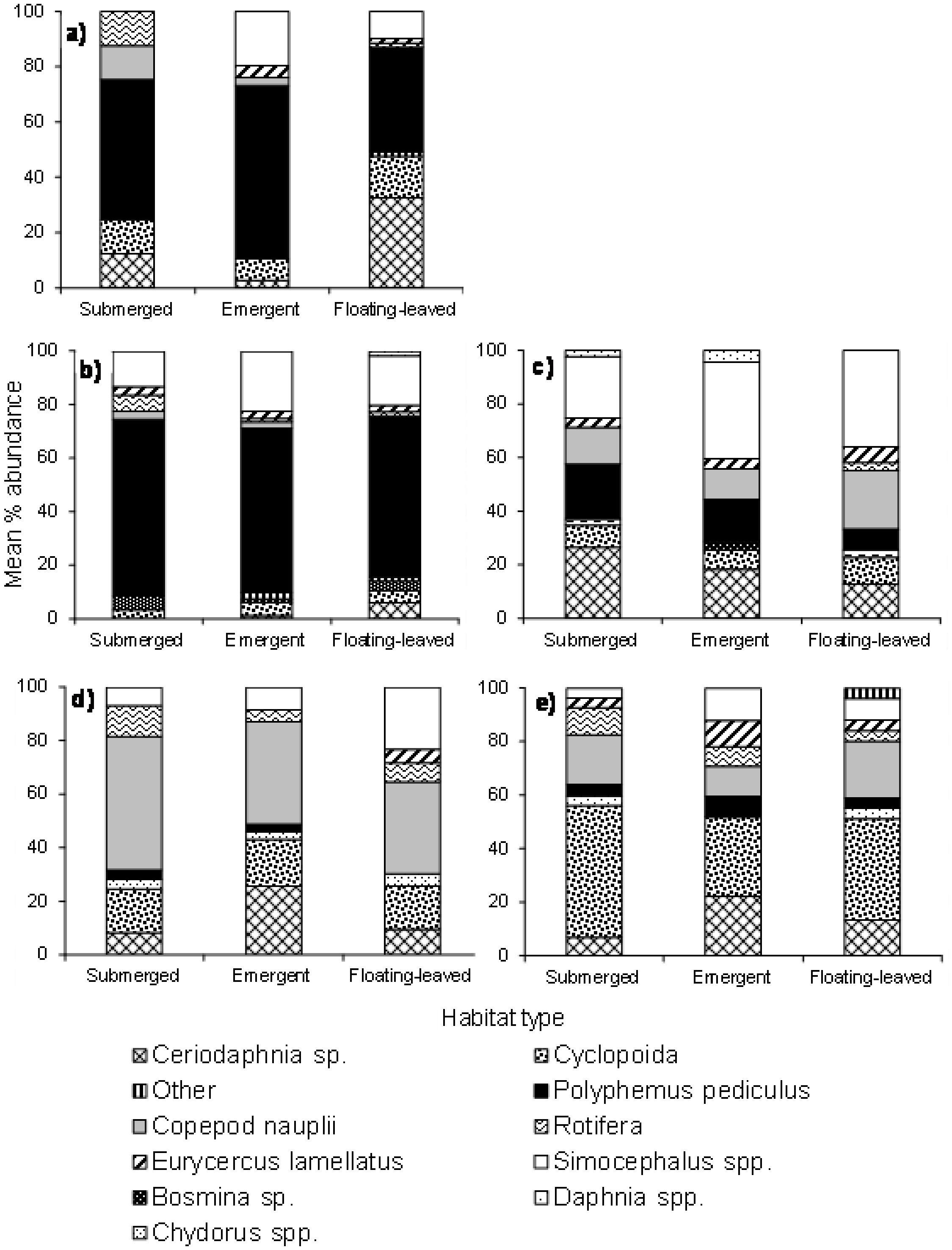


Fig. 4.2 Zooplankton composition in submerged, emergent and floating-leaved vegetation in the River Ancholme on a) 17 May, b) 27 May, c) 7 June, d) 16 June and e) 1 July 2011.

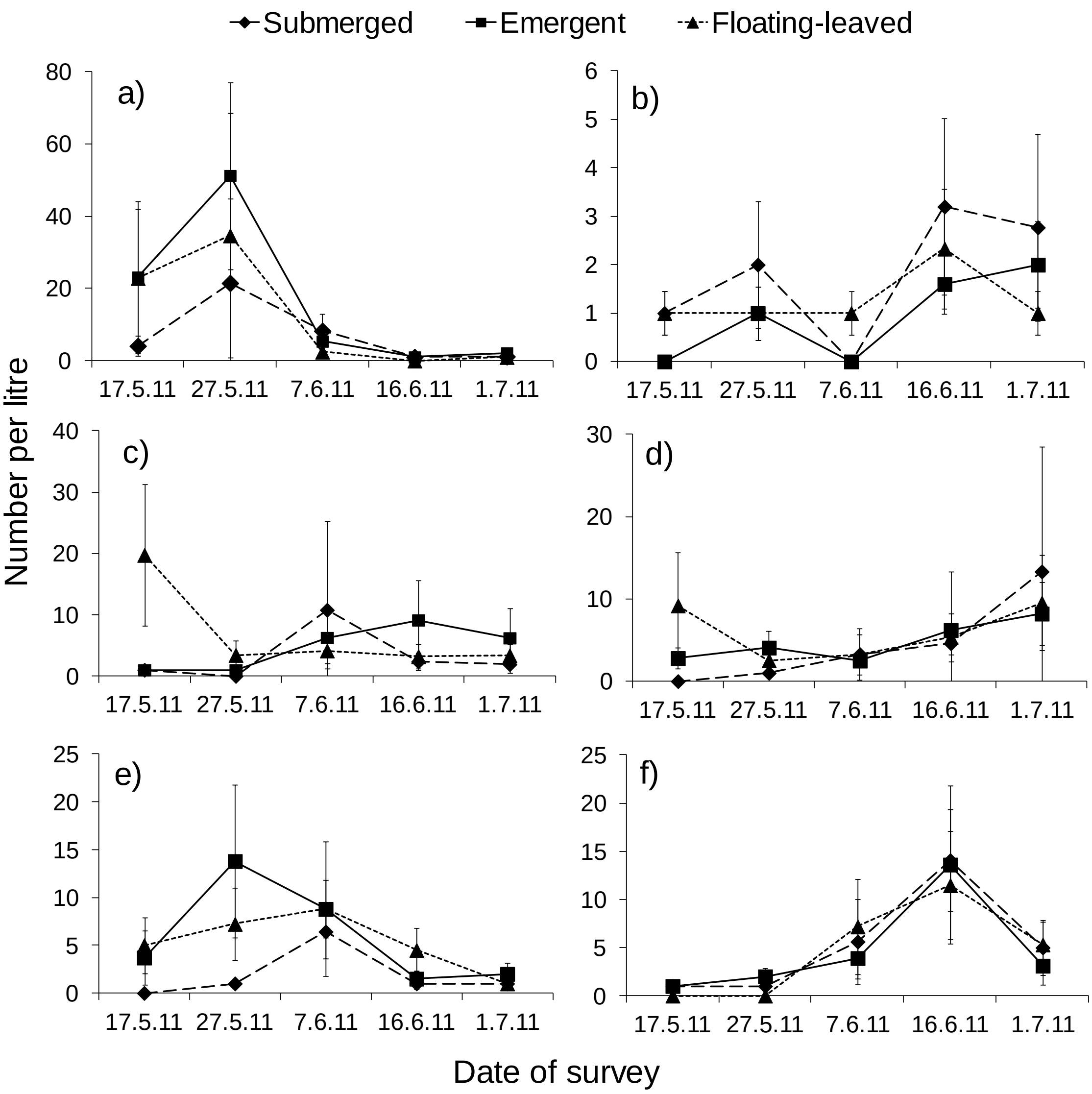


Fig. 4.3 Number per litre with standard deviations of a) *Polyphemus pediculus*, b) Rotifera, c) *Ceriodaphnia* sp., d) Cyclopoida, e) *Simocephalus exspinosus* and f) copepod nauplii in submerged (♦), emergent (■) and floating-leaved (▲) vegetation in the River Ancholme on five sampling occasions.

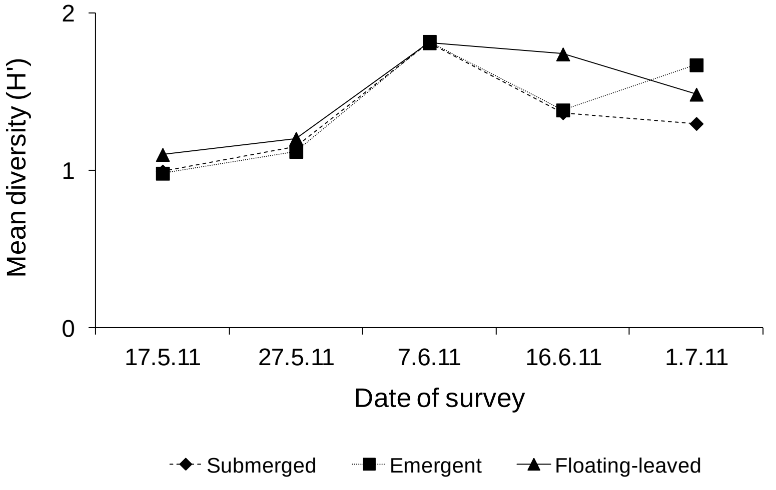


Fig. 4.4 Mean zooplankton diversity (H') in submerged (♦), emergent (■) and floating-leaved (▲) vegetation in the River Ancholme over five surveys.

4.3.2 INFLUENCE OF HABITAT STRUCTURE ON DIET COMPOSITION, DIVERSITY AND EVENNESS, AND FEEDING ACTIVITY OF 0+ FISHES

A total of 481 points was sampled over five surveys, of which 161 were dominated by floating-leaved vegetation, 90 were dominated by emergent vegetation, 36 were dominated by filamentous algae, 35 were dominated by submerged vegetation and 159 were characterised by mixed vegetation. Only 17% of points contained fish (Table 4.1), with roach (*n* = 273) and bream (*n* = 185) being the most abundant (100% of total 0+ catch) (Table 4.2). In the first survey all fish were finfold larvae, in the second, third and fourth surveys all fish were finformed larvae, and in the last survey all fishes were 0+ juveniles. Catches from emergent vegetation were insufficient for analysis of roach.

Table 4.1 Number of points sampled and containing fish in each vegetation category in the River Ancholme.

Vegetation category	Number of points sampled	Number of points containing fish	% of points containing fish
Submerged	35	8	23
Emergent	90	1	1
Floating-leaved	161	28	17
Filamentous algae	36	33	91
Mixed vegetation	159	13	8

Table 4.2 Number of fish examined for diet analysis in each vegetation category, S = submerged, E = emergent, F = floating-leaved, A = filamentous algae and M = mixed vegetation, in the River Ancholme.

		Vegetation category					
Species	Ecospecies	S	E*	F	A	M	Total
Roach	YL	6	0	49	36	0	91
	OL	14	0	64	27	31	136
	J	0	0	14	27	5	46
Bream	YL	20	0	45	32	0	97
	OL	23	8	25	23	0	79
	J	0	0	5	3*	1*	9
	Total	63	8	202	148	37	458

*Catches from emergent vegetation were insufficient for analysis of roach and juvenile bream for filamentous algae and mixed vegetation. NB: YL = finfold larvae, OL = finformed larvae and J = 0+ juveniles.

In the first two surveys, the feeding activity of finfold and finformed roach larvae was higher in floating-leaved vegetation (3.63 and 7.28 respectively) and filamentous algae (3.83 and 7.85 respectively) than in submerged vegetation (2.16 and 6.7 respectively) (Fig. 4.5a-e). By contrast, there were no significant differences in the feeding activity of finformed roach larvae between vegetation categories in the third and fourth surveys (Fig. 4.5a-e) or of 0+ juvenile roach in the last survey (independent samples *t*-test, *P*>0.05; Fig. 4.5a-e).

The feeding activity of finfold bream larvae in the first survey was higher in floating-leaved vegetation (2.725) and filamentous algae (3.03) than in submerged vegetation (1.76) (Fig. 4.6a-d), by comparison in the second survey the feeding activity of finformed bream larvae was highest in floating-leaved vegetation (5.1) (Fig. 4.6a-d). Insufficient numbers of bream were captured for analysis in the third survey (Fig. 4.6a-d). No significant differences were found in the feeding activity of finformed bream larvae between vegetation categories in the fourth survey (independent samples *t*-test $P > 0.05$; Fig. 4.6a-d), and only enough 0+ juvenile bream were found in one vegetation category (floating-leaved vegetation) in the last survey to calculate feeding activity (Fig. 4.6a-d).

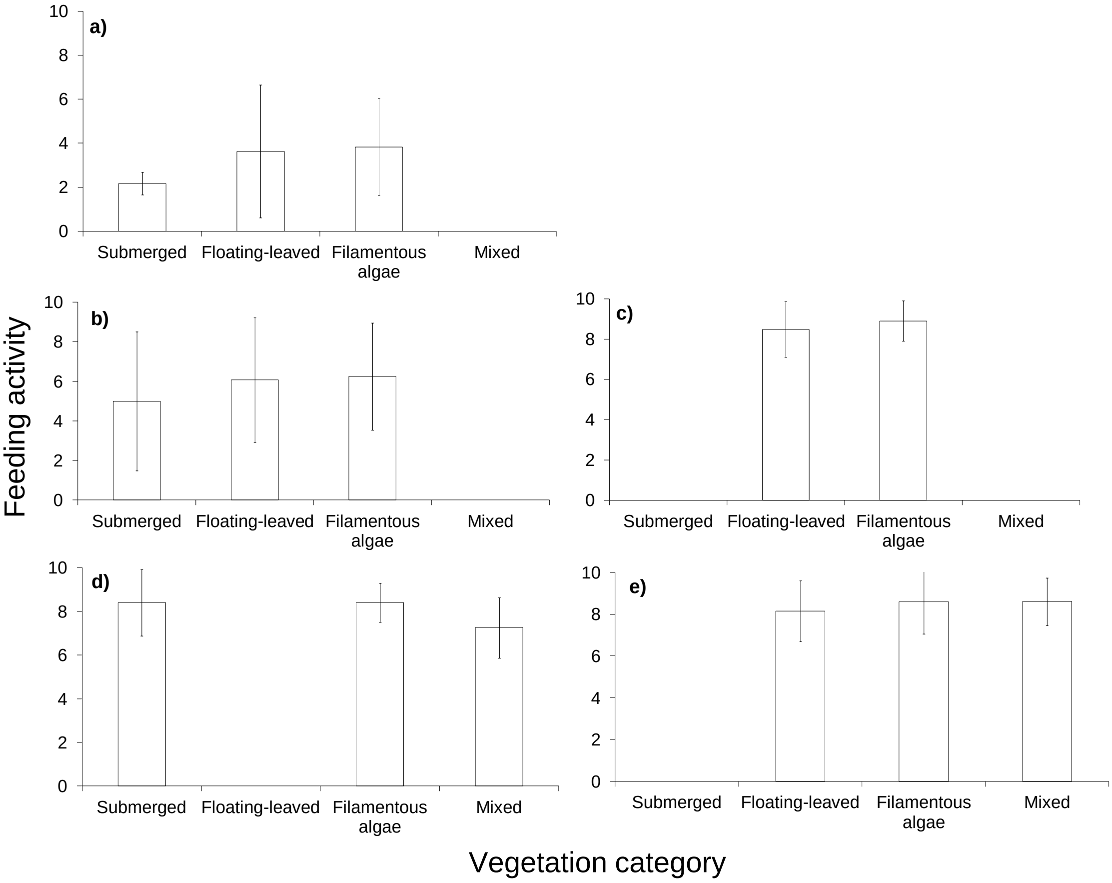


Fig. 4.5 Mean feeding activity with standard deviation of 0+ roach (*n* = 273) in each vegetation category, over five sampling occasions a) 17 May (finfold), b) 27 May (finformed), c) 7 June (finformed), d) 16 June (finformed) and e) 1 July 2011 (0+ juvenile), in the River Ancholme. NB: Catches from emergent vegetation were insufficient for analysis of roach.

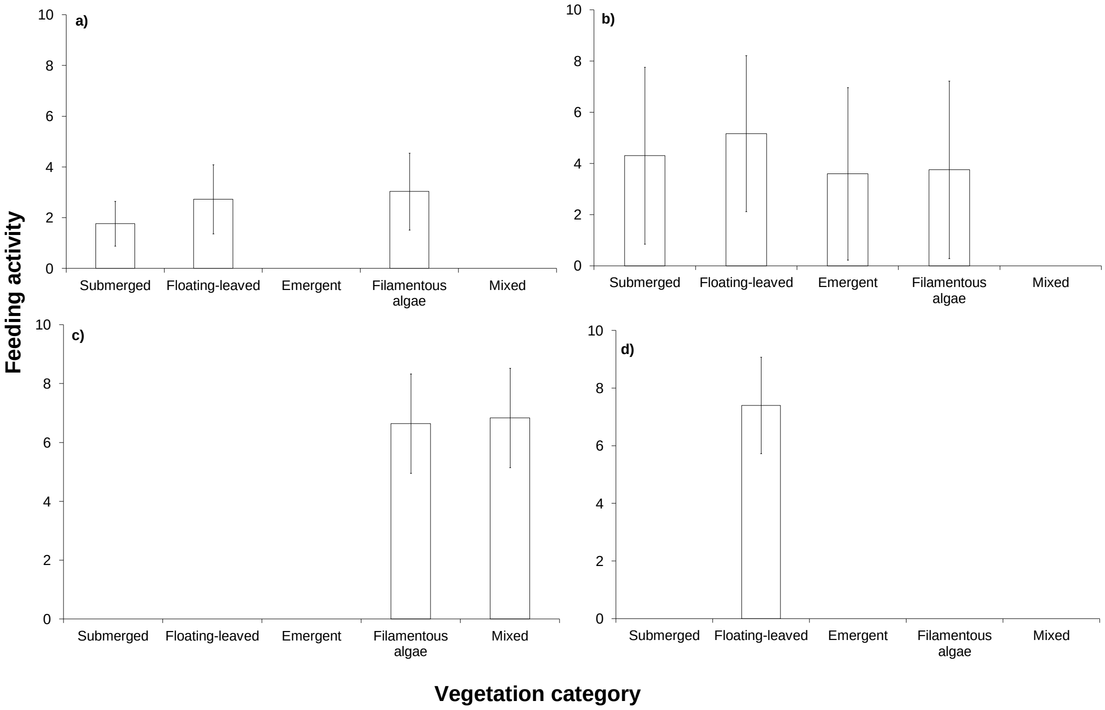


Fig. 4.6 Mean feeding activity with standard deviations of 0+ bream (*n* = 185) in each vegetation category, over five sampling occasions a) 17th May (finfold), b) 27th (finformed) May, c) 7th June (finformed), d) 16th June (finformed) and e) 1st July 2011 (0+juveniles), in the River Ancholme . NB: no bream were caught on 7th June 2011.

The main prey of roach and bream varied between vegetation categories. In the first survey, the main prey of finfold roach larvae were Rotifera (50%), *Bosmina* sp. (33.33%) and copepod nauplii (16.66%), but relative abundance varied between vegetation categories (submerged, filamentous algae and floating-leaved) (Fig. 4.7a). In floating-leaved vegetation, fewer Rotifera (27.78%) but more copepod nauplii (34.58%), cyclopoid copepods (12.97%) and *Ceriodaphnia* sp. (13.96%) were consumed than in submerged vegetation (Fig. 4.7a). By contrast, the diet of finfold roach larvae in filamentous algae consisted of more copepod nauplii (54.89%) but fewer *Ceriodaphnia* sp. (3%), *Bosmina* sp. (5%) and cyclopoid copepods (9.12%) than in submerged and floating-leaved vegetation (Fig. 4.7a). The diet composition of finfold roach was significantly different between floating-leaved and submerged vegetation in the first survey (Monte-Carlo test, $P<0.05$; Table 4.3; Fig. 4.9).

In the second survey, the mean percent abundance of *P. pediculus* in the diet of finformed roach larvae was higher than all other taxa in submerged, filamentous algae and floating-leaved vegetation (Fig. 4.7b). A higher percentage of Rotifera were consumed by finformed roach larvae in submerged (33.33%) than in filamentous algae (2.7%) and floating-leaved vegetation (0%) (Fig. 4.7b). A mixture of other species (*S. exspinosus*, cyclopoid copepods and *Ceriodaphnia* sp.) were consumed in small numbers in filamentous algae and floating-leaved vegetation (Fig. 4.7b). No significant differences in diet composition between vegetation categories were recorded in the second survey (Monte-Carlo tests, *P*>0.05; Table 4.3; Fig. 4.10)

In the third survey, *E. lamellatus* and *Ceriodaphnia* sp. were abundant in the diet of finformed roach larvae in filamentous algae (41.66% and 31.64%) respectively) (Fig. 4.7c). A mixture of species, namely *S. exspinosus* (21.71%)*, Ceriodaphnia* sp. (13.34%) and *P. pediculus* (13.44%), made up the diet of finformed roach larvae in floating-leaved vegetation, with no single taxon dominating the diet. No significant differences in diet composition between vegetation categories were recorded in the third survey (Monte-Carlo tests, *P*>0.05; Table 4.3; Fig. 4.11)

In the fourth survey, finformed roach larvae consumed a high percentage of *S. exspinosus* in mixed vegetation (54.38%) and filamentous algae (69.88%), with the rest of the diet comprising smaller amounts of *E. lamellatus*, *P. pediculus*, *Ceriodaphnia* sp. and cyclopoid copepods (Fig. 4.7d). By comparison, the diet of finformed roach larvae in submerged vegetation was dominated by chironomid larvae, comprising 70% of the diet (Fig. 4.7d), with significantly fewer *S. exspinosus* (6.49%) consumed than in the other vegetation categories (Kruskal-Wallis tests, *P*<0.05). There were significant differences in the diet composition of roach between vegetation categories (Monte-Carlo tests, *P*<0.05; Table 4.3; Fig. 4.12).

In the last survey, the mean percent abundance of *E. lamellatus* and cyclopoid copepods was high in the diets of 0+ juvenile roach in mixed vegetation (61.47% and 56.62% respectively), filamentous algae (29.82% and 56.62% respectively) and floating-leaved (20.81% and 49.96% respectively) vegetation. There were significant differences in the diet composition of roach between vegetation categories (Monte-Carlo tests, *P*<0.05; Table 4.3; Fig. 4.13). The main difference was the greater amount of *Ceriodaphnia* sp. (16.1%) consumed in floating-leaved vegetation compared with mixed vegetation (5.1%) and filamentous algae (0.9%) (Fig. 4.7e). Further investigation revealed that the diet of roach was influenced by the composition of the mixed vegetation (Fig. 4.7e). For example, there were significantly more *S. exspinosus* in the diets of 0+ juvenile roach larvae in submerged vegetation consisting of *Potamogeton* spp. and filamentous algae than in submerged vegetation consisting mainly of yellow water-lily and filamentous algae or horned pondweed and filamentous algae (Kruskal-Wallis test, *P*<0.05; Fig. 4.8). Additionally, the mean percent abundance of chironomid larvae was significantly higher in mixed vegetation consisting of *Potamogeton* spp. and filamentous algae than mixed vegetation comprising yellow water-lily and filamentous algae or horned pondweed and filamentous algae (Kruskal-Wallis tests, *P*<0.05; Fig.

4.8). The mixed vegetation in the last survey comprised yellow water-lily and filamentous algae only, so no further analysis was possible.

In the first survey, there were no substantial differences in the diversity or evenness of the diets of finfold roach larvae in floating-leaved vegetation and filamentous algae (Fig. 4.14a). In the second survey, diversity and evenness were higher in filamentous algae than in submerged and floating-leaved vegetation (Fig. 4.14b). By comparison, in the third survey diversity and evenness were higher in floating-leaved vegetation than in filamentous algae (Fig. 4.14c). In the fourth survey, diversity and evenness were higher in mixed vegetation than in submerged vegetation and filamentous algae (Fig. 4.14d). In the last survey, diversity and evenness were higher in mixed and floating-leaved vegetation than in filamentous (Fig. 4.14e).

Table 4.3 PERMANOVA output examining the influence of vegetation category (submerged, floating-leaved and mixed) on the diet composition of 0+ roach. **Bold values** = significant result.

Date	Ecospecies	Source	DF	SS	MS	Pseudo-F	P(Monte-Carlo)
17.5.2011	Finfold	Veg Cat	2	11862	5931.2	2.274	**0.0194**
27.5.2011	Finformed	Veg Cat	2	9926.4	4963.2	1.762	0.0968
7.6.2011	Finformed	Veg Cat	1	3742.9	3742.9	1.8755	0.1224
16.6.2011	Finformed	Veg Cat	2	15481	7740.6	4.861	**0.0026**
1.7.2011	0+ juveniles	Veg Cat	2	10435	5217.6	3.5284	**0.0028**

Degrees of freedom (DF), Sum of squares (SS), Mean square (MS). Pseudo-F is based on expected mean squares as in univariate ANOVA and P(Monte-Carlo) is used when there are very few possible permutations.

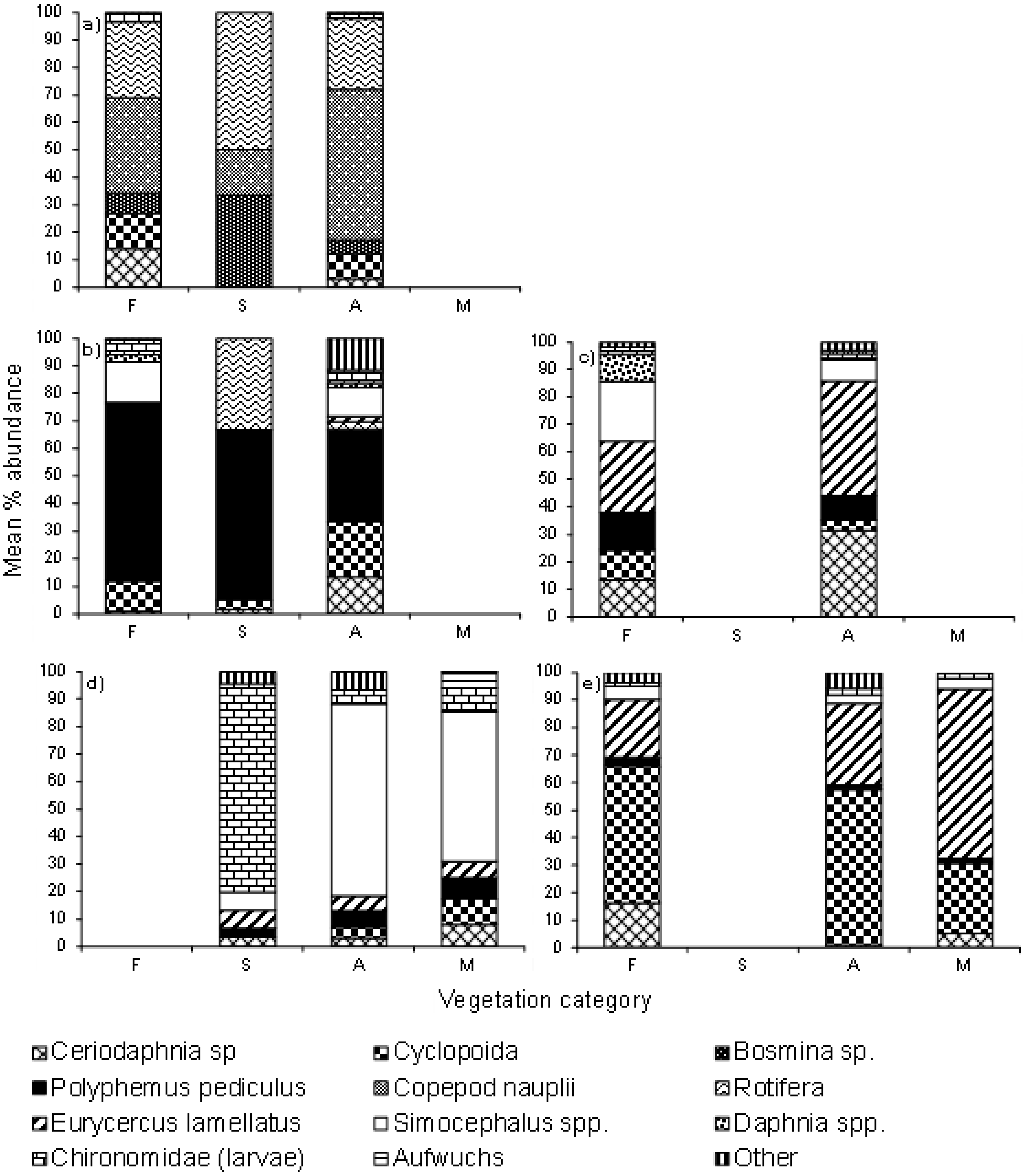


Fig. 4.7 Diet composition of 0+ roach on a) 17 May (finfold roach), b) 27 May (finformed roach), c) 7 June (finformed roach), d) 16 June (finformed roach) and e) 1 July (0+ juvenile roach) 2011, in submerged vegetation (S), Floating-leaved vegetation (F), filamentous algae (A) and mixed vegetation (M) in the River Ancholme.

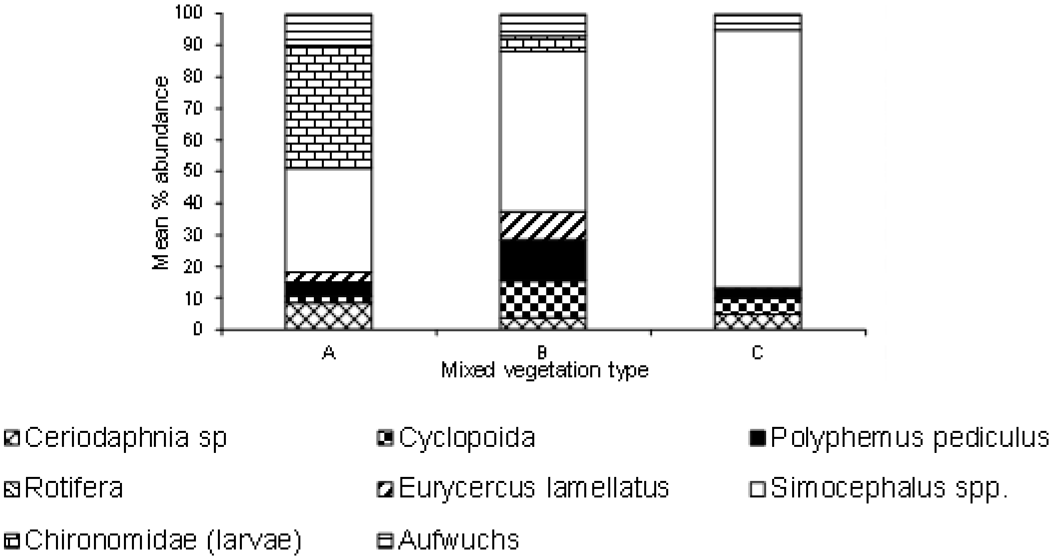


Fig. 4.8 Diet composition of finformed roach larvae on 16 June 2011 in three sub-categories of mixed vegetation, where A = *Potamogeton* spp. and filamentous algae, B = yellow water-lily and filamentous algae and C = horned pondweed and filamentous algae.

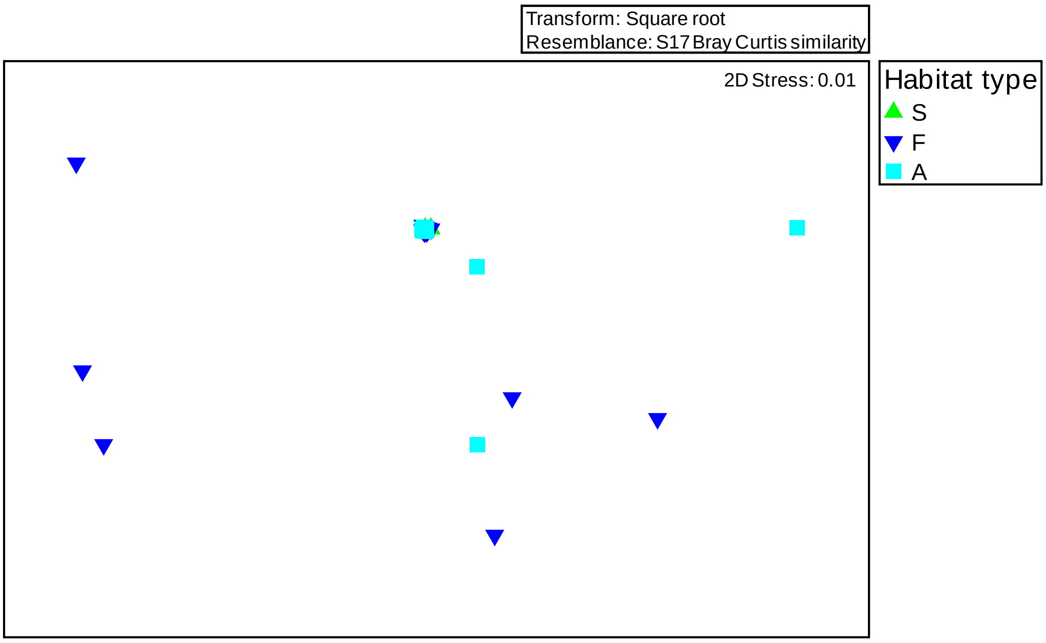


Fig. 4.9 Non-metric multidimensional scaling plot of the similarity in the diet composition of finfold roach in submerged vegetation (S), floating-leaved vegetation (F) and filamentous algae (A) on 17 May 2011, River Ancholme.

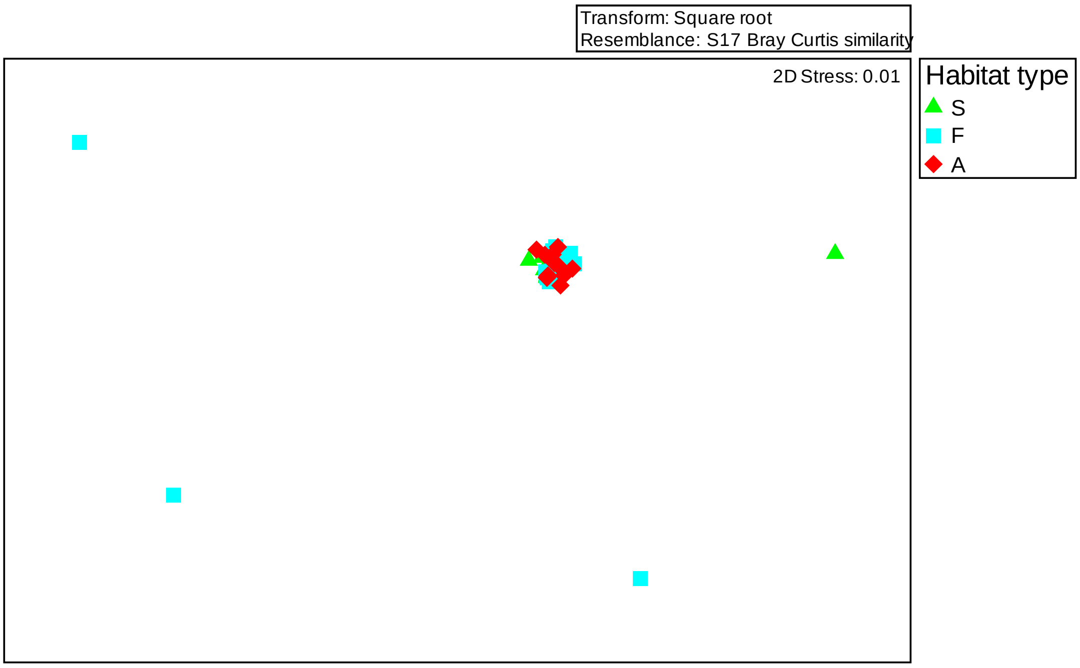


Fig. 4.10 Non-metric multidimensional scaling plot of the similarity in the diet composition of finformed roach in submerged vegetation (S), floating-leaved vegetation (F) and filamentous algae (A) on 27 May 2011, River Ancholme.

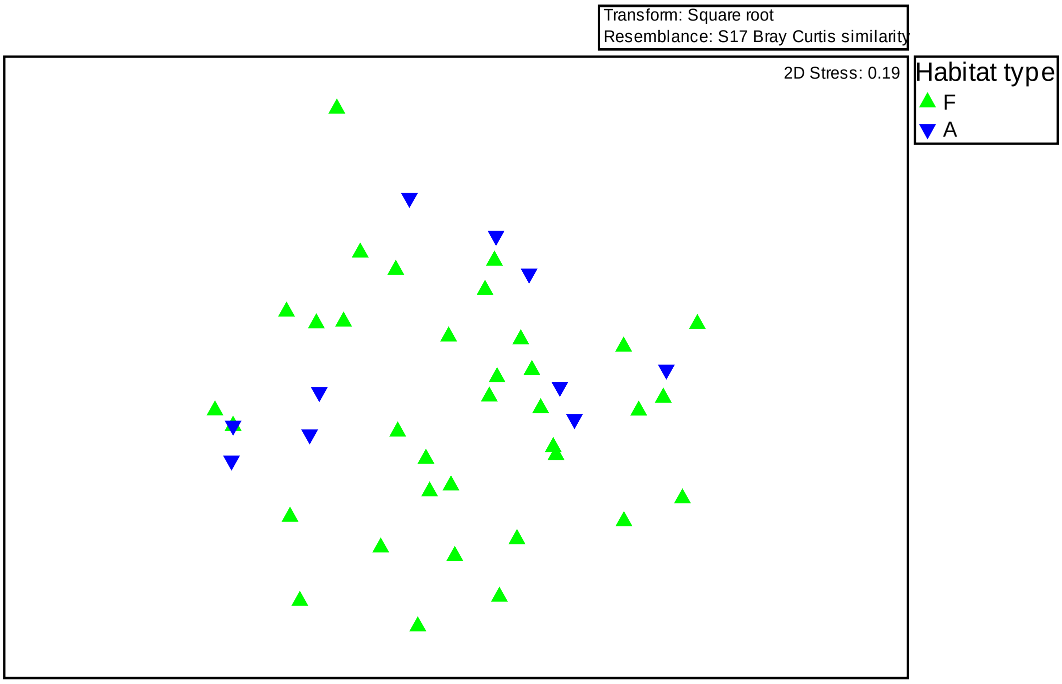


Fig. 4.11 Non-metric multidimensional scaling plot of the similarity in the diet composition of finformed roach in submerged vegetation (S), floating-leaved vegetation (F) and filamentous algae (A) on 7 June 2011, River Ancholme.

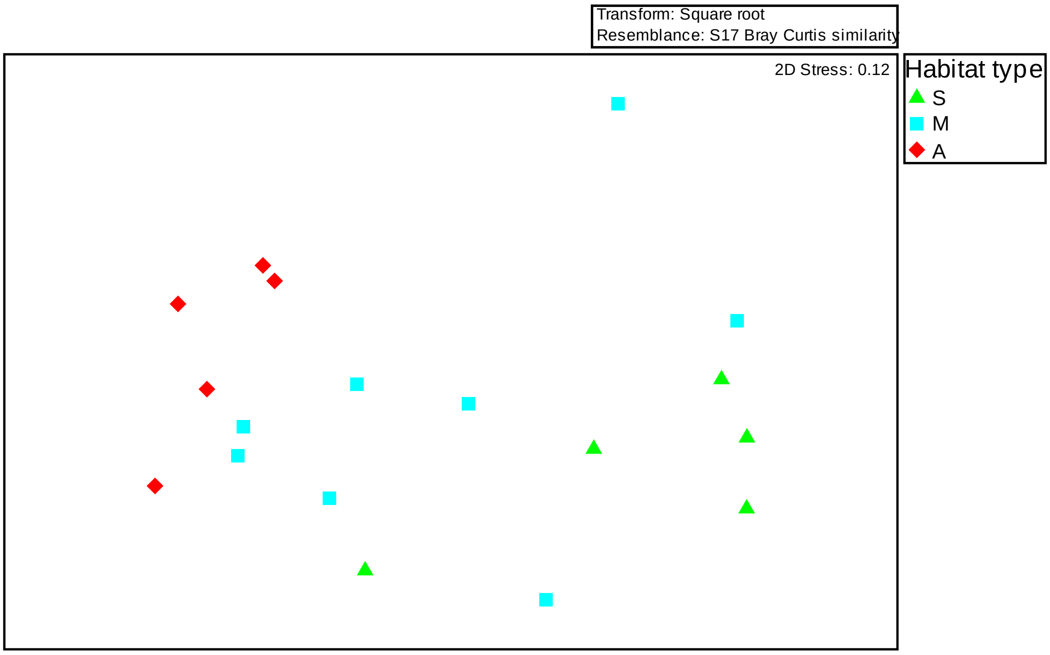


Fig. 4.12 Non-metric multidimensional scaling plot of the similarity in the diet composition of finformed roach in submerged vegetation (S), floating-leaved vegetation (F) and filamentous algae (A) on 16 June 2011, River Ancholme.

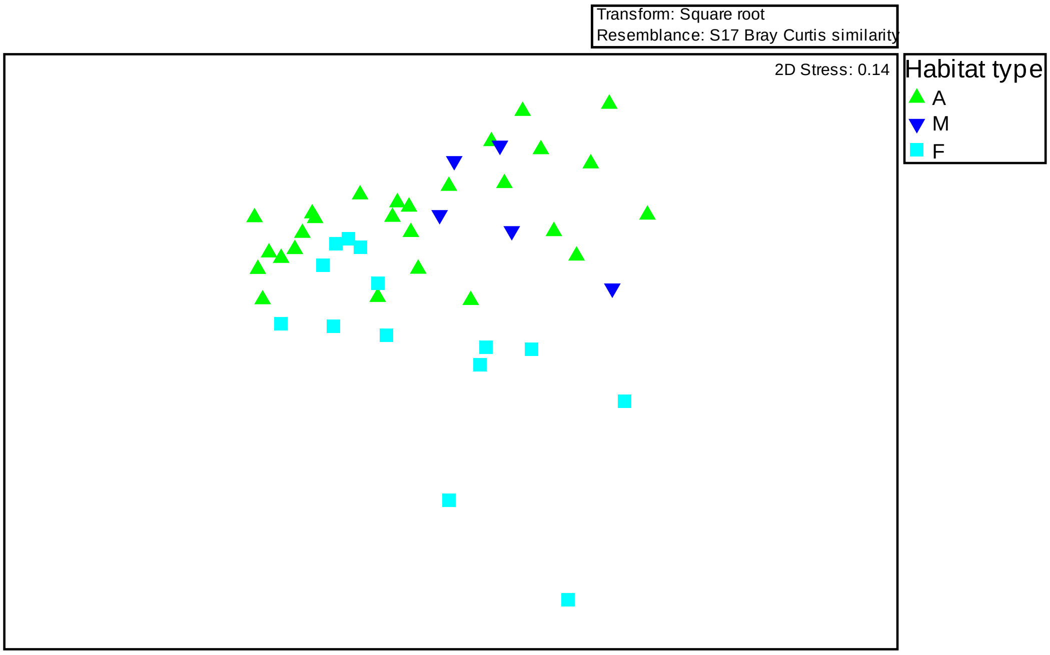


Fig. 4.13 Non- metric multidimensional scaling plot of the similarity in the diet composition of 0+ juvenile roach in submerged vegetation (S), floating-leaved vegetation (F) and filamentous algae (A) on 1 July 2011, River Ancholme.

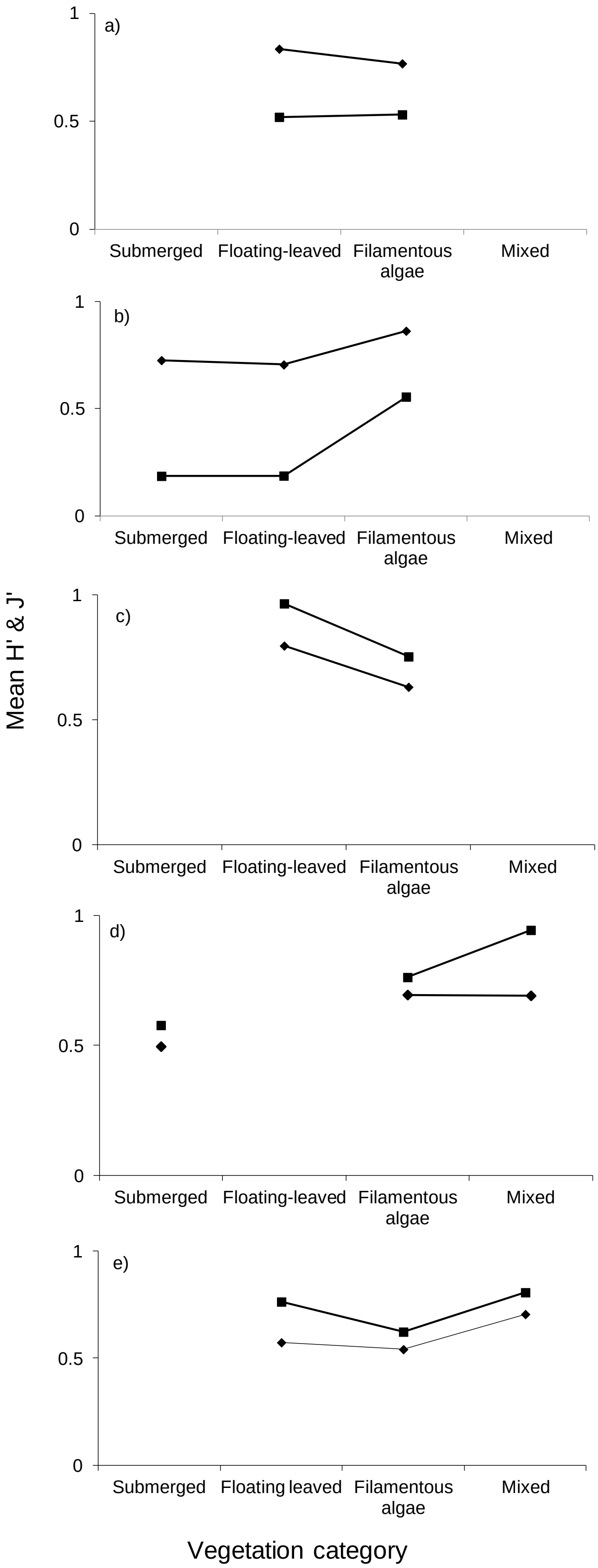


Fig. 4.14 Mean diversity (H' ■) and evenness (J ♦) of the diets of 0+ roach in four vegetation categories on the River Ancholme on a) 17 May (finfold roach), b) 27 May (finformed roach), c) 7 June (finformed roach), d) 16 June (finformed roach) and e) 1 July (0+ juvenile roach), 2011.

In the first survey, the mean percent abundance of rotifers in the diets of finfold bream larvae was higher than all other taxa, comprising 45% of the diet in submerged vegetation (Fig. 4.15a). The rest of the diet was made up of copepod nauplii (14.5%), *Ceriodaphnia* sp. (16.2%), cyclopoid copepods (6.3%) and *Bosmina* sp. (11.90%) (Fig. 4.15a). In floating-leaved vegetation, the diet consisted of a mixture of taxa, namely copepod nauplii (32.4%), *Ceriodaphnia* sp. (20.5%), Rotifera (13.8%) and cyclopoid copepods (12.96%) (Fig. 4.15a). By comparison, copepod nauplii (60%) were the most common prey in filamentous algae, with smaller numbers of rotifers (15.6%), *Ceriodaphnia* sp. (5.46%) and cyclopoid copepods (3.48%) also consumed (Fig. 4.15a). The diet composition of finfold bream was significantly different between vegetation categories in the first survey (Monte-Carlo test, $P<0.05$; Table 4.4; Fig. 4.16).

In the second survey, the diets of finformed bream larvae consisted of a mixture of taxa, namely *P. pediculus*, cyclopoid copepods, Rotifera, *Ceriodaphnia* sp. and *Daphnia* spp., in submerged vegetation, floating-leaved vegetation and filamentous algae (Fig. 4.15b). In contrast, the diets in emergent vegetation were dominated by cyclopoid copepods, which comprised 61% of the gut content with the rest of the diet consisting of *Bosmina* sp. and chironomid larvae (Fig. 4.15b). Nonetheless, the diet composition of finformed bream was not significantly different between vegetation categories (Monte-Carlo test, $P>0.05$; Table 4.4; Fig. 4.17).

No bream were caught in the third survey. In the fourth survey, finformed bream larvae were only captured in mixed vegetation and filamentous algae. In both habitats, the diets were dominated by *Ceriodaphnia* sp., with the mean percent abundance being 58% in filamentous algae and 75% in mixed vegetation (Fig. 4.15c). The rest of the diet consisted of a small number of cyclopoid copepods, *Daphnia* spp., *Simocephalus* spp. and *E. lamellatus* (Fig. 4.15c). The diet of finformed bream were not significantly different between vegetation categories in this survey (Monte-Carlo test, $P>0.05$; Table 4.4; Fig. 4.18)

In the last survey, 0+ juvenile bream were only captured in sufficient numbers for analysis in floating-leaved vegetation, where the mean percent abundance of *Ceriodaphnia* sp. was 73%, with small numbers of cyclopoid copepods (13.13%) and *E. lamellatus* (5.8%) also consumed (Fig. 4.15d).

The diversity and evenness of the diets of finfold bream were highest in floating-leaved vegetation and filamentous algae than in submerged vegetation in the first survey (Fig.

4.19a). In the second survey, diversity was highest in filamentous algae than in submerged vegetation, floating-leaved and emergent vegetation, whereas evenness was highest in emergent vegetation than in filamentous algae, submerged vegetation and floating-leaved vegetation (Fig. 4.19b). No bream were caught in the third survey. In the fourth survey, diversity and evenness were highest in filamentous algae than in filamentous algae (Fig. 4.19c). Bream were only caught in floating-leaved vegetation in the fifth survey so no comparisons could be made.

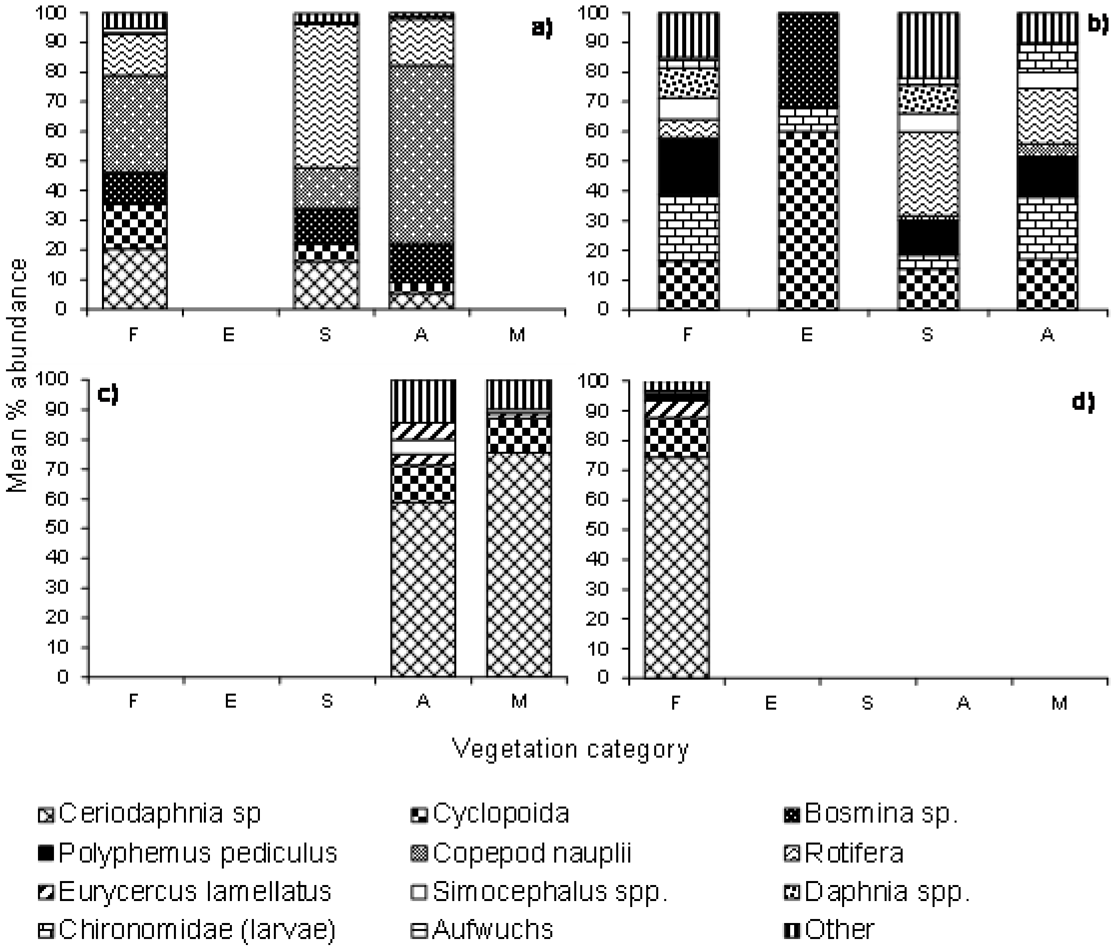


Fig. 4.15. Diet composition of 0+ bream on a) 17 May (finfold bream), b) 27 May (finformed bream), c) 16 June (finformed bream) and d) 1 July (0+ juvenile bream), 2011, in submerged vegetation (S), Emergent vegetation (E), Floating-leaved vegetation (F), filamentous algae (A) and mixed vegetation (M) in the River Ancholme.

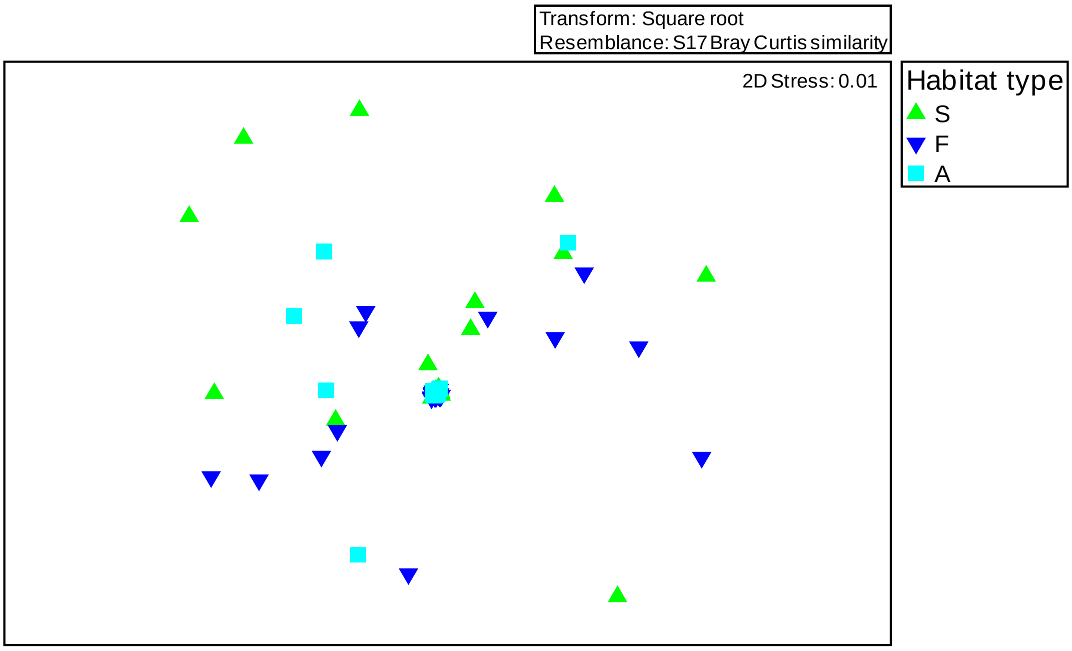


Fig. 4.16 Non-metric multidimentional scaling plot of the similarity in diet composition of finfold bream in submerged vegetation (S), floating-leaved vegetation (F) and filamentous algae (A) on 17 May 2011, River Ancholme.

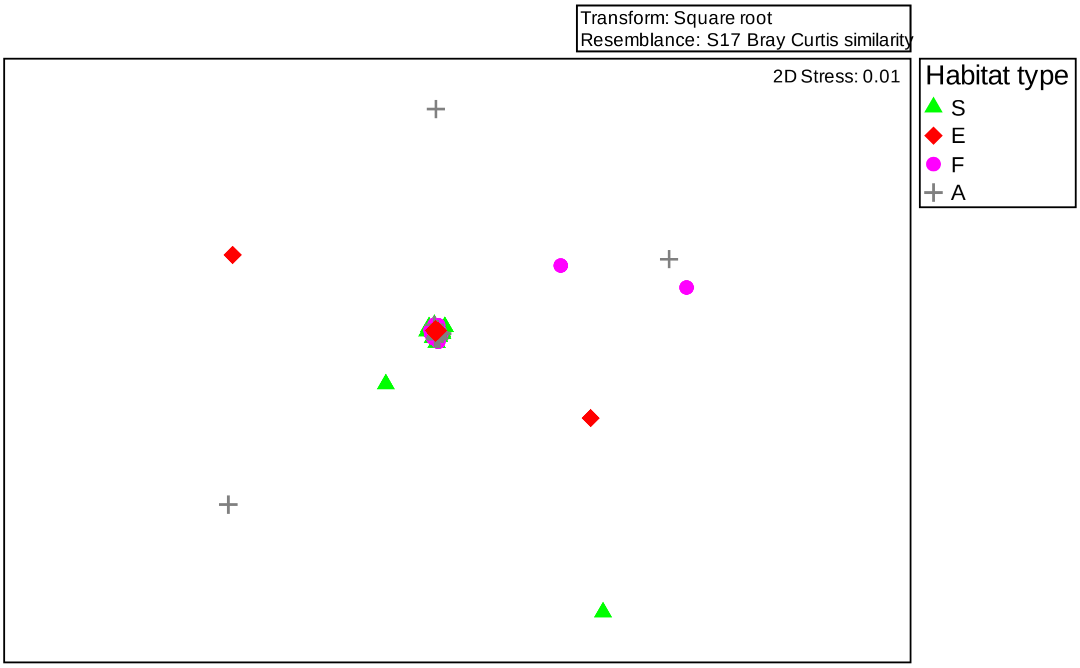


Fig. 4.17 Non-metric multidimentional scaling plot of the similarity in diet composition of finformed bream in submerged vegetation (S), floating-leaved vegetation (F), emergent vegetation (E) and filamentous algae (A) on 27 May 2011, River Ancholme.

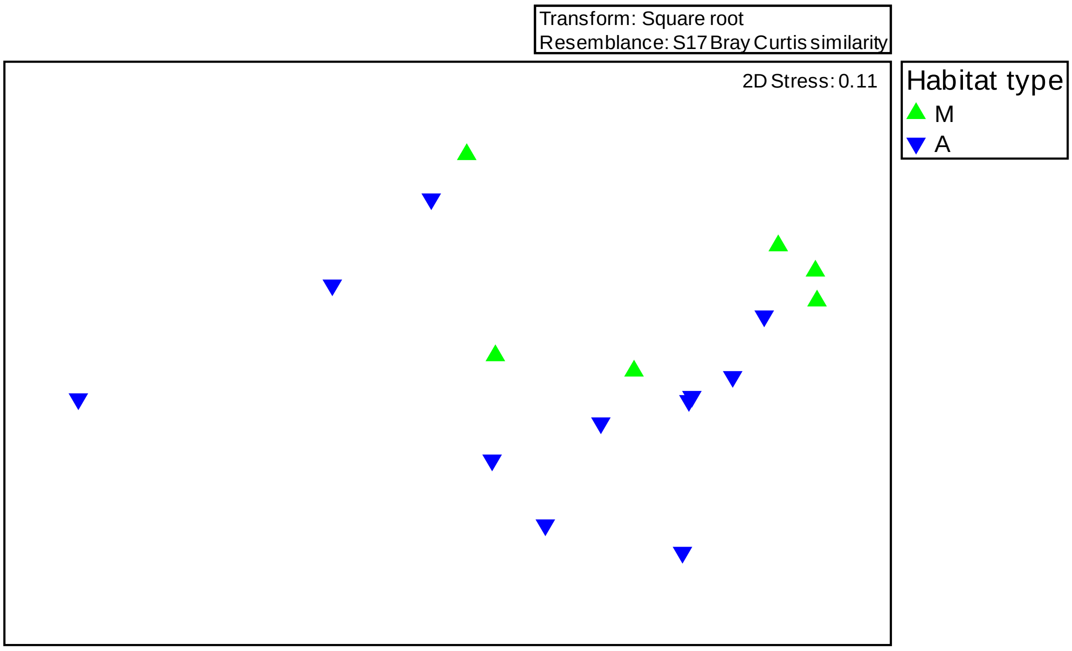


Fig. 4.18 Non-metric multidimentional scaling plot of the similarity in the diet composition of finformed bream in mixed vegetation (M) and filamentous algae (A) on 16 June 2011, River Ancholme.

Table 4.4 PERMANOVA output examining the influence of the vegetation categories (submerged, emergent, floating leaved and mixed) on the diet of bream. **Bold values** = significant result.

	Source	DF	SS	MS	Pseudo-F	P(MC)
17.5.2011	Veg Cat	3	34252	17126	5.1809	**0.0001**
27.5.2011	Veg Cat	4	15309	5103	1.3425	0.1567
7.6.2011	Veg Cat	-	-	-	-	-
16.6.2011	Veg Cat	1	2356.3	2356.3	1.242	0.2906
1.7.2011	Veg Cat	-	-	-	-	-

- no bream were captured on 7.6.2011 and were only captured from one vegetation category on 1.7.2011. NB: All fish analysed on 17.5.2011 were finfold larvae, all fish analysed on 27.5.2011 and 16.6.2011 were finformed larvae. Degrees of freedom (DF), Sum of squares (SS), Mean square (MS). Pseudo-F is based on expected mean squares as in univariate ANOVA and P(Monte-Carlo) is used when there are very few possible permutations.

In general, 0+ roach avoided or consumed *Ceriodaphnia* sp. in proportion to their abundance, irrespective of vegetation category (Fig. 4.20). By comparison, *E. lamellatus* and *Daphnia* spp. were generally selected, irrespective of vegetation category. No other consistent patterns in electivity indices were found for 0+ roach, but electivity indices did differ between vegetation categories in some surveys. For example, in the first survey, selection of copepod nauplii and cyclopoid copepods by finfold roach larvae was stronger in floating-leaved (+1 and -0.2 respectively) than in submerged vegetation (+0.2 and -1 respectively) (Fig. 4.20). Conversely, *Ceriodaphnia* sp. were consumed in proportion to their abundance in submerged vegetation (0), but avoided in floating-leaved vegetation (-0.7) (Fig. 4.20). In the second survey, *S.*

exspinosus were avoided in submerged vegetation (-1), but selected in floating-leaved vegetation (+0.5).

Ceriodaphnia sp., rotifers and *Bosmina* sp. were generally selected or consumed in proportion to their abundance by 0+ bream, irrespective of vegetation category (Fig. 4.21). Conversely, *P. pediculus* and *S. exspinosus* were generally avoided, irrespective of vegetation category, although avoidance was invariably strongest in emergent vegetation (both -1). Again, some survey-specific differences in electivity indices between vegetation categories were noted. For example, in the second survey, finformed bream larvae selected cyclopoid copepods in floating-leaved vegetation (+0.5), but avoided them in emergent vegetation (-0.7) (Fig. 4.21). There were no significant differences in the condition of larval and 0+ juvenile roach and bream between vegetation categories (independent samples *t*-tests, all P>0.05) (Table 4.5).

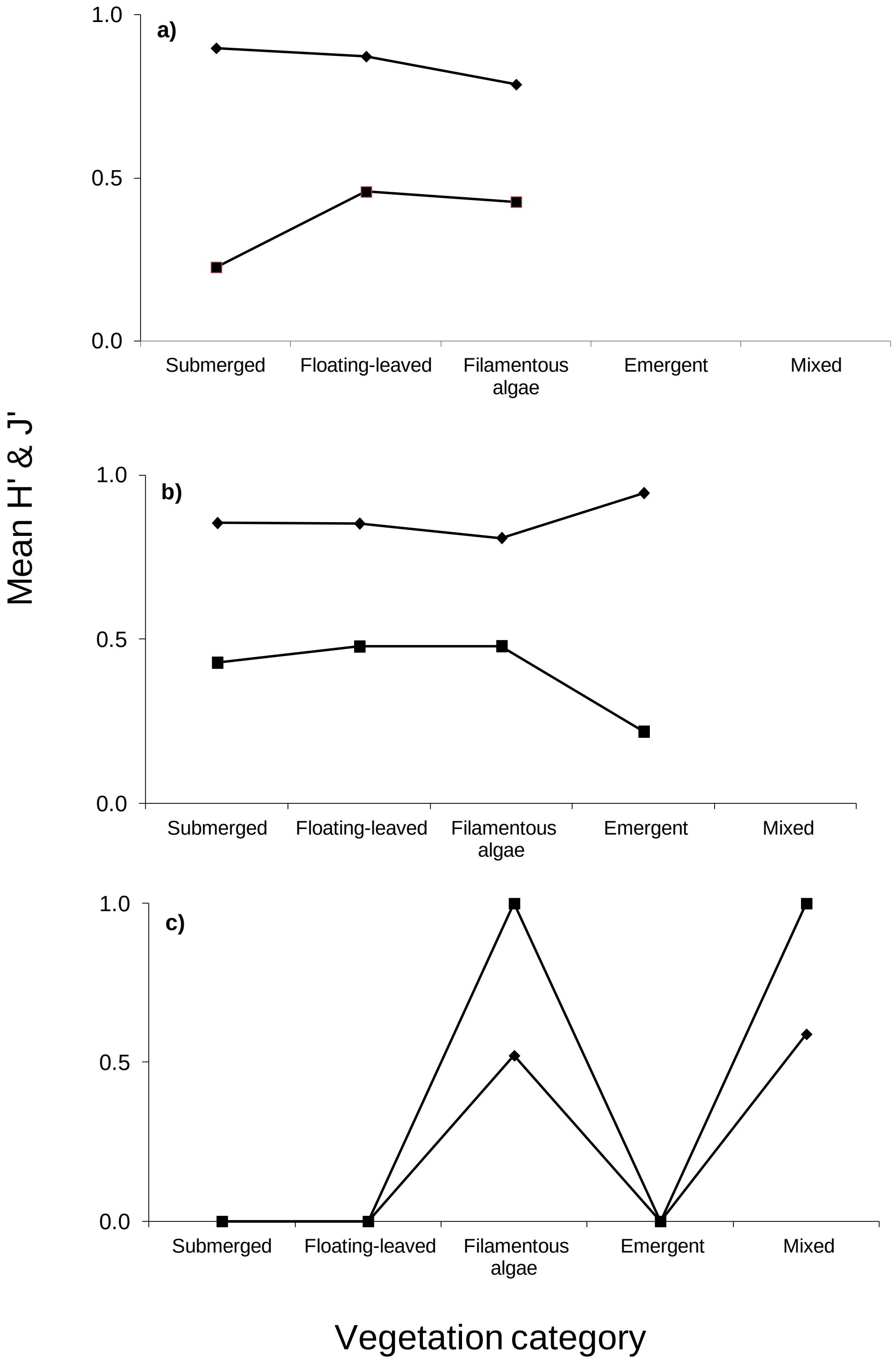


Fig. 4.19 Mean diversity (H’) and evenness (J’) of the diet of 0+ bream from different vegetation categories on the River Ancholme on a) 17 May (finfold bream), b) 27 May (finformed bream) and c) 16 June (0+ juvenile bream).

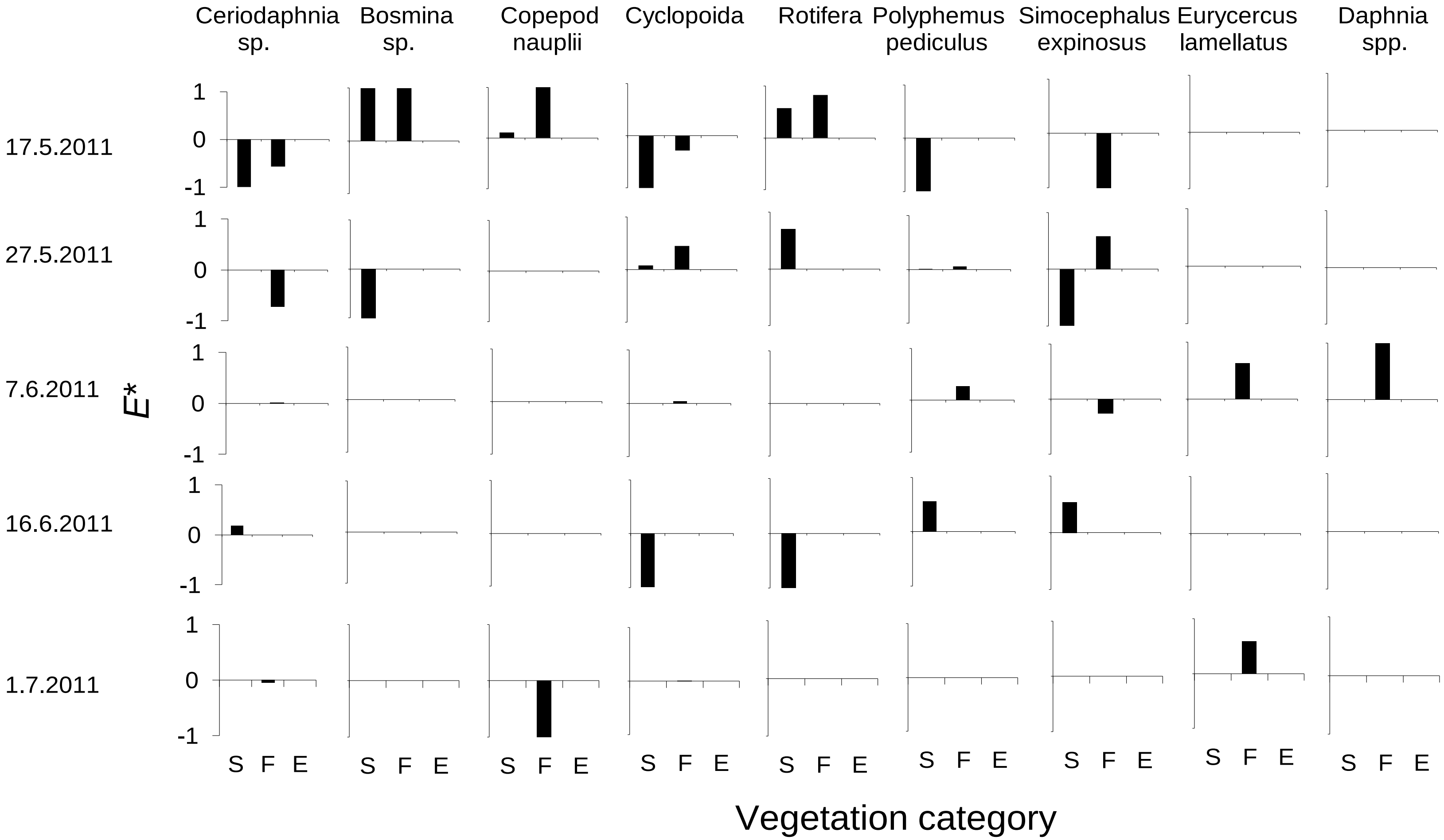


Fig. 4.20 Mean electivity (*E**) of nine zooplankton taxa for 0+ roach over five surveys on the River Ancholme in two vegetation categories; submerged (S) and floating-leaved (F). (No roach were caught in emergent vegetation). NB: All fish analysed on 17.5.2011 were finfold larvae, all fish analysed on 27.5.2011, 7.6.2011 and 16.6.2011 were finformed larvae and on the 1.7.2011 they were all 0+ juveniles.

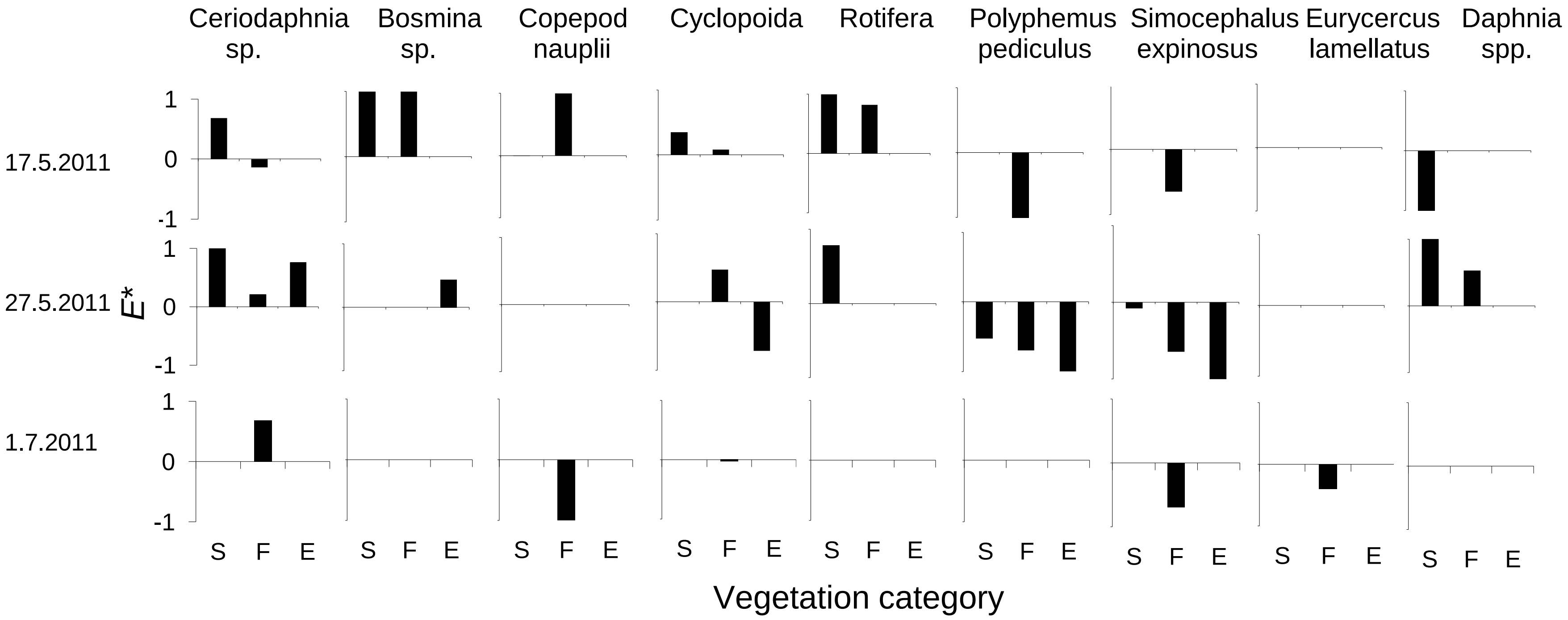


Fig. 4.21 Mean electivity (*E**) of nine zooplankton taxa for 0+ bream over five surveys on the River Ancholme in three vegetation categories, submerged (S), floating leaved (F) and emergent (E). NB: All fish analysed on 17.5.2011 were finfold larvae, all fish analysed on 27.5.2011 were finformed larvae and on the 1.7.2011 they were all 0+ juveniles.

Table 4.5 Mean (± SD) condition of finfold (Fld), finformed (Fmd) and 0+ juvenile (J) roach and bream captured from submerged (S), floating-leaved (F), emergent (E), filamentous algae (A), and mixed (M) vegetation categories on the River Ancholme 2011.

			Vegetation category				
Survey date	Species	Ecospecies	S	F	E	A	M
17.5.2011	Roach	Fld	1.00 (± 0.06)	1.00 (± 0.08)	–	1.00 (±0.07)	–
	Bream	Fld	1.00 (± 0.05)	1.00 (± 0.08)	–	1.00 (± 0.06)	–
27.5.2011	Roach	Fmd	1.00 (± 0.03)	1.00 (± 0.04)	–	1.00 (± 0.15)	–
	Bream	Fmd	1.00 (± 0.02)	1.00 (± 0.08)	1.00 (± 0.05)	1.00 (± 0.03)	–
7.6.2011	Roach	Fmd	–	1.00 (± 0.04)	–	1.00 (± 0.06)	1.00 (± 0.02)
	Bream	Fmd	–	–	–	–	–
16.6.2011	Roach	Fmd	1.00 (± 0.01)	–	–	1.00 (± 0.05)	1.00 (± 0.02)
	Bream	Fmd		–	–	1.00 (± 0.01)	1.00 (± 0.02)
1.7.2011	Roach	J	–	1.04 (± 0.06)	–	1.00 (± 0.05)	1.00 (± 0.02)
	Bream	J	–	1.00 (± 0.01)	–	–	–

– catches insufficient for analysis

4.4 DISCUSSION

Habitat structure is one of the fundamental factors determining the distribution of organisms at all spatial scales (Garner, 1996b; McAbendroth *et al.*, 2005; Thomaz & Cunha, 2010; Nunn *et al.*, 2012). Aquatic vegetation is particularly important, especially in freshwater ecosystems, as the high diversity of biomasses and morphologies provide a wide range of habitat structure and complexity for associated fauna (van der Velde, 1981; Dvořaki & Bestz, 1982; Stansfield *et al.*, 1997; Grenouillet *et al.*, 2002; Nurminen & Horppila, 2002; Cazzanelli *et al.*, 2008). Many factors influence the distribution of prey that are suitable for consumption by 0+ fishes. For example, different habitats support different zooplankton populations (Savino & Stein, 1982; Werner *et al.*, 1983; Richardson, 1992; Persson & Eklöv, 1995; Bass *et al*., 1997; Perrow *et al.*, 1999; Basu *et al.*, 2000; Burks *et al.*, 2002; van Donk & van de Bund, 2002; Mazzeo *et al.*, 2003; Okun & Mehner, 2005; Agostinho *et al.*, 2007; Nunn *et al.*, 2012). For example, Kuczyńska-Kippen, (2006a) found that the stem length of different macrophyte structures appeared to be the best predictor of all macrophyte parameters in addition to pH and chlorophyll *a* for the chemical variables, for explaining variation in rotifer densities. In addition, densities of zooplankton including open water species of cyclopoid copepods have been found to be higher in complex beds of stonewart (*Chara* *tomentosa*, L.) compared to less complex beds of lesser bulrush (*Typha angustifolia,* L.) in shallow lakes in Poland (Kuczynska-Kippen, 2006b).

All macrophyte species support communities of epiphytic algae, Protozoa and detritus, which in turn provide food for zooplankton (Eminson & Moss, 1980; Thiel-nielsen & Søndergaard, 1999; Duggan *et al.*, 2001; Kuczyńska-Kippen & Nagengast, 2003). In addition, the areas of reduced flow that occur around macrophytes provide suitable conditions for plankton development due to increased water-retention times (Bass *et al.*, 1997; Spaink *et al.*, 1998; Nunn *et al.*, 2007b). It is therefore widely believed that diverse beds of aquatic macrophytes are ideal nursery habitats for many fish species (Sheaffer & Nickum, 1986; Dewey & Jennings, 1992; Nunn *et al.*, 2007b), providing abundant and diverse communities of invertebrates, which are needed by 0+ fishes during ontogeny, and which allow species-specific dietary specialization (Werner *et al.*, 1977; Cyr & Downing, 1988; Bryan & Scarnecchia, 1992; Bass *et al.*, 1997; Dewey *et al.*, 1997; Garner, 1997; Stansfield *et al.*, 1997; Cattaneo *et al.*, 1998; Grenouillet *et al.*, 2000, 2001b; Nunn *et al.*, 2007a). Indeed, higher densities of 0+ fishes have been found in macrophytes compared with open-water habitats (Venugopal & Winfield, 1993; Dibble *et al*., 1996), with water bodies without macrophytes generally less productive than those with macrophytes (Northcott, 1979; Laughlin & Werner, 1980; Whiteside *et al.*, 1985; Killgore *et al.*, 1989; Bryan & Scarnecchia, 1992).

As the River Ancholme is highly regulated and has a high biomass and diversity of vegetation, it was expected that density and diversity of zooplankton would be high. Indeed, another study on the Ancholme found that zooplankton richness and density were considerably higher than in the rivers Trent, Don and Yorkshire Ouse, which support lower biomasses and diversities of vegetation, with cyclopoid copepods, rotifers and daphnids being particularly abundant (Taylor, 2012). In this study, the floating-leaved vegetation category (dominated by yellow water-lily) created the least complex habitat structure (i.e. sparse stems and broad floating leaves) compared with the submerged, emergent and filamentous algae vegetation categories. It is often found in close proximity to open water making yellow water-lily a favourable refuge for open water zooplankton species (Kuczyńska-Kippen & Nagengast, 2006). Similarly, the structure of the emergent vegetation category, which was dominated by common reed and greater reedmace was relatively simple but created an intermediate level of habitat complexity because of their higher stem densities (Kuczyńska-Kippen & Nagengast, 2006). The submerged vegetation category was dominated by *Potamogeton* spp., which have a higher surface area to volume ratio than do the floating-leaved and emergent vegetation categories, making it more suitable for phytophilic taxa. The filamentous algae vegetation category created the most complex habitat because of its very high density and surface area to volume ratio. In this study, it was generally found that the highest densities of most zooplankton taxa were found in emergent and floating-leaved vegetation (the least complex habitats) rather than submerged vegetation (the most complex habitats). For example, in the first and second surveys, although *P. pediculus* dominated in all habitats, higher densities were found in floating-leaved and emergent vegetation than in submerged vegetation.

Differing macrophyte structures provide numerous benefits for many fish species and their prey, for example, providing refuge from predators and high flows (Bass *et al*., 1997; Perrow *et al.*, 1999; Basu *et al.*, 2000; Burks *et al.*, 2002; van Donk & van de Bund, 2002; Mazzeo *et al.*, 2003; Okun & Mehner, 2005; Agostinho *et al.*, 2007; Nunn *et al*., 2007c; Nunn *et al.*, 2012). Stansfield *et al.* (1997) demonstrated some refuge effect in *Daphnia* spp. as they perisisted in macrophyte stands after they had been eliminated from open water. Burks *et al*. (2001) similarly demonstrated that daphnids sought macrophyte refuge in the presence of roach and perch. Moreover, Bean & Winfield (1995) found that both roach and rudd increased the amount of time spent in structured areas in the presence of predators. Furthermore, Diehl & Eklov (1995) demonstrated how 0+ perch increased their use of vegetation in the presence of piscivores. Nonetheless, high biomasses or a high complexity of macrophytes are not necessarily beneficial to invertebrate and fish communities. Lauridsen *et al.* (1996) suggested that small dense macrophyte beds may be better refuges for open water species of zooplankton such as *Daphnia* spp. than large beds of the same density, as they aggregate at the edge of macrophyte beds when seeking refuge, and densities of potential competitors (such as *Simocephalus* spp.) are higher in macrophyte beds of larger sizes (Perrow *et al.*, 1999). Many studies have also shown that fish predation success decreases with increasing structural complexity (Heck & Thoman, 1981; Minello & Zimmerman, 1983; Anderson, 1984; Nelson & Bonsdorff, 1990; Dionne & Folt, 1991; Manatunge *et al.*, 2000; Fantin-Cruz *et al.*, 2008). Fish foraging success may decline with increasing structural complexity as predators become visually restricted or more obstructed in their movements (Crowder & Cooper, 1982; Savino & Stein, 1982; Nunn *et al*., 2012). For example, Diehl (1988) found that that the foraging efficiency of roach, bream and perch was lower in vegetation/dense vegetation than in open water/sparse vegetation. Nonetheless, in the present study there was little evidence of structural complexity influencing the feeding activity of 0+ roach or bream. Contrary to expectations, the gut fullness of roach larvae was highest in filamentous algae in the first and second surveys, suggesting that the complex structure did not negatively affect their feeding activity. It is possible that this may or may not have been a true representation of feeding activity in filamentous algae if the fish moved between vegetation categories.

The limitations that dense macrophyte beds may impose on fishes inevitably differ between species. Winfield (1986) showed that 0+ perch were more efficient feeders in structured environments than 0+ roach, but roach are more efficient than perch at evading predators when they are in vegetation (Persson, 1993). Thus, when 0+ fishes are faced with finding habitats to forage and avoid predation, many species show a ‘trade-off’ by opting for habitats with ‘intermediate levels of complexity’ to maximise foraging success whilst minimising predation risk (Werner *et al.*, 1983; Power *et al.*, 1985; Schriver *et al.*, 1995; Dibble *et al.*, 1996; Miranda & Hodges, 2000; Agostinho *et al.*, 2007). In this study, it is possible to speculate that roach had better foraging efficiency than did bream in all macrophyte structures as feeding activity was always higher in all vegetation categories compared to bream. However, this had no influence on the condition of 0+ roach or bream, this remained constant at one (the best it can be) in all vegetation categories.

This study revealed differences in the diet composition and prey selection of larval and 0+ juvenile roach and bream in vegetation of contrasting structural complexity, although there were no consistent patterns across surveys. Generally, selection was stronger in simple (floating-leaved) than in more complex (submerged and emergent) vegetation. Copepod nauplii were most abundant in submerged vegetation and many were consumed by finfold roach larvae in filamentous algae. However, selection of copepod nauplii was strongest in floating-leaved vegetation, indicating that availability was not the only factor influencing diet composition. The simple complexity of the floating-leaved vegetation may have increased the fish’s relative efficiency when feeding on certain prey. Indeed, Winfield (1986) demonstrated that complex macrophyte-like structures impaired the foraging efficiency of juvenile roach, but dense stands of simple *Nuphar* sp. had no affect on the feeding rate of zooplanktivorous roach. Similarly, Moss *et al.* (1998) showed that predation by perch on *Daphnia* spp. increased in less-dense stands of water lilies. This may have influenced results in the present study, as finformed roach larvae consumed more *E. lamellatus* in filamentous algae than in floating-leaved vegetation, but selection was stronger in floating-leaved vegetation. Moreover, finformed bream larvae avoided cyclopoid copepods in emergent vegetation, but selected them in floating-leaved vegetation. Dionne & Folt (1991) demonstrated that macrophyte growth forms are not all similar in their effects on fish foraging. They showed that *S. crystallina* capture rates by pumpkinseed (*Lepomis gibbosus* (L.)) foraging in *Scirpus validus* (Vahl) (cylindrical stems) were 53% times greater than in *Potamogeton amplifolius* (Tuck) (leafy stems). Furthermore, Manatunge *et al.* (2000) found that the foraging efficiency of *Pseudorasbora parva* (Temminck & Schlegel) decreased significantly with increasing habitat complexity. The decline in feeding efficiency was related to submerged vegetation impeding swimming ability and obstructing sight when foraging. Although a number of studies have observed differences in prey selection by fish between taxa, for example, slow versus fast moving (Winfield, 1983), this study demonstrated variations in prey selection within a taxon between habitats of contrasting complexity. This is important as it shows that prey availability is not the only influence on the prey selection of 0+ fishes and that habitat complexity does have an effect on prey choice. Differences in prey selection may also be a result of differences in the sizes of individuals of some prey taxa occupying different habitats. For example, large and small individuals of the same species may have different habitat requirements.

Spatial variations in other food sources such as benthic invertebrates (Bass *et al*., 1997) and aufwuchs (Marker & Collett 1997b) should also be considered when studying species and rivers where these are important. For example, 0+ juvenile perch may consume a large amount of benthic invertebrates (Persson & Greenberg, 1990; Mehner *et al.*, 1995; Nunn *et al.*, 2007a). Furthermore, Nunn *et al.* (2007a) found that the main food of finformed roach larvae in the River Trent was aufwuchs, which was possibly related to a lack of planktonic prey. Taylor (2012) also found that there was a high abundance of chironomid larvae in the diets of roach in the River Ancholme, compared to a lower importance in the diets of roach from other rivers (Don, Ouse and Trent), which may suggest that macrophytes are an important habitat for benthic macroinvertebrates (Garner *et al.*, 1996; Bass *et al.*, 1997). By comparison, in this study chironomid larvae were only important in the diets of roach in one survey, in submerged vegetation (complex habitat). This suggests that the larger and slower-moving benthic invertebrates in this habitat may have been easier to capture than faster-moving and more transparent planktonic prey, as fish mobility and vision are restricted in more complex habitats (Crowder & Cooper, 1982). Finally, differences in predation risk or competition between habitats may cause differences in prey selection. For example, 0+ fishes may be forced to select smaller, less profitable prey when in the presence of potential predators or competitors. Persson (1993) found that in the absence of piscivorous perch, juvenile roach fed predominantly on *Bosmina* sp*.,* but switched to detritus/algae in the presence of predators.

Knowledge on the impacts of macrophyte structure on zooplankton and 0+ fish communities can be applied to river enhancement schemes. For example, Langler &

Smith (2001) examined the effectiveness of an enhancement scheme on the Huntspill River in Somerset, England, with 0+ cyprinid fish assemblages in manipulated habitats compared with those in unmanipulated sites. The scheme involved reducing bank gradients and constructing off-channel back waters, which were planted with willow (*Salix* sp.) and common reed. The abundance and diversity of 0+ fishes was significantly higher in manipulated habitats than unmanipulated habitats. As such, it is believed that microhabitats for spawning, nursery and refuge sites produced by habitat enhancement schemes play a significant role in improving cyprinid fish populations.

CHAPTER FIVE

THE INFLUENCE OF INTERSPECIFIC INTERACTIONS ON THE DIET COMPOSITION, PREY SELECTION, GROWTH AND CONDITION OF 0+ ROACH AND BREAM

5.1 INTRODUCTION

A number of factors can influence the growth and survival of 0+ fishes, including predation, competition, food availability and environmental conditions such as temperature and flow (Brabrand, 1985; Borcherding *et al.*, 2000; Beeck *et al.*, 2002; Nunn *et al.*, 2003, 2007a, b). In the first few weeks of life, fluctuations in prey availability are of particular importance (Graeb *et al.*, 2004). At this time, fish larvae have poorly-developed fins and vision, and a small gape size, limiting their ability to locate, capture and ingest prey. As such, low prey availability can cause a reduction in fish growth, possibly leading to starvation and death. In addition, competition can have implications for growth, survival and, subsequently, recruitment success. Interspecific dietary overlap can be indicative of competition, and is often greatest amongst young larvae as they are morphologically and behaviourally undifferentiated (Garner, 1996a). This can result from overlap in habitat use and prey types between species, increasing the potential for competition. This emphasises the importance of increasing knowledge of the influence of interspecific interactions on the diet composition, prey selection and growth and condition of 0+ fishes, which ultimately influence recruitment success (DeVries *et al.*, 1998). Although the feeding habits and diets of the larvae of some fish species are known (Winfield *et al.*, 1983; Skrzypczak *et al.*, 1998; Nunn *et al.*, 2007a), it is unclear how interspecific interactions influence their feeding ecology.

The aim of this study was thus to investigate the influence of interspecific interactions on the feeding ecology of 0+ fishes. Specifically, the objectives were to compare the: (1) diet composition; (2) prey selection; (3) growth and (4) condition of 0+ fishes in sympatry and allopatry. The hypothesis was that interspecific interactions will be reflected by differences in the diet composition, prey selection, growth and condition of 0+ fishes in sympatry and allpatry, which will subsequently be reflected by recruitment success. This study will improve knowledge of the implications of interspecific interactions on the population dynamics of 0+ fishes, and will provide information on how to manage aquatic habitats and aquaculture facilities for fish and fisheries, especially how to provide optimum habitat conditions in the drive to improve the ecological status of rivers and lakes under the European Union Water Framework Directive (Kallis & Butler, 2001).

5.2. MATERIALS AND METHODS

Calverton Fish Farm was used to investigate the influence of interspecific interactions on the diet composition, prey selection, growth and condition of larval and 0+ juvenile roach and bream (Plates 5.1 & 5.2) in June 2008. These species were chosen because they are two of the most abundant fish in lowland rivers in North-West Europe and, hence, may compete for resources. Moreover, they have similar habitat requirements, such as slow-flowing waters with muddy or clay bottoms (Garner, 1996a) and vegetation for spawning and refuge for their young. Calverton Fish Farm is a 4 ha site with 35 ponds, operated by the Environment Agency (EA) in the East Midlands (National Grid Reference: SK6456148580).

First-feeding larvae are reared on Artemia in the hatchery at Calverton and then stocked (1,000,000-1,500,000 larvae/ha) into specially prepared ponds, which provide a natural food source. The ponds range from 100 m^2 to 350 m^2 in size and have an average depth of 0.8 m. Dried poultry waste is used to manure the ponds, which are filled with water 2 to 4 weeks before the predicted stock-out date of the larvae. This promotes the growth of phytoplankton, which are then preyed upon by small zooplankton such as rotifers, which are ideal food for larvae. Polythene-covered horticultural tunnels are used to increase water temperatures, which in turn increases the growth and survival rates of the larvae. The enclosures used in this experiment (Chapter 5) were placed in one of these ponds with a polythene covered tunnel (http://www.environment-agency.gov.uk/research/commercial/32864.aspx).

Nine enclosures (60 cm × 60 cm × 100 cm, 1-mm mesh) were arranged in a pond using a Latin-square experimental design to avoid location-related bias (Plate 5.3):

Plate 5.1 Finformed roach larva.

Plate 5.2 Finformed bream larva.

Plate 5.3 Experimental enclosures at Calverton Fish Farm.

1	3	2
2	1	3
3	2	1

where treatment 1 contained roach, 2 contained bream, and 3 contained roach and bream. Sufficient space was left between the enclosures to allow water movement and zooplankton dispersal.

A total of 100 larvae was stocked into each enclosure on 4 June 2008 (278 fish m^{-2}):

- treatment 1 – 100 roach larvae stocked into each enclosure;
- treatment 2 – 100 bream larvae stocked into each enclosure;
- treatment 3 – 50 roach and 50 bream larvae stocked into each enclosure.

Although this density was higher than those in the ponds at Calverton Fish Farm (usually 100-150 fish m^{-2}), it was necessary to provide sufficient fish for sub-samples to be removed for diet analysis. Moreover, the density is within the ranges observed in the wild (Section 5.3.3).

A second experiment was conducted at Calverton Fish Farm from 14 May 2009, focusing on the impacts of interspecific interactions on growth and condition. As in 2008, nine enclosures were arranged using a Latin-square experimental design to avoid location-related bias.

A total of 100 larvae was stocked into each enclosure:

- treatment 1 – 100 roach larvae stocked into each enclosure;
- treatment 2 – 100 bream larvae stocked into each enclosure;
- treatment 3 – 50 roach and 50 bream larvae stocked into each enclosure.

To compare the experimental results with conditions in the wild, fish were collected from the River Trent at Attenborough (see Section 3.2.2; Plate 5.4) using a micromesh seine net (25 m long by 3 m deep, 3 mm hexagonal mesh). This site was chosen because roach and bream are the two most abundant 0+ fish species at Attenborough, together comprising >80% of catches (Andy Nunn PhD thesis, page 39).

Plate 5.4 Survey site and sampling at Attenborough on the River Trent.

5.2.1 Experimental procedure

For the first experiment at Calverton samples were taken every 2-3 days between 6 and 19 June 2008, taking care to minimise disturbance of the pond bed:

- a sample (treatments 1 and 2, $n \approx 10$; treatment 3, $n \approx 30$) of fish was removed from each enclosure and preserved in 4% formalin solution. The larger sample taken from treatment 3 was intended to ensure that adequate numbers of both fish species were obtained. Fish that were removed were replaced (using spare stock from the hatchery) to maintain a constant density. Replacement fish were of a similar stage of development/size to those removed.
- a zooplankton sample was collected from each enclosure by pouring 10 L of water through a sieve (100-μm mesh), and preserved in 4% formalin solution.

At the end of the experiment (when the natural food sources had been exhausted/artificial feeding commenced), all fish were removed from the enclosures for analysis in the laboratory.

For the second experiment, the fish were left in the enclosures for the whole experimental period, until the natural food resources had been exhausted on 4 June 2009. The fish were then removed from the enclosures with fine-meshed hand nets.

Fishes from the wild were analysed (Table 5.1) from samples when roach were more abundant than bream but not necessarily the most abundant species in the sample, and when bream were more abundant than roach, again they were not necessarily the most abundant species in the sample. Also, roach when roach and bream were approximately equally abundant and bream when roach and bream were approximately equally abundant. Corresponding zooplankton samples were also collected and analysed as described in Section 3.2.1.

Table 5.1. Species, density, number and larval step of 0+ roach and bream used for analysis for samples from the River Trent

	Species	Date	Density (/m^2) (total fish)	Number of fish analysed	Larval step
Sample 1	roach (when roach were more abundant than bream)	6 June 2010	5	10	6
Sample 2	Bream (when bream were more abundant than roach)	17 July 2010	5.8	10	6
Sample 3	Roach and bream in equal abundance	30 Aug 2010	6.7	20*	6

* 10 of each species (roach and bream)

5.2.2 Laboratory analysis

In the laboratory, fish were identified to species (Pinder, 2001) and measured for total length (TL, nearest 0.1 mm). Prior to analysis, fish were categorised as either finfold larvae, finformed larvae or 0+ juveniles as they represent distinct ‘ecospecies’ in terms of their diet composition (Section 3.2.1; Nunn *et al.*, 2007a). Larval steps were identified according to Peňáz (2001) (see Section 3.2.1).

For the second experiment, all fishes were identified to species and measured (SL, nearest 0.1 mm), and 30 fish from each enclosure were weighed (nearest 0.01 mg) using a digital scale and blotting off any excess water to determine weight-length relationships.

For samples taken from the wild, ten roach and ten bream from each sample (*n* = 40) were identified to larval step (Peňáz, 2001), measured (SL, nearest 0.1 mm), and weighed to the nearest g to determine weight-length relationships in the laboratory. For each fish, the contents of the entire gastrointestinal tract were removed and identified as described in Section 3.2.1.

5.2.3 Data analysis

For the first Calverton experiment a Bray-Curtis similarity matrix (Czekanowski, 1913; Bray & Curtis, 1957) was calculated in the PRIMER (Plymouth Routines In Multivariate Ecological Research) statistical package, using the mean percent abundance of each zooplankton taxon in each enclosure on each sampling occasion, and presented as a non-metric multidimensional scaling (MDS) plot to test for an effect of treatment (roach, bream, roach and bream) on zooplankton composition (as described in Section 3.2.1). Prey selection by roach and bream was calculated where sufficient numbers of each developmental step were captured. If there was less than five in the larval step then selection was not calculated (see Section 3.2.1). These methods were repeated for results from the wild.

PERMANOVA was conducted (using the number of each prey category found in the gastrointestinal tract of individual fish, square root transformed) to test for differences in the diet composition of finformed larvae (bream on their own, bream with roach, roach on their own, and roach with bream). As before, the Monte Carlo *P*-value was used, where a value <0.05 is significant and a value ≥0.05 is not significant. Prey selection by roach and bream was investigated using the relativized electivity index (*E**) of Vanderploeg & Scavia (1979) as described in Section 3.2.1. This method was also repeated for results from the wild.

For the second Calverton experiment all data were tested for normality and homogeneity of variances using one-sample Kolmogorov-Smirnov and Levene tests, respectively (Dytham, 2003). Mean lengths and weights were compared between treatments using independent samples *t*-tests (Dytham, 2003). The relationship between wet weight (g) and SL (mm) was investigated for roach and bream from the three treatments. Wet weight-SL relationships were calculated using natural logarithm-transformed data by linear regression. No significant differences were found in the relationships between replicates (Analysis of Covariance [ANCOVA], $P > 0.1$), so data were combined for each treatment. Wet weight-SL relationships were compared between treatments using ANCOVA.

The weight-length relationships were used to calculate the relative body condition factor (*K*) of roach and bream in the three treatments (Bagenal & Tesch, 1978) as described previously in Section 3.2.1. Mean condition of roach and bream was compared between single- and mixed-species enclosures using independent samples *t*-tests (Dytham, 2003). For results from the wild, Bray-Curtis similarity matrices were calculated, using the mean percent abundance of each prey category in the diet of roach and bream on each sampling occasion, and presented as an MDS plot to test for similarities in diet composition as described in Section 3.2.1.

For results from the wild all the lengths and weights of roach and bream from each sample were log-transformed and used to calculate weight-length relationships using linear regression; they were compared using ANCOVA and independent samples *t*-tests to samples where bream were more abundant than roach and when roach and bream were approximately equally abundant, the same was done with bream. The weight-length relationships were used to calculate the relative body condition factor (*K*) (see Section 3.2.1) of roach and bream in the three situations described above. The number of fish in each sample was used to calculate the mean (± SD) density (fish m^{-2}).

5.3 RESULTS

5.3.1 THE INFLUENCE OF INTERSPECIFIC INTERACTIONS ON THE DIET COMPOSITION AND PREY SELECTION OF 0+ FISHES

Ostracoda, Rotifera and copepod nauplii were the principal components of the zooplankton in the enclosures (Fig. 5.1). Cladocera present in the zooplankton samples included *Bosmina* sp., *Chydorus* spp. and *Alona* spp., with the most abundant species being *Daphnia magna* Straus. Cyclopoid copepods were also commonly found in all samples. Temporal variations in zooplankton composition were found (Fig. 5.2), but there was no significant treatment effect. There was more temporal variation in zooplankton composition than there was between treatments and replicates (the closer the markers, the greater the similarity between samples; Fig. 5.2).

A total of 956 fish was dissected and assessed for diet composition (Table 5.2). The diets of roach and bream included cyclopoid copepods and *D. magna*, but few other Cladocera (*Bosmina* sp., *Chydorus* spp. and *Alona* spp.; Fig. 5.3). Additionally, a substantial amount of chironomid larvae was found in their diets. The main change in the diet of roach was the increase in copepod nauplii in sympatry (58.4%) compared to allopatry (17.3%) (Fig 5.3). There was an increase in cyclopoid copepods and *Daphnia magna* in the diet of bream when in sympatry (11% and 7% respectively) compared to allopatry (3.9% and 4.6% respectively) (Fig 5.3) Similarly, both species consumed less

Rotifera in sympatry compared to allopatry (roach from 41% in allopatry to 21% in sympatry; bream from 47% in allopatry to 40% in sympatry) . Although the dominant taxa in the diet matched those in the zooplankton, it is evident that there was a lower richness of taxa in the zooplankton than in the diets of roach and bream (Fig. 5.3).

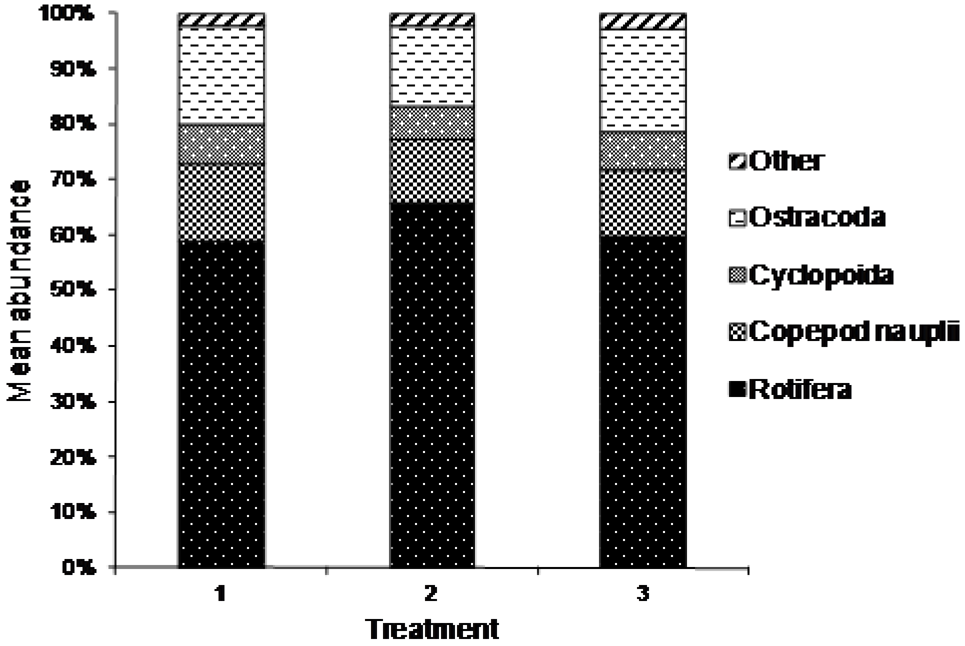


Fig. 5.1. Mean percent abundance of zooplankton taxa in Calverton enclosures, where treatment 1 = roach only, 2 = bream only and 3 = roach and bream.

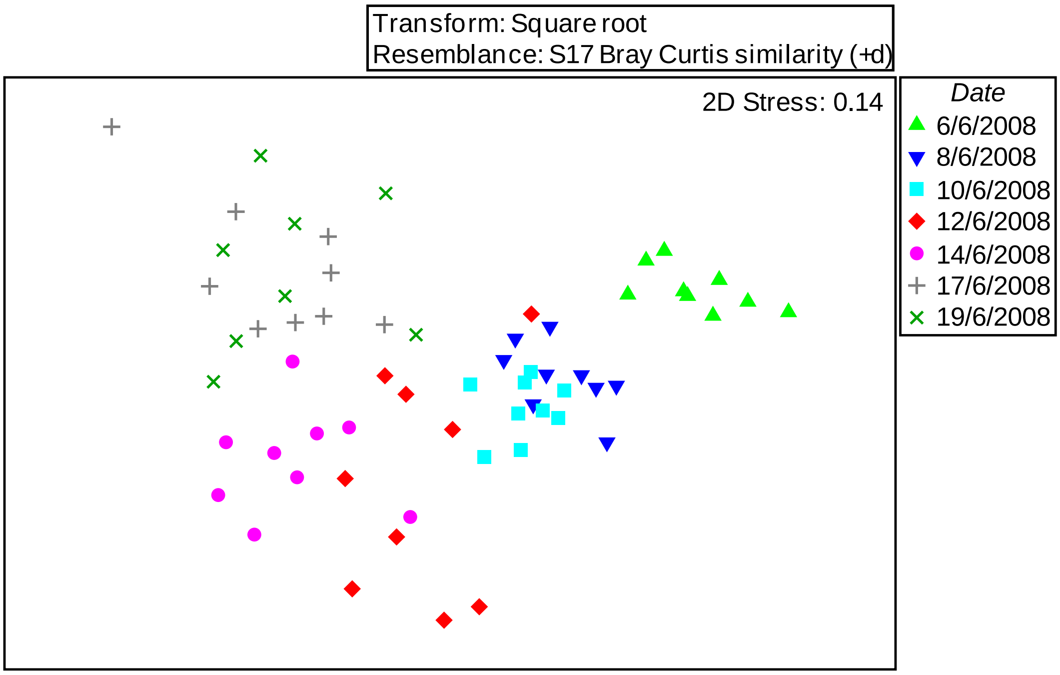


Fig. 5.2 Non-metric multidimensional scaling plot of the similarity in zooplankton composition in nine experimental enclosures on seven sampling occasions.

Table 5.2 Number of fish examined to assess the influence of interspecific interactions on the diet composition and prey selection of 0+ roach and bream at Calverton Fish Farm.

	Roach	Bream
Larval step 1*	0	0
Larval step 2	28	10
Larval step 3	30	11
Larval step 4	224	165
Larval step 5	78	171
Larval step 6	58	106
Juvenile	29	46
Total	**447**	**509**

* L1 fish were absent as the fish were stocked out at L2.

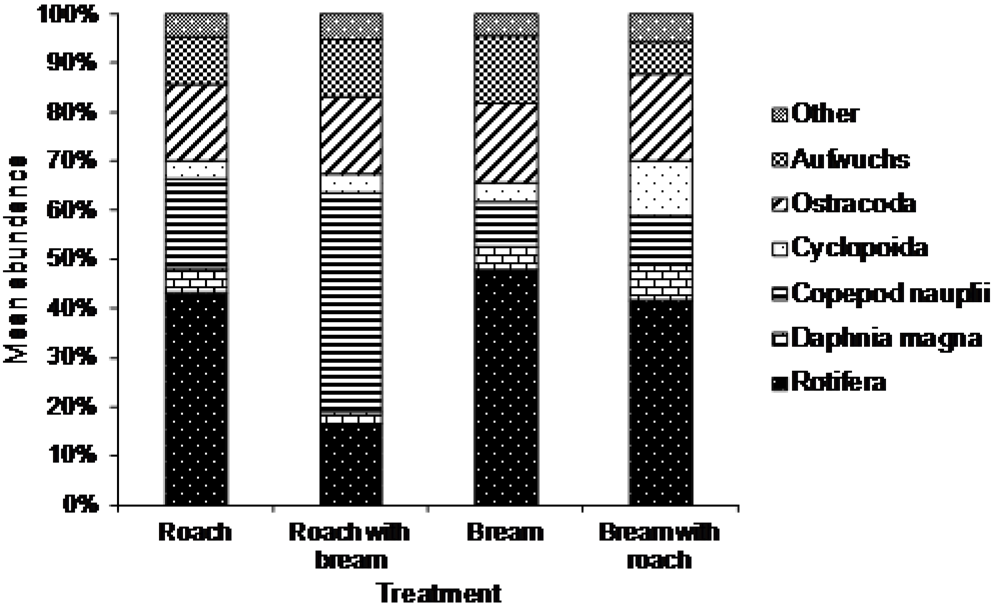


Fig. 5.3 Mean percent abundance of prey taxa in the diets of roach and bream in allopatry (single-species enclosures) and sympatry (mixed-species enclosures).

Rotifera was the main food source of roach in single-species enclosures, but its importance in the diet generally declined as the fish developed, with relative abundance highest in L2 and lowest in L6 (Fig. 5.4a). Copepod nauplii consumption was greatest between larval steps 2 and 4, before gradually declining to zero by L6 (Fig. 5.4b). Roach consumed only small numbers of Ostracoda in larval steps 2-4, but this increased in steps L5-J, with numbers peaking at L6 (Fig. 5.4c). There were few or no cyclopoid copepods consumed between larval steps 2 and 5, but there was a slight increase at L6 and J (Fig. 5.4d). Consumption of *D. magna* was low for L2-L4, and then increased at later larval and juvenile steps (Fig. 5.4e).

Consumption of copepod nauplii followed a similar pattern in mixed- and single-species enclosures, but peaked at L2 in mixed-species enclosures instead of L4 (Fig. 5.4b). Consumption of Ostracoda was similar in single- and mixed-species enclosures during early development (L2-L4), but was suppressed in mixed-species enclosures in L5, L6 and J (Fig. 5.4c). The relative importance of cyclopoid copepods in the diets of roach larvae was approximately the same in single- and mixed-species enclosures from L2 to L5 (0-1.6%), but consumption was higher in mixed-species enclosures at L6 and J (19.6% & 13.2% respectively; Fig. 5.4d). Consumption of *D. magna* was generally higher in mixed- (0-14.4%) than in single-species enclosures (0-9.4%) (Fig. 5.4e).

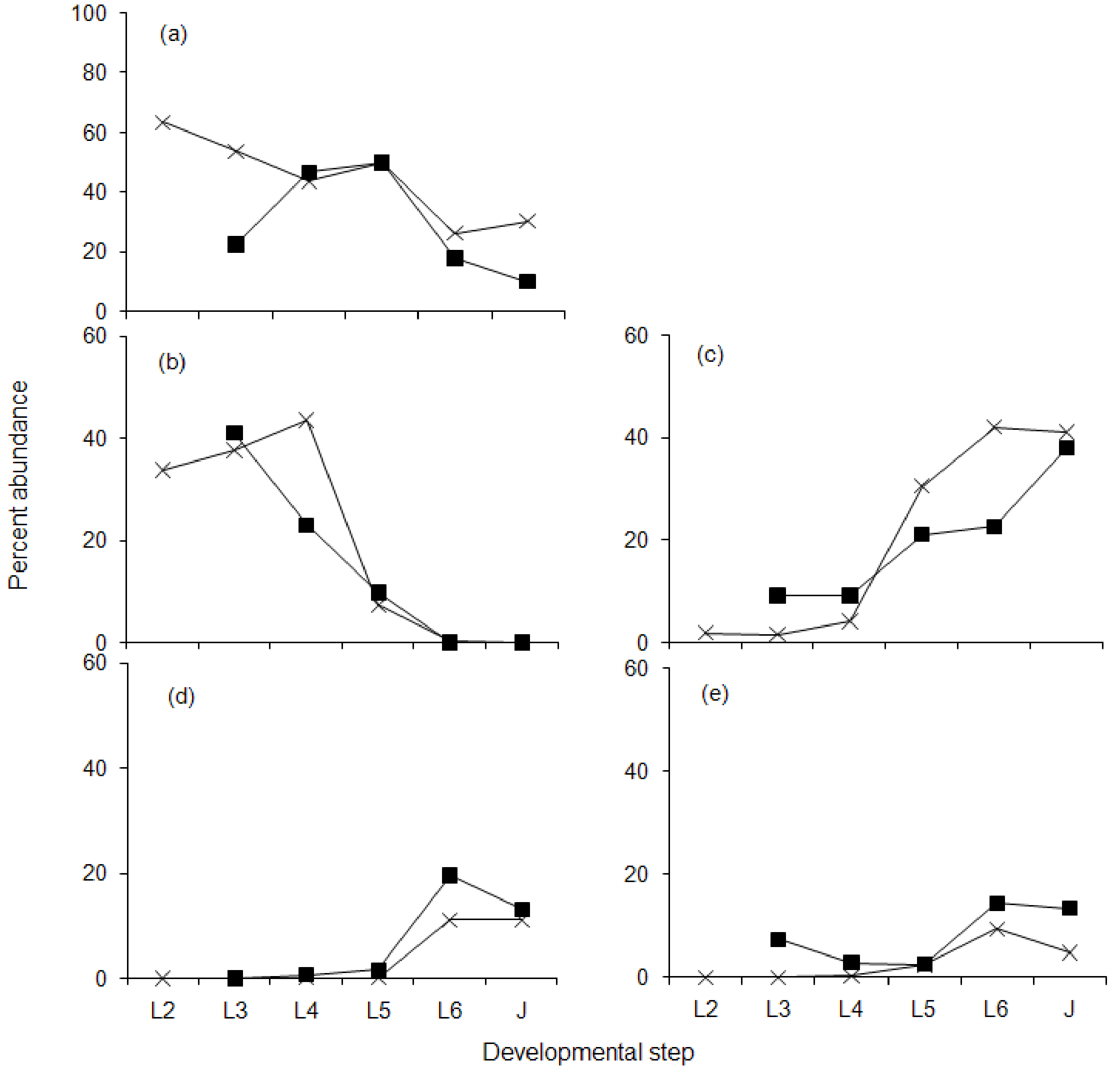


Fig. 5.4 Mean percent abundance of (a) Rotifera, (b) copepod nauplii, (c) ostracods, (d) Cyclopoida and (e) *Daphnia magna* in the diets of larval (L2-L6) and juvenile (J) roach in single- (×) and mixed-species (■) enclosures.

Rotifera consumption by bream in single-species enclosures peaked at L2 (100%) then gradually declined to zero at J (Fig. 5.5a). Bream generally consumed only small numbers of copepod nauplii, with the highest abundance in L3 (21.3%) and the lowest in L6 and juvenile (8% & 0% respectively; Fig. 5.5b). Ostracoda were consumed from L3 to J, with relative abundance generally increasing with development (Fig. 5.5c). Few or no cyclopoid copepods were consumed in L2-L4, but there was a slight increase in L5 and L6 followed by a reduction at J (Fig. 5.5d). There was no consumption of *D. magna* between L2 and L3, but this gradually increased from L4 and peaked at J (15.8%; Fig. 5.5e).

The diets of bream larvae were generally similar in both single- and mixed-species enclosures. In mixed-species enclosures, Rotifera consumption was zero at L2 but then followed a similar pattern to in single-species enclosures (Fig. 5.5a). Copepod nauplii consumption also followed a similar pattern compared with single-species enclosures, but peaked in L4 (24.3%) instead of L3, and none were eaten by L6 and J fish (Fig. 5.5b). Bream consumed similar amounts of Ostracoda in single- and mixed-species enclosures between L4 and J (Fig. 5.5c). Cyclopoid copepod consumption was higher in mixed- than in single-species enclosures in L6 and J but, again, few or none were eaten by earlier larval steps (Fig. 5.5d). Consumption of *D. magna* followed a similar pattern in single- and mixed-species enclosures (Fig. 5.5e).

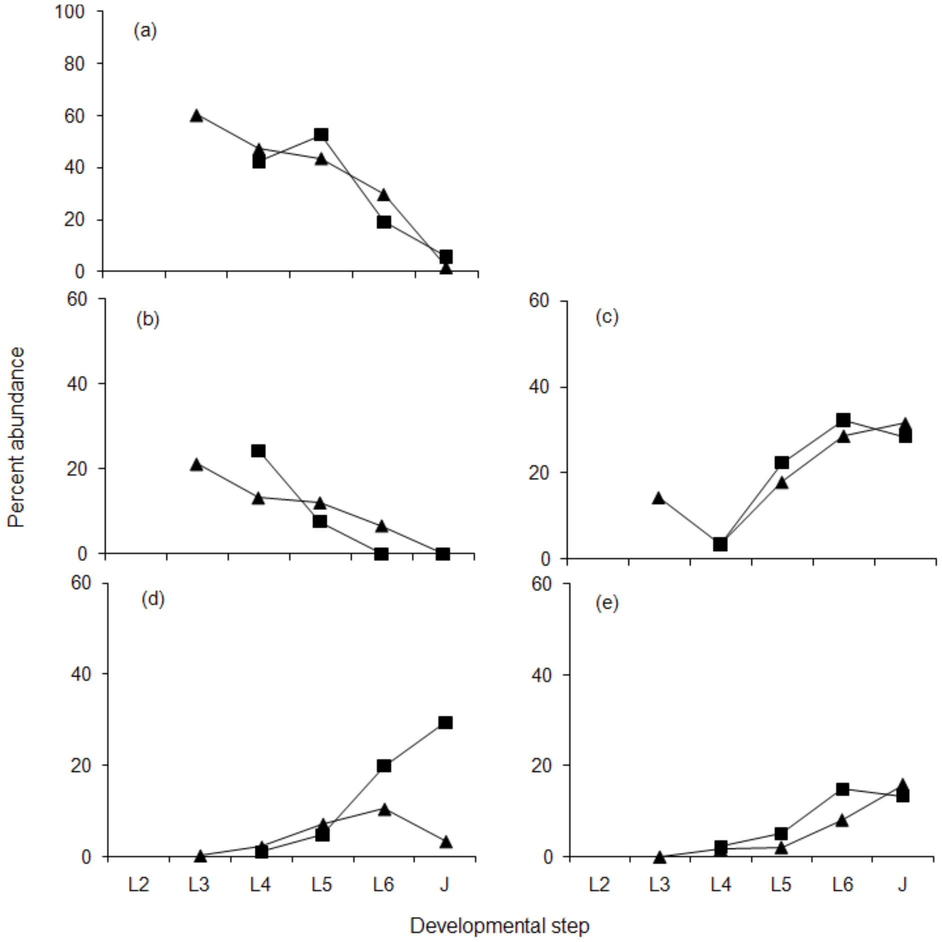


Fig. 5.5 Mean percent abundance of (a) Rotifera, (b) copepod nauplii, (c) Ostracoda, (d) Cyclopoida and (e) *Daphnia magna* in the diets of larval (L2-L6) and juvenile (J) bream in single- (▲) and mixed-species (■) enclosures.

PERMANOVA analysis confirmed that there was no significant difference between replicates within treatments in the diets of roach (Table 5.3, Monte-Carlo test, *P* = 0.7137). Replicates were therefore combined for subsequent analysis. Dietary overlap between roach and bream in mixed-species enclosures was high (89% similarity). However, the diets of finfold roach larvae were significantly different between single- and mixed-species enclosures (Tables 5.3 & 5.4; Monte-Carlo test, *P* = 0.0042 & 0.0209), suggesting that bream had a negative influence on the diet of finfold roach larvae, but there was no significant influence of bream on the diets of finformed larvae and juvenile roach (Table 5.4; *P* = 0.1275 and 0.2334). In particular, the percent abundance of rotifers in the diet was substantially lower for roach in mixed (0-24.5%) - than in single-species enclosures (26-63%), with the exceptions of during L4 and L5.

Table 5.3 PERMANOVA output examining the influence of treatment (Tr), ecospecies (Ec) and replicate (Rep) on the diet composition of roach. **Bold values** = significant result.

Source	DF	SS	MS	Pseudo-F	P(Monte-Carlo)
Tr	1	6251.2	6251.2	4.5332	**0.0062**
Ec	2	30457	15229	9.7893	**0.0001**
Rep(Tr)	4	4846.2	1211.5	0.74406	0.7137
Tr x Ec	2	11927	5963.5	3.8334	**0.0042**
Ec x Rep(Tr)	7	10631	1518.7	0.93271	0.549
Res	373	6.0735	1628.3		
Total	389	6.8748			

NB: Degrees of freedom (DF), Sum of squares (SS), Mean square (MS). Pseudo-F is based on expected mean squares as in univariate ANOVA and P(Monte-Carlo) is used when there are very few possible permutations.

Table 5.4 PERMANOVA Pair-wise test output examining the influence of treatments (Tr) on the diet composition of roach ecospecies (Ec). **Bold values** = significant result.

	Ec	Tr	P(perm*)	P(Monte-Carlo)
Groups single, mixed	Finfold	2.4998	0.0154	**0.0209**
	Finformed	1.5093	0.1282	0.1275
	0+ Juvenile	1.2693	0.2149	0.2334

* Permutation *P*-value is used when there are a large number of possible permutations, when there are very few possible permutations, the Monte Carlo *P*-value should be used in preference.

There was a significant difference between replicates within treatments for bream (Table 5.5, *P* = 0.01), this can be explained by the increase in consumption of rotifer in one of the replicates compared with the other two, so replicates were not combined for subsequent analysis. The presence of roach had no influence on the diets of bream. Unlike roach, there was no significant interaction between treatment and ecospecies for bream (Monte-Carlo test, *P* = 0.32) (Table 5.5). Replicates and ecospecies were then tested for any significance nested within the treatment, which again demonstrated no significant interaction (Monte-Carlo test, *P* = 0.10), thus indicating no significant interaction between replicates, ecospecies or treatment.

Table 5.5 PERMANOVA output examining the influence of treatment (Tr), ecospecies (Ec) and replicate (Rep) on the diet composition of bream. **Bold value** = significant result.

Source	DF	SS	MS	Pseudo-F	P(Monte-Carlo)
Tr	1	1649	1649	0.62604	0.66
Ec	2	35971	17985	7.9984	**0.0001**
Rep(Tr)	5	17400	3480	1.9039	**0.01**
Tr x Ec	2	5436.7	2718.4	1.2089	0.32
Ec x Rep(Tr)	9	21658	2406.5	1.3165	0.10
Res	442	8.07915	1827.9		
Total	461	9.59275			

NB: Degrees of freedom (DF), Sum of squares (SS), Mean square (MS). Pseudo-F is based on expected mean squares as in univariate ANOVA and P(Monte-Carlo) is used when there are very few possible permutations.

There were no major differences in prey selection for roach between single- and mixed-species enclosures, but marginal differences were recorded for certain zooplankton taxa, such as rotifers and *Alona* spp. Electivity values for rotifers were highest for young larvae, with *E** declining and becoming negative with development in single-species enclosures (Fig. 5.6a). A similar pattern was followed in mixed-species enclosures, where selection was either the same or less than in single-species enclosures (Fig. 5.6a). In single-species enclosures, copepod nauplii were generally selected or consumed by L2, L3 and L4 roach in proportion to their abundance in the environment, but were avoided as fish developed from L5 onwards. A similar pattern was followed in mixed-species enclosures, but values were slightly higher until L5, then declined and became negative for L6 and J fish (Fig. 5.6b). Ostracoda were avoided by L2-L5 roach in both single- and mixed-species enclosures, but *E** values were higher from L6-J (Fig. 5.6c). Cyclopoid copepods were also avoided by L3-L5 roach and were not selected until late in development (L6-J) in both single- and mixed-species enclosures (Fig. 5.6d). Values for L6 fish were higher in mixed- than in single-species enclosures. In both single- and mixed-species enclosures, *E** values for *D. magna* were typically negative for L2-L5 roach, but positive for L6 and J fish, the exception being J fish in single-species enclosures (-0.3) (Fig. 5.6e). In single-species enclosures, *Bosmina* sp. was selected by L2-L6 fish and consumed by J fish in proportion to its abundance in the environment (0). In mixed-species enclosures, *Bosmina* sp. was selected by all developmental steps (Fig. 5.6h). There were no distinct patterns for non-planktonic cladocerans (*Alona* spp. and *Chydorus* spp.). *Alona* spp. were always avoided by L3-L6 fish, with *E** values nearer to zero for J fish in single-species enclosures. In mixed-species enclosures, *Alona* spp. were selected by L3 fish (+1), but then avoided from L4-J (Fig. 5.6 f & g). *Chydorus* spp. followed a similar pattern in both mixed- and single-species enclosures, with younger larval steps avoiding them (-1) and L6 and J fish selecting them (+0.3) (Fig. 5.6g).

Bream generally selected rotifers from L3-L5 in both single- and mixed-species enclosures, but avoided them during L6 and J (Figs 5.6a). Copepod nauplii were selected by L3 fish (+0.4), but selection declined with development from L4-J in single-species enclosures. In mixed-species enclosures, copepod nauplii were consistently avoided by all developmental steps of bream, with the strength of the avoidance increasing with development (Fig. 5.6b). *E** values for Ostracoda were negative throughout development, but the strength of the avoidance declined as the bream developed in both single- and mixed-species enclosures (Fig. 5.6c). Cyclopoid copepod *E** values were negative from L3-L5 in both single- and mixed-species enclosures, but the trend diverged between treatments as the fish developed. In single-species enclosures, the *E** value was approximately zero for L6 larvae but negative for J fish (-0.1) (Fig. 5.6d). By contrast, in mixed-species enclosures, cyclopoid copepods were strongly selected by both L6 and J bream (Fig. 5.6d). *Daphnia magna* electivity followed a similar pattern in both single- and mixed-species enclosures, with young larvae avoiding them and a trend towards positive values for older larvae and J fish (Fig. 5.6e). Bream avoided *Bosmina* sp. during L3, but its importance in the diet matched that in the environment from L4-L6, and it was selected by J bream in single-species enclosures. In comparison, *Bosmina* sp. was selected from L4-J in mixed-species enclosures (Fig. 5.6h). Non-planktonic cladocerans followed similar patterns in mixed- and single-species enclosures. *Alona* spp. were always avoided from L3-L6 and only selected by J bream in mixed-species enclosures (+0.16) (Fig. 5.6f). *Chydorus* spp. were principally avoided by younger larvae, but selected by later larval steps and J bream in both single- and mixed-species enclosures (Fig. 5.6g).

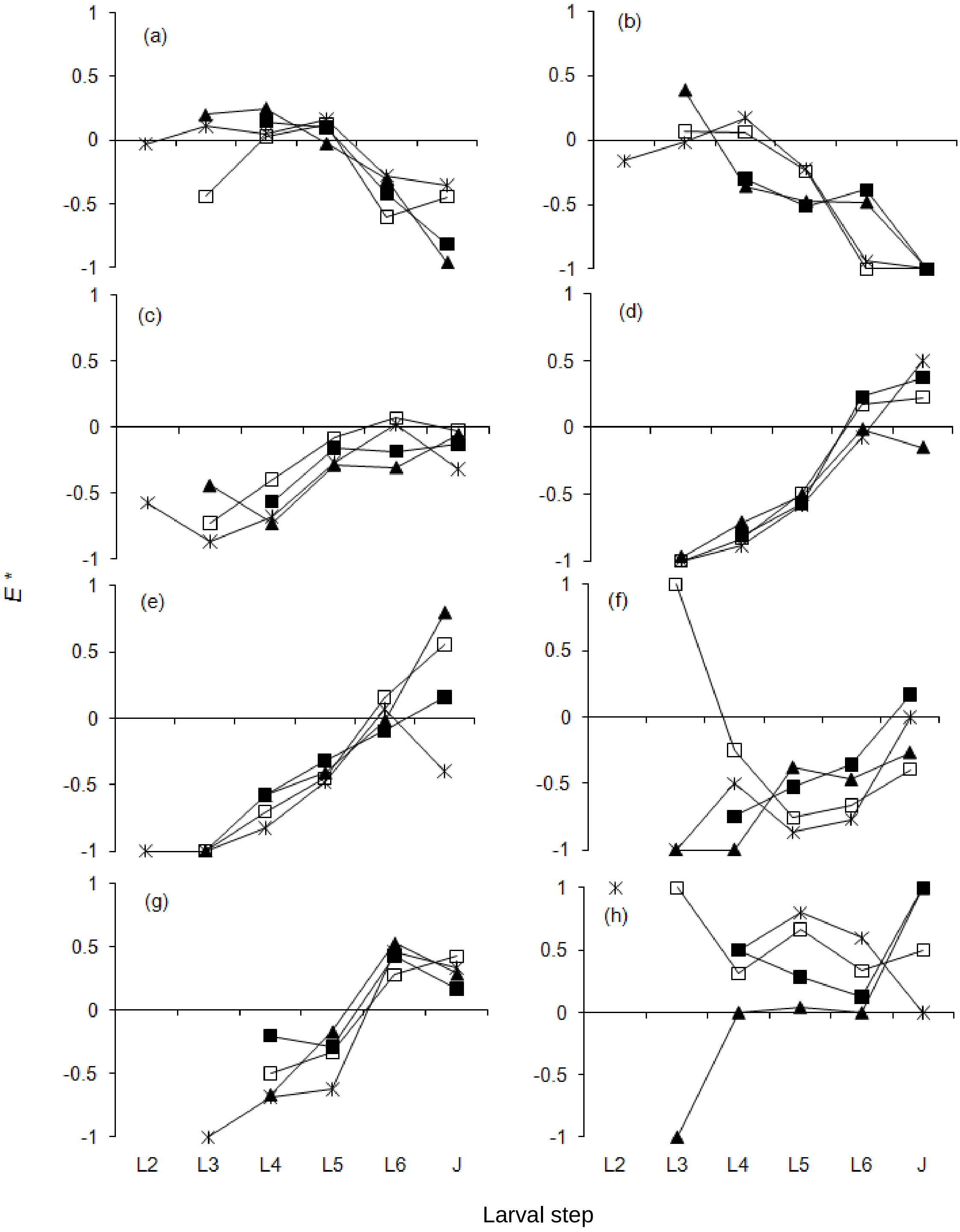


Fig. 5.6 Mean electivity values (*E**) for roach (✳), bream (▲), roach with bream (☐), and bream with roach (■) preying upon (a) Rotifera, (b) copepod nauplii, (c) Ostracoda, (d) Cyclopoida, (e) *Daphnia magna*, (f) *Alona* spp., (g) *Chydorus* spp. and (h) *Bosmina* sp.

5.3.2 THE INFLUENCE OF INTERSPECIFIC INTERACTIONS ON THE LENGTH, WEIGHT AND CONDITION OF 0+ FISHES

The condition of roach was not significantly affected by the presence of bream (P>0.05), but there was a small but significant deterioration in the condition of bream in the presence of roach (P<0.05) (Table 5.6). ANCOVA and independent samples *t*-tests showed that there were no significant differences in the weight (roach P>0.05; bream

P>0.05), length (roach *P*>0.05; bream *P*>0.05) or weight-length relationships (roach *P*>0.05; bream *P*>0.05) of roach and bream between single- and mixed-species enclosures (Figs 5.7 & 5.8).

Table 5.6 The mean length, weight and condition of roach and bream in allopatry (single-species enclosures) and sympatry (mixed-species enclosures). The mean *K* indicates whether the fish are in better (*K*=1) or poorer (*K*<1) condition than average.

	Mean length (mm)	Mean weight (mg)	Mean condition (*K*)
Bream	17.9	0.070	1.00
Bream with roach	17.6	0.065	0.97
Roach	20.0	0.110	1.00
Roach with bream	20.5	0.121	1.00

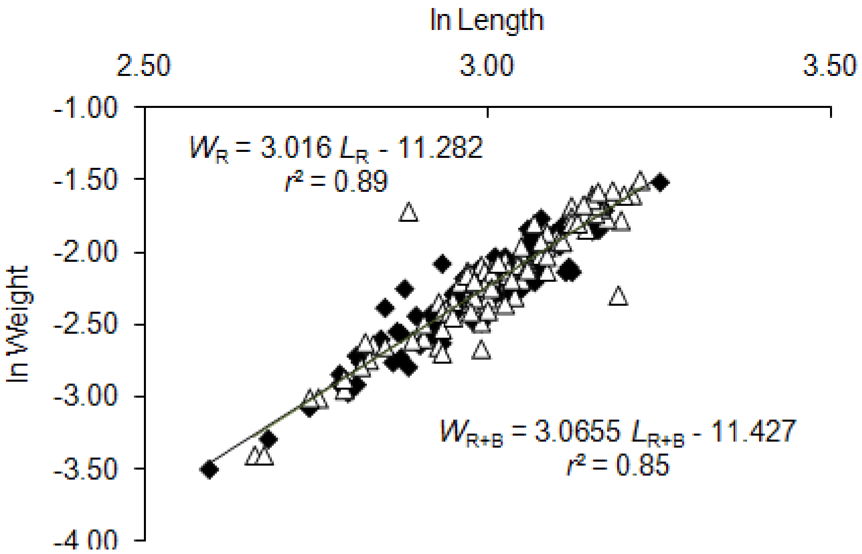


Fig. 5.7 Linear regression relationship between the natural logarithm (ln) of wet weight (*W*, g) and total length (*L*, mm) for roach in single- (R △) and mixed-species (R+B ◆) enclosures.

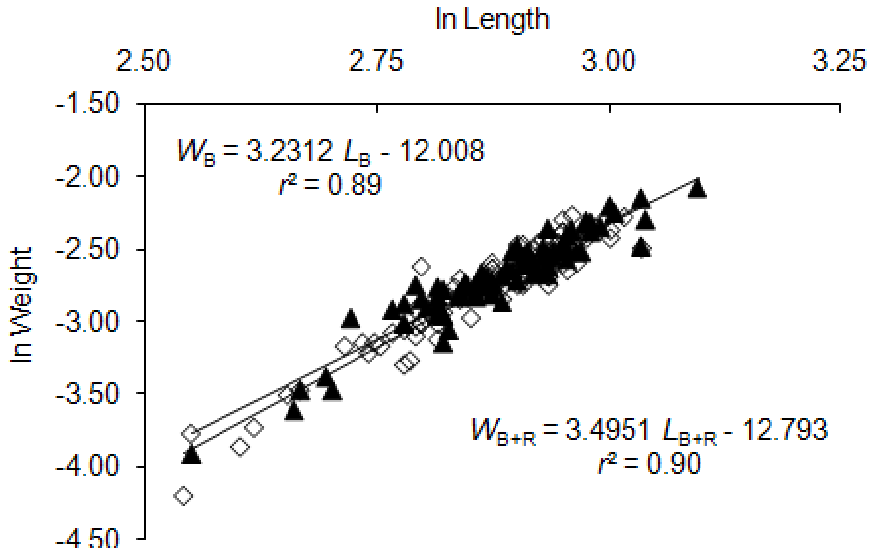


Fig. 5.8 Linear regression relationship between the natural logarithm (ln) of wet weight (W, g) and total length (L, mm) for bream in single- (B ▲) and mixed-species (B+R ◇) enclosures.

5.3.3 THE INFLUENCE OF INTERSPECIFIC INTERACTIONS ON THE DIET COMPOSITION AND PREY SELECTION OF 0+ FISHES IN THE WILD

Cyclopoid copepods, Rotifera and copepod nauplii were the principal components of the zooplankton in water samples taken from the River Trent. Cladocera present in the zooplankton included *Bosmina* sp. and *Daphnia* spp. A total of 40 roach and bream from the wild was dissected and assessed for the influence of diet composition. All fish were finformed (L6) larvae as insufficient finfold roach and bream larvae were captured together in the same samples. The composition of the zooplankton was not reflected in the diets of either roach or bream larvae, which consumed mainly *Bosmina* sp., *Daphnia* spp. and aufwuchs (Fig. 5.9.). The diets of roach and bream also included *E. lamellatus,* chironomid larvae, filamentous algae and phytoplankton, such as *Closterium* spp. and *Eudorina* spp., but few other Cladocera (*Chydorus* spp.) (<6%) and very few Rotifera (<0.1). Aufwuchs (40%) and *Bosmina* sp. (16%) were the main food sources of roach when it was more abundant than bream (Fig. 5.9). *Bosmina* sp. was also the most important food source for bream when bream was more abundant than roach (94%). When roach and bream were equally abundant, roach consumed less aufwuchs (0%), but more *Daphnia* spp. (50%) than when roach was most abundant. By comparison, bream consumed larger amounts of *Daphnia* spp. (8%) and cyclopoid copepods (15%) when roach and bream were equally abundant than when bream was more dominant than roach (0% and 1% respectively) (Fig. 5.9). The differences in the diet of roach when in the presence of bream, compared with when roach were more dominant than bream, were more substantial than the difference in the diet of bream in the presence of roach, compared with when bream were more dominant than roach, as shown by the distance between the markers in Fig. 5.10 (the closer the markers, the greater the similarity between samples).

Further analysis confirmed that there was a significant difference between the diets of roach and bream when roach was the most abundant species in the sample and when bream was the most abundant species in the sample (Monte-Carlo test, $P<0.05$) (Table 5.7). In addition, the diets of roach were significantly different when it was the dominant species compared with when roach and bream were equally abundant (Monte-Carlo test, $P<0.05$). Similarly, the diets of bream were significantly different when it was the dominant species compared with when roach and bream were equally abundant (Monte-Carlo test, $P<0.05$), although the difference in the diets of bream was not as significant as it was for roach, which supports the outcome of the MDS plot (Fig. 5.10). There was no significant difference in the condition of roach when it was the dominant species and when bream was the dominant species (independent samples *t*-tests, *P*>0.05), and the condition of bream was not significantly affected by the presence of roach (independent samples *t*-tests, *P*>0.05).

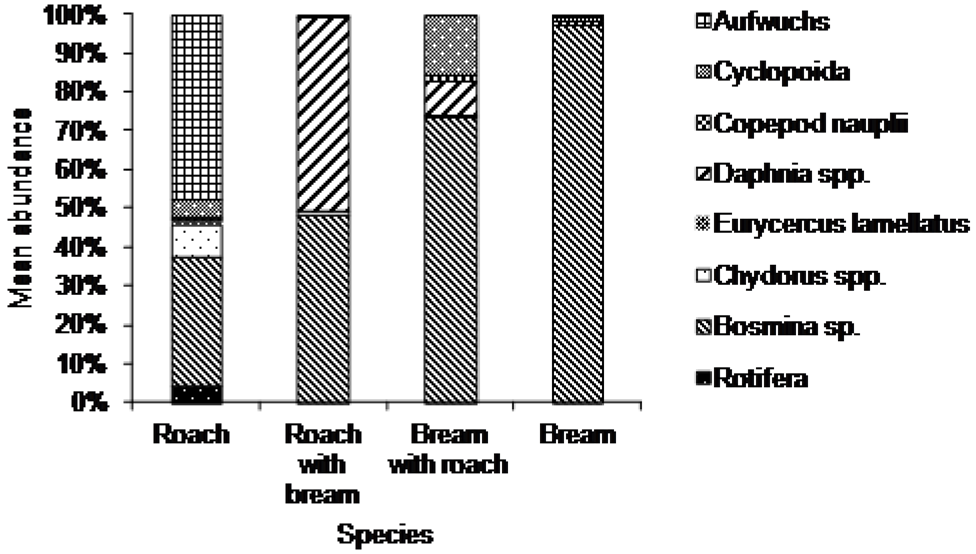


Fig. 5.9 Diet composition of finformed roach and bream larvae in the River Trent at Attenborough. Roach = roach diet when roach was the dominant species, Roach with bream = roach diet when roach and bream were equally abundant, Bream with roach = bream diet when bream and roach were equally abundant and Bream = bream diet when bream was the dominant species.

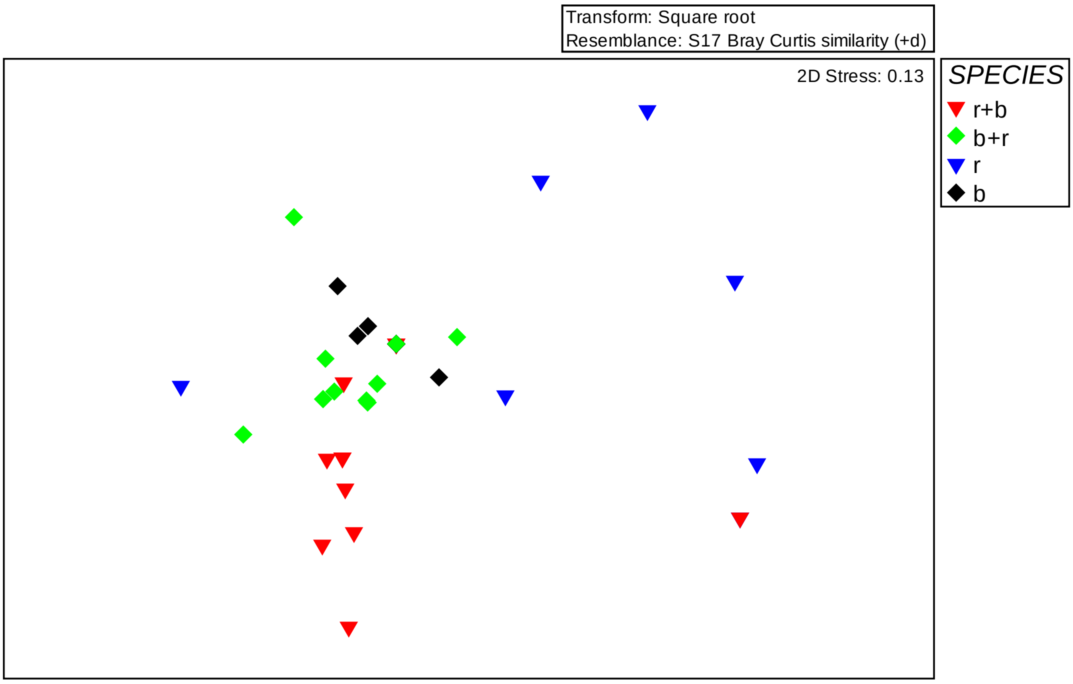


Fig. 5.10 Non-metric multidimensional scaling plot of the similarity in diet composition between samples (roach (r), roach with bream (r+b), bream (b) and bream with roach (b+r) in the River Trent.

Table 5.7 PERMANOVA pair-wise test output comparing the diet composition of roach, roach in the presence of bream (r+b), bream and bream in the presence of roach (b+r) in the River Trent. **Bold values** = significant result.

Groups	Tr*	P(perm)	P(Monte-Carlo)
Roach, r+b	2.8627	0.0001	**0.0003**
Roach, bream	3.2115	0.0002	**0.0002**
Bream, b+r	2.0523	0.0062	**0.0222**

*Tr = treatment, although in this case it was not a treatment per se. It describes species composition when comparing roach with roach in the presence of bream (r+b) and bream with bream in the presence of roach (b+r) in the River Trent.

In samples when roach was more dominant than bream, roach selected *Chydorus* spp. (+1) and cyclopoid copepods (+1), but had no preference for any other food type (Fig. 5.11). In samples when roach and bream were equally abundant, roach selected *Bosmina* sp. (+0.7) and *Chydorus* spp. (+1), but avoided rotifers (-1), copepod nauplii (-0.8) and cyclopoid copepods (-0.7) (Fig. 5.11). Bream selected *Bosmina* sp. (+0.7), but avoided rotifers (-1), copepod nauplii (-0.9) and cyclopoid copepods (-0.9) in samples when bream were more abundant than roach (Fig. 5.11). In samples when bream and roach were equally abundant, bream showed a similar preference for all food types; but there was a decline in preference for *Bosmina* sp. Even though they were still selected (+0.4) (Fig. 5.11).

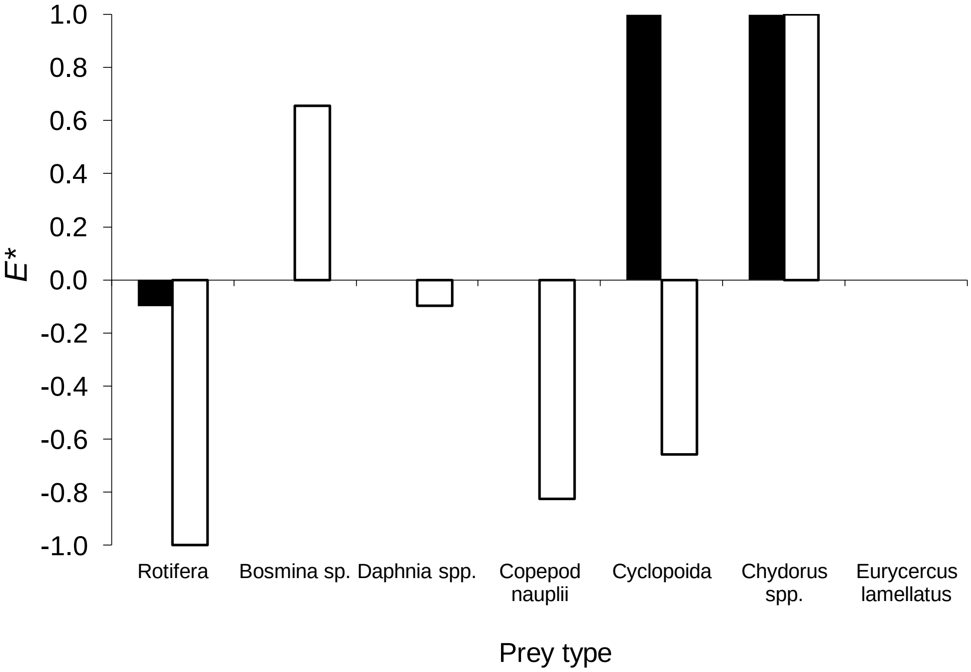


Fig. 5.11 Mean electivity values (*E**) for food type preferences of roach (when roach were dominant) (■) and roach (roach and bream equal abundance) (□).

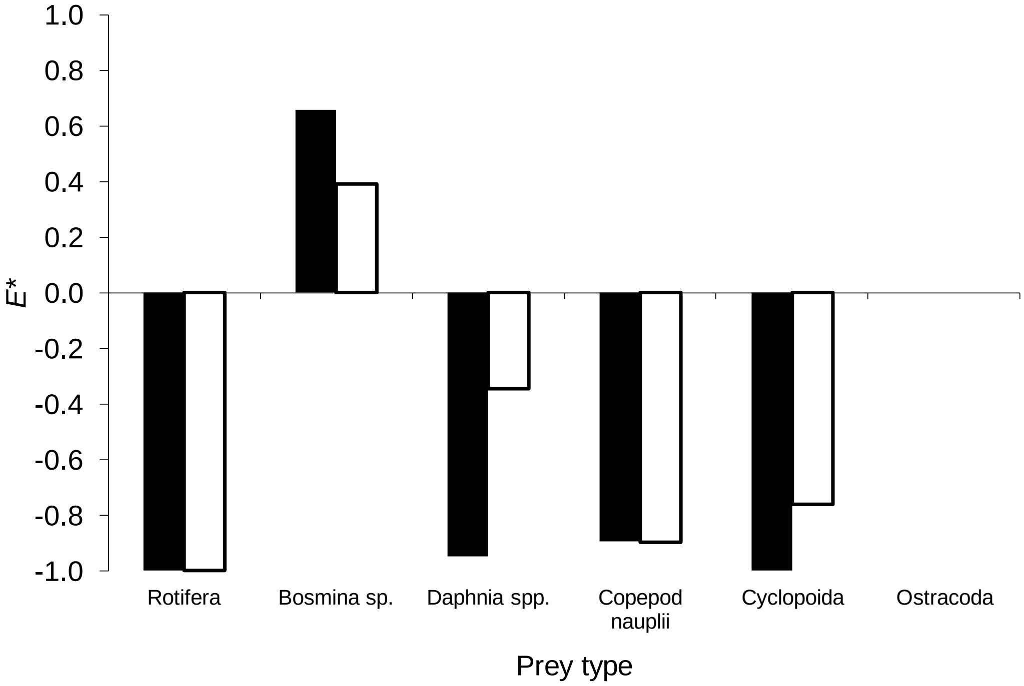


Fig. 5.12 Mean electivity values (*E**) for food type preferences of bream (when bream were dominant) (■) and bream (bream and roach equal abundance) (□).

The density of fish used in the experiments at Calverton was higher than those in the ponds in the fish farm, to allow for fish to be removed, however, it fell within the natural range of the densities in the wild samples found in the River Trent (Table 5.8).

Table 5.8 Comparison of 0+ fish densities in the experimental enclosures, Calverton Fish Farm ponds and the River Trent.

	Fish density (no. m^{-2})
Experimental enclosures	278
Calverton Fish Farm	100-150
River Trent*	5-7
River Trent**	0-463

*this study
**range in densities from Hull International Fisheries Institute's 0+ fish dataset, 1999-2009

5.4 DISCUSSION

Diet composition and zooplankton availability play an important role in the early development of fishes (Mann, 1997; Mann *et al.*, 1997; DeVries *et al.*, 1998), because growth in the first few weeks of life is key to survival and recruitment success (Nunn *et al.,* 2003). The growth of larval fishes is influenced by the availability of suitable food items (Welker *et al.*, 1994), with most species relying on small zooplankton because of their limited gape width (Mehner *et al.*, 1998). Consequently, lack of suitable prey can cause either reduced growth or starvation (Graeb *et al.*, 2004; Hoxmeier *et al.*, 2004).

Interspecific competition, of which dietary overlap can be indicative, is an important factor that can have implications for growth, survival and recruitment success (Nunn *et al.*, 2007c, d; Nunn *et al*., 2012). In the present study, a series of experiments was conducted in enclosures to investigate the influence of interspecific interactions on the diet composition, prey selection, growth and condition of larval and 0+ juvenile roach and bream; these results were then compared with samples from the River Trent.

Interspecific dietary overlap is frequently high in young larvae, suggesting that the fishes are still morphologically and behaviourally undifferentiated during this period (Garner, 1996a). This study found that finfold roach and bream larvae consumed a considerable amount of rotifers and copepod nauplii compared with other zooplankton taxa in the enclosures at Calverton. However, overlap does not necessarily imply competition, given that competition only occurs in situations where demand for a particular food item exceeds the immediate supply (Zaret & Rand, 1971). Nunn *et al.* (2007b), for example, found that dietary overlap was greatest among 0+ fishes feeding on rotifers and aufwuchs, which are generally abundant food types. The consumption of aufwuchs by finformed roach larvae in this study corroborates other studies on the summer diet of this fish species (Garner, 1996a; Nunn *et al.*, 2007a), especially when few animal prey are available. Similarly, Cowx (1989) found that when adult roach and dace co-existed in the River Exe catchment, their diets overlapped greatly, but this was mainly plant material, including algae, macrophytes and detritus, which was usually not restricted in supply. This situation was also true in the present investigation, with the most abundant zooplankton found in the diets of the fish also being highly abundant in the water column, and dietary overlap was significant. The results from the River Trent generally appeared to support the findings of the experiments at Calverton Fish Farm, even though fish densities in the river were lower than in the enclosures. For example, dietary overlap between roach and bream was high in the River Trent (both dominated by *Bosmina* sp.).

Notwithstanding, it appears that interspecific interactions influenced diet composition of roach and bream in the experimental enclosures. Although rotifers and copepod nauplii were the two main taxa consumed by both finfold roach and bream larvae, diet composition differed when the two species were in sympatry and allopatry. The main differences were a lower importance of rotifers and a greater importance of copepod nauplii in the diet of roach when in sympatry with bream than when in allopatry, implying that roach changed their behaviour in the presence of bream. Moreover, given Nunn *et al.* (2007b) observed that roach larvae preferentially selected rotifers over copepod nauplii of the same size, it is possible that the switch to copepod nauplii in the presence of bream could have negative impacts on fish growth, condition and survival.

In the present study, roach and bream consumed fewer cyclopoid copepods than most other prey taxa when in allopatry. However, there was an increase in cyclopoid copepod consumption by bream when in sympatry with roach, and roach exhibited a similar shift, although the increase was less than for bream. Bream in the River Trent showed a similar pattern. Cyclopoid copepods were the most abundant zooplankters consumed by bream when roach and bream were equally abundant, whereas bream consumed fewer copepods when they were the dominant fish species. By comparison, roach consumed very few cyclopoid copepods in all circumstances. Winfield *et al.* (1983) carried out laboratory tests on the efficiency of 0+ juvenile roach and bream at capturing prey, and found both species had more difficultly capturing copepods than cladocerans. However, bream were more efficient than roach at catching copepods, probably because they have a greater strike ability than roach, likely related to the more protrusible mouth of bream. Hoogenboezem *et al.* (1992) also stated that bream are able to switch between particulate- and filter-feeding, which might give them an advantage over roach when feeding on copepods. This could explain the electivity indices in the current study. When in allopatry, finformed bream larvae and 0+ juveniles selected *D. magna*, a large and slow-moving cladoceran, whereas (fast-moving) cyclopoid copepods were selected when in sympatry. This suggests that although bream are capable of capturing cyclopoid copepods, they prefer not to (e.g. in allopatry) as they are more difficult to catch than other prey. Bream in the River Trent demonstrated similar behaviour as cyclopoid copepods were avoided on all occasions, even though cyclopoid copepod numbers in the diet were higher when roach and bream were equally abundant.

Finformed roach and bream larvae generally consumed greater amounts of planktonic and non-planktonic cladocerans than did finfold larvae. However, differences were found in behaviour between treatments. For example, selection of planktonic cladocerans by roach was stronger (e.g. *D. magna*, *Bosmina* sp.) in sympatry than in allopatry, suggesting resource partitioning between roach and bream. Similarly, Winfield *et al.* (1983) found that roach and bream exhibited food resource partitioning, with planktonic cladocerans predominating in the diets of roach, and copepods and non-planktonic cladocerans comprising the majority of the diets of bream. The results of the present study are similar to those of Winfield *et al.* (1983), *viz*. larger numbers of copepods were found in the diets of bream in mixed-species enclosures compared to single-species enclosures, and a preference for roach to select more planktonic cladocerans with development in mixed-species enclosures. Similar results were found in the River Trent, where the diets of finformed roach larvae in samples where roach were more dominant than bream consisted mainly of *Bosmina* sp. and aufwuchs, whereas when roach and bream were equally abundant fewer *Bosmina* sp. and no aufwuchs, but more *Daphnia* spp., were consumed. The importance of aufwuchs when roach was dominant could be related to temporal variations in animal prey and/or intraspecific competition (Mann, 1997; Mann *et al.*, 1997; Nunn *et al.*, 2007a, b). Similarly, roach could simply have consumed more *Daphnia* spp. if more were present in the water column when roach were more dominant than bream, which again may have been a consequence of seasonal variations in zooplankton abundance and composition, but the fact that roach avoidance of *Daphnia* spp. increased in the presence of bream (i.e. electivity values were negative, despite the importance of *Daphnia* spp. in the diet) suggests that roach were forced to switch to this prey type. Bream followed the same pattern always avoiding *Daphnia* spp., but selection increased for this taxon in the presence of roach (electivity values were still negative), suggesting that they were forced to feed on *Daphnia* spp. This may have had a negative effect on the condition of bream, as the condition of bream declined in sympatry compared to allopatry.

Although interspecific interactions caused a shift in the foraging behaviour of roach and, to a lesser extent, bream in the experimental enclosures, the differences in diet composition and prey selection when in sympatry and allopatry were not sufficient to have an impact on their length, weight or weight-length relationships. However, impacts might have become more apparent if the experiment was conducted over a longer time period or at higher densities. The condition of roach was not affected by the presence of bream, but there was a small but significant deterioration in the condition of bream when in the presence of roach. This may have been because of the increase in copepod consumption by bream in the presence of roach and, thus, the increased energy expended in capturing this prey may have affected their condition. In addition, the condition of finformed roach and bream larvae did not appear to be affected by interspecific interactions in the River Trent. Notwithstanding, the high densities of 0+ fish inhabiting the margins of many rivers in early summer (e.g. Baras *et al.*, 1994 found as many as 15,000 25 mm fish m^{-2}) may intensify the effects of interspecific interactions on feeding behaviour, which could have important implications for the growth and survival of 0+ fishes, with a number of studies demonstrating a negative relationship between fish growth and density (e.g. Byström & García-Berthou, 1999; Romare, 2000). Persson & Greenberg (1990), for example, demonstrated that the individual growth rates of 0+ perch decreased with increasing roach density, and Cryer *et al.* (1986) and Perrow & Irvine (1992) demonstrated that abundant 0+ roach can sometimes show poor growth as a result of depression of their prey populations. Similarly, Welker *et al.* (1994) suggested that the growth and survival of planktivorous gizzard shad (*Dorosoma cepedianum* (LeSueur) larvae and the growth of bluegill (*Lepomis macrochirus* Rafinesque) larvae are affected by the availability of zooplankton, which may become limiting when larval fish densities are high. Indeed, Grenouillet *et al.* (2001a) stated that the survival of roach in the first year of life was density-dependent, and that intraspecific competition within the 0+ cohort could influence recruitment to older age classes. Furthermore, competition for food resources may influence the overwinter survival of 0+ fishes, which is positively related to fish length, although it is the energy stored by the fish (which is a function of length), rather than length itself, that is the key factor (Griffiths & Kirkwood, 1995; Kirjasniemi & Valtonen, 1997, Hurst, 2007). These studies suggest that fish densities *per se* may not be important, but that there may be a threshold density (relative to food availability) at which fish deplete food resources to an extent that impacts on growth and survival may occur.

CHAPTER SIX

6.1 GENERAL DISCUSSION

There are many external factors, either anthropogenic or natural, that affect the numbers of fish that recruit to adulthood (Mills & Mann 1985; Miller *et al*., 1988; Gliwicz, 1994; Houde, 2002; Ondračková *et al*., 2002; Nunn *et al*., 2003, Quist, 2004; Longshaw *et al*., 2005; Longshaw *et al*., 2010; Nunn *et al*., 2012). Diet composition and zooplankton availability play an important role in the early development of fishes, because growth in the first few weeks of life is key to survival and recruitment success (Cryer *et al*., 1986; Bass *et al*., 1997; Barriga *et al*., 2011; Nunn *et al*., 2012; Fig. 6.1). This thesis explores temporal, spatial and interspecific influences on the feeding ecology of 0+ fishes; and this chapter integrates the knowledge gained from the previous three chapters, and provides recommendations for further study.

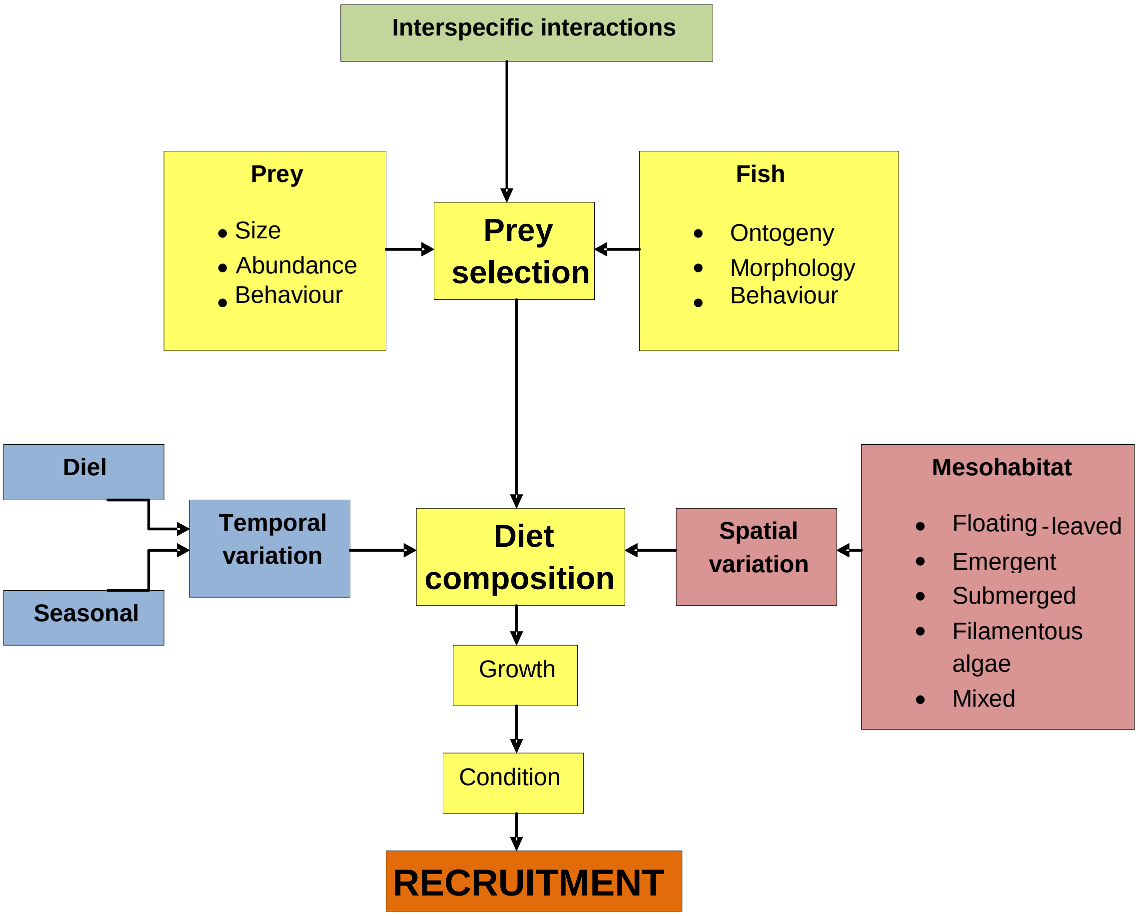


Fig. 6.1 Summary diagram of topics covered within thesis (blue = Chapter 3, red = Chapter 4, green = Chapter 5, yellow = fundamental topics explored within each Chapter).

6.1.1 TEMPORAL VARIATIONS

Temporal (diel and seasonal) variations in prey availability influenced the feeding behaviour and diet composition of 0+ roach, perch and bream in this thesis (Chapter 3). Emphasising the need for further study on how temporal variations, such as vertical and horizontal migration of zooplankton, may influence fish condition and consequently recruitment success (Lampert, 1993; Scheffer, 1998; Wojital *et al*., 2003). There were diel variations in the feeding ecology of 0+ fishes, with juvenile perch and roach having a higher gut fullness at night than during daylight, compared with a reduction in gut fullness at night for larval roach and perch, indicating a switch in feeding behaviour during ontogeny. This highlights the need to better understand how different ecospecies respond to temporal changes in food availability (Reyesmarchant *et al*., 1992; Nunn *et al*., 2007a). Additionally, diel variations can influence patterns of fish distribution, with fish occupying habitats that are profitable in terms of food resources and predator avoidance (Jacobsen *et al*., 1997; Jacobson & Perrow, 1998; Olsson *et al*., 2007). This can have implications for sampling strategies depending on the target species and ecospecies (Wolter & Freyhof, 2004). In this study, there was a significant increase in the abundance of spined loach, pike and bullhead at night. Therefore, surveys undertaken in daylight could seriously underestimate population sizes of some species. In addition, habitat use by 0+ fishes could have changed in response to predators, using marginal habitat as refuge areas over the 24-h cycle, influencing their diet composition and prey selection. Densities of 0+ fishes were highest during daylight in two of the surveys, which may have been a consequence of predator avoidance due to an increase in the numbers of piscivorous pike and perch in marginal areas at night.

Electivity values and prey availability also suggested a switch in feeding behaviour in larval and 0+ juvenile roach between day and night. For example, electivity values of *E. lamellatus* for roach larvae generally increased at night. By contrast, electivity values for *E. lamellatus* declined at night for 0+ juvenile roach in 2009*,* indicating a switch in diel feeding behaviour and feeding activity with ontogeny, but this only occurred in 2009 and was not repeated in 2010. Temporal variations in prey availability can have vital consequences for the growth and development of larval and juvenile fish, potentially influencing their survival and subsequent recruitment success. The study in (Chapter 5) demonstrated how diel changes in zooplankton populations influence the types and abundance of prey available to 0+ fishes. There was circumstantial evidence of zooplankton migrations, as densities of Rotifera in the margins declined at night, suggesting migration into open waters.

Seasonal variations in feeding activity, and diet composition can also have ramifications for recruitment success as the condition of fish may be affected, reducing their chances of survival through the winter (DeVries *et al*., 1998; Hoxmeier *et al*., 2004; Nunn *et al*., 2012; Chapter 3). It is therefore important that peaks in the availability of specific sizes and types of prey coincide with the suitable stages of fish development. Seasonal variations in this thesis included a significant reduction in the feeding activity of 0+ juvenile roach and bream from summer to winter. There were significant seasonal differences in the diet composition of bream, but no significant seasonal variations were found in the diet composition of 0+ juvenile roach, suggesting that bream are more specialised feeders than roach. The diversity and evenness of the diets of 0+ juvenile bream were higher in winter than summer. This could indicate a preference for a certain prey type (such as cyclopoid copepods) in summer that was not available in winter, which consequently led to a more varied winter diet. By contrast, the diversity of 0+ juvenile roach diets was lowest in winter, although there was a greater evenness in the taxa consumed than summer. There was also more individual specialism in autumn and winter by 0+ juvenile roach than in the summer. Nonetheless, any seasonal changes in feeding activity or diet composition of roach and bream did not affect the condition of the fish, which remained constant across all seasons. However, the duration of this study may have been inadequate to detect reductions in condition, especially those that are inherent from fish reaching smaller sizes towards the end of the first growing season or taking longer to reach the size where they can exploit different food types.

6.1.2 SPATIAL VARIATIONS

The influence of macrophyte structure on zooplankton distribution, prey selection and feeding activity of 0+ fishes was examined in Chapter 4. Habitat structure/complexity can influence zooplankton composition (density/diversity), which consequently can affect the foraging ecology and diet composition of 0+ fishes (McAbendroth *et al*., 2005; Thomaz & Cunha, 2010; Nunn *at al*., 2012). In this thesis, it was generally found that highest densities of most zooplankton taxa in emergent and floating-leaved vegetation (the least complex habitats) rather than submerged vegetation (the most complex) this suggests that habitat structure influences prey availability to 0+ fishes. Similarly, prey selection of most taxa by 0+ fish was always highest in the simple vegetation categories compared with complex vegetation categories, even though similar taxa were available in most habitats. Other influences such as how habitat complexity affects the mobility of fishes also need to be taken into consideration when studying the feeding ecology of fish (Winfield, 1986; Dibble *et al*., 1996; Agostinho *et al*., 2007). Contrary to expectations, there was little evidence of structural complexity influencing the feeding activity of 0+ roach or bream in this thesis. This may have been a result of high prey availability or movement of fish between vegetation categories to avoid predation or because feeding activity varies temporally.

6.1.3 INTERSPECIFIC INTERACTIONS

The effects of interspecific interactions on the diet composition, prey selection, growth and condition of 0+ roach and bream in experimental and wild conditions were explored in Chapter 5. Dietary overlap was high in both instances. The diets of larval fishes are restricted, and there is often a distinct shift in diet composition and feeding behaviour from the larval to juvenile period (Nunn *et al*., 2012). Selection of smaller and slower moving zooplankton species is more prevalent in finfold fishes compared to finformed fishes that are more developed, this makes them more capable of feeding on larger and more mobile zooplankton species (Garner, 1996a; Mehner *et al*., 1998; Nunn *et al*., 2007b). Nevertheless, there was evidence of resource partitioning when 0+ roach and bream were in sympatry, which suggested the feeding behaviour of both species was negatively affected by interspecific interactions, with fish selecting less profitable prey in terms of energy gained relative to energy expended. Many factors influence the feeding ecology of 0+ fishes, including interspecific interactions (Garner, 1996a). As finfold fish are morphologically and behaviourally undifferentiated during this period dietary overlap is frequently high (Garner 1996a) and this can negatively affect fish growth and condition (Persson & Irvine, 1992; Welker *et al*., 1994; Grenouillet *et al*., 2001a). In this thesis interspecific interactions influenced the diet composition of roach and bream in experimental enclosures, as a consequence, there was a small but significant deterioration in the condition of bream when in the presence of roach compared to when bream were in an enclosure on their own. Nonetheless, this did not affect the length or weight of roach or bream, but did significantly influence the condition of bream. It can be speculated that fish densities *per se* may not be important, but that there may be a threshold density (relative to food availability) at which fish deplete food resources to an extent that impacts on condition and subsequent survival.

6.2 CONCLUSIONS AND RECOMMENDATIONS

6.2.1 TEMPORAL VARIATIONS

Temporal variations in prey selection and diet composition can have important implications for the growth, condition and survival of fishes. This study found diel variations in the feeding activity, prey selection and diet composition of larval and 0+ juvenile fishes, as well as the composition and abundance of zooplankton. The feeding activity of 0+ juvenile roach, for example, was significantly higher at night than during daylight in 2009, whereas finformed roach larvae were most active during daylight. It is recommended that further diel studies are carried out that incorporate samples from open-water as well as marginal areas. Although in this study there was circumstantial evidence of zooplankton and predator migrations into and out of the margins, samples from open-water habitats could provide support for or refute this theory. This study was carried out in a marina, so comparisons to the main river channel would provide beneficial comparisons to back water habitats and how species in the areas utilise them. It would also be valuable to compare different river systems such as northern rivers to southern rivers in the UK to improve knowledge of fish feeding ecology on a wider scale. Additionally, this study focused on 0+ roach and perch, future studies should consider all important fishes of angler interest within the Trent system such as chub, dace, barbel and bream. The outcomes of such investigations should affirm the key times and areas used by foraging 0+ fishes.

Fish species composition and densities also varied over the 24-h periods. Densities of larval fishes throughout June were generally higher in daylight than night, but in July, when most cyprinid fish species were 0+ juvenile, densities where higher at night than during daylight. These ontogenetic shifts in feeding behaviour may influence their diet and in turn their condition, affecting their chances of recruiting to adulthood. There was a significant increase in the size and abundance of piscivorous predators such as perch and pike and a significant increase in the densities of spined loach and bullhead in hours of darkness. This has ramifications for sampling protocols (e.g. EU LIFE monitoring) as daylight surveys may seriously underestimate species demographics. It is therefore recommended that sampling for spined loach and bullhead should be done at night.

There was a significant reduction in the feeding activity of 0+ juvenile roach and bream in winter compared with summer, although it did not affect their condition. As mentioned previously (Chapter 2), the most widely-used and reliable index of nutritional condition of larval and juvenile fishes appears to be the ratio of tissue RNA to DNA (Ferron & Leggett, 1994; Folkvord *et al*., 1996; Rooker & Holt, 1996) and may be a better indicator of fish condition compared to standard length/weight comparisons. Whereas the amount of RNA in cells varies in proportion to protein synthesis, DNA concentrations remain fairly constant, even during starvation (Caldarone *et al*., 2006). RNA-DNA ratios can be used to determine the nutritional status both of populations of larvae and individual fish, and for comparison of cultured and wild fishes (Bulow, 1987; Steinhart & Eckmann, 1992; Buckley *et al*., 1999), and are a more accurate index of metabolic activity than RNA concentration alone as they are unaffected by the number or size of cells in tissue samples (Haines, 1973). Correlations between food availability and RNA-DNA ratios have been reported for the larvae of a number of fish species (Buckley, 1980; Buckley *et al*., 1984; Buckley & Lough, 1987; Theilacker *et al*., 1996). It is recommended that targeted surveys are conducted to investigate species-specific, ontogenetic and seasonal changes in feeding behaviour. The studies should be carried out over a longer period of time than in the current study (for example, 1 year) to examine seasonal variations in 0+ fish diet composition and prey selection, and whether this influences fish condition. It is recommended that the RNA-DNA technique described previously is used in future studies in addition to or replacement of standard length/weight relationships to calculate condition. Further and more intensive studies of interannual variations (for example, over a 10 year period) in diet composition and prey availability may allow a causal link between 0+ fish growth and survival and food resources to be identified. Again, RNA-DNA ratios should be used to identify any relationship between annual variations in fish diet and condition of key fish species in a variety of UK rivers. It may also be useful to compare years of differing environmental conditions (e.g. high or low flows) to identify any trends, for example, Nunn *et al*., (2003) suggests that temperature influences the growth of fishes at the end of their first year.

6.2.2 SPATIAL VARIATIONS

Macrophyte structure can influence prey availability and thus the diet composition of 0+ fishes, which consequently can have important implications for the growth, condition and survival of fishes. This study found variations in the diet composition of 0+ roach and bream, as well as the composition and abundance of zooplankton between habitats of differing structural complexity. Generally, zooplankton population densities were higher in the least complex macrophyte structures (emergent and floating-leaved). Similarly, 0+ fishes were more likely to select prey in the least complex macrophyte structures than more complex structures (submerged plant species). Although habitats differ in the densities and size ranges of potential prey found, there is little evidence that this corresponds to habitat-specific differences in diet, or that such habitats offer a nutritional advantage over others. It appears that habitat structural complexity influences the feeding activity of 0+ fishes, but did not affect the condition of 0+ fishes. Although in this instance condition appeared not to be influenced, structural complexity influenced feeding behaviour. In other situations, a change in feeding behaviour may influence the growth and subsequent survival of 0+ fishes.

It is recommended that further studies are conducted to investigate the influence of habitat use on the diet composition, prey selection, growth, condition and survival of 0+ fishes. This study focused on a regulated river and on 0+ roach and bream. Future studies should incorporate other fish species and, where possible, be conducted in a natural river system where there is distinct groupings of differing macrophyte structures. These studies should incorporate other variables such as prey size, temperature and dissolved oxygen (DO) levels, and take into consideration the effect of predator abundance on feeding behaviour.

There are many approaches that could be used when taking into account temperature. To rule out temperature as an influence on the condition of fishes between different macrophyte structures, temperature readings should be taken at each point where fish are stunned. Alternatively, one temperature reading could be taken from each habitat category on each survey date. In addition to this data, it may be useful to record temperature on a daily basis over the survey period (one from each habitat category), so that the number of degree days above 12^{o}C can be recorded. It has been found that growth in cyprinids occurs above this temperature (Nunn *et al*., 2003). Therefore, recording temperature can identify any correlations between growth and temperature or growth and temperature within differing macrophyte structures. It is recommended that DO level readings are also taken within each habitat category (one in each) on each survey date, so that any correlations between DO levels within differing macrophyte structures and condition of the fishes can be identified. The number of piscivorous fish that are stunned at each point should also be recorded within each habitat category. This will help identify any correlations between predator abundance and feeding behaviour, which in turn could influence fish condition. Such knowledge has fundamental implications for conservation projects and can be applied to increase the habitat available to all life stages and species of fish in river rehabilitation schemes. If possible, such surveys should employ a point sampling strategy in an attempt to identify variations in fish habitat use and zooplankton distribution. This strategy will further enable a better understanding of the role of habitat morphology and hydrology in food availability and foraging success. For example, measuring flow in differing macrophyte structures may provide vital information linking water retention times with zooplankton abundance/composition. It is recommended that one flow reading is taken within each habitat category studied on each survey date. It is generally found that areas of reduced flow provide better conditions for plankton development due to the increase in water retention times (the length of time water remains in one place) (Reckendorfer *et al*., 1999; Schiemer *et al*., 2001). Therefore, variances in flow rates within differing macrophyte structures may influence prey availability and therefore fish feeding behaviour and condition. In addition, this knowledge will facilitate the management of river habitats and aquaculture facilities for fish and fisheries, especially how to provide optimum habitat conditions in the drive to improve the ecological status of rivers and lakes under the EU WFD.

6.2.3 INTERSPECIFIC INTERACTIONS

This study demonstrated a significant influence of interspecific interactions on the diet composition and prey selection of 0+ roach and bream. There was evidence of resource partitioning when roach and bream larvae were in sympatry (i.e. in mixed-species enclosures). Finfold roach larvae consumed fewer rotifers but more copepod nauplii, and bream consumed more adult cyclopoid copepods than when in allopatry (i.e. in single-species enclosures). The increased importance of copepod nauplii and adult cyclopoid copepods in the diets when in sympatry, both of which were avoided in allopatry, suggests the feeding behaviour of both species was negatively affected by interspecific interactions. Such knowledge of the dietary requirements of larval and juvenile fishes is essential for the management of their populations and habitats. It is recommended that the study is repeated under similar conditions but using different combinations and ratios of fish species. For example, dace and chub are likely to compete for resources in the wild as well as aquaculture. By manipulating the ratios (increasing the amount of one species compared to the other) could demonstrate the influence of interspecific interactions on the diet composition and prey selection of different fish species and the thresholds when species switch prey items. Various combinations of feeding guilds could be studied, for example surface- and benthic-feeding species, to identify the species most likely to compete for resources. The calorific value of different prey types could also be studied using the ash-free dry weight of each zooplankton species (Davis, 1993) to determine if any changes in prey choice affect condition. For example, the energy needed to capture a certain prey may out-weigh its energy gain.

Interspecific interactions had no significant influence on the length, weight or weight-length relationships 0+ roach and bream. In addition, the condition of roach was not affected by the presence of bream, but there was a small but significant deterioration in the condition of bream when in the presence of roach. The deterioration in bream condition could be related to a switch in diet, with bream consuming more cyclopoid copepods when in the presence of roach, as cyclopoid copepods are fast moving and require more energy to capture than other zooplankters. It is recommended that the experiment is repeated at higher stocking densities (300, 350, 400 or more fish/m^2) to help establish a threshold density at which fish deplete resources to an extent that impacts on growth or condition. Also, carrying out this experiment over a longer time period may help identify the densities at which interspecific, and intraspecific, interactions manifest in differences in growth and survival rates. The density of fish in the experiments was higher than the stocking density at Calverton Fish Farm, indicating that there are unlikely to be any negative impacts on the growth or survival of roach and bream larvae under the current management regime. Further experiments could be conducted on different combinations and ratios of fish species that are likely to compete either in aquaculture facilities, such as dace and chub. In addition, it may be useful to see if there is any dietary overlap or changes in feeding behaviour in species that would not be expected to compete for resources such as barbel and dace. This will help determine species-specific optimal stocking densities for fish farms, both for single- and mixed-species ponds. This will not only enhance fish stocks and recruitment in fish farms, but in turn will provide vital information and benefit to our understanding of fish ecology and aquaculture in general.

This study has ramifications for husbandry protocols and stocking densities in fish-production facilities. There is effectively a trade-off between stocking density and fish growth/survival. Whereas stocking at high densities may produce large numbers of relatively small fishes, stocking at lower densities may produce smaller numbers of larger fishes. Thus, it is critical that the correct densities and combinations of fish are used in production facilities, and that adequate food is available to larvae when they are stocked: if a fish species influences the growth or condition of another species, it could affect survival in the facility and once released into the wild, thus reducing stocking success. The current husbandry practices at Calverton Fish Farm have been developed over many years and appear to meet these requirements. The ponds are primed to provide fish larvae with abundant zooplankton, with stock-out generally coinciding with peak rotifer densities, and supplementary feeds are provided once natural food resources have been depleted. In addition, the fishes are stocked at a lower density than previously, which has increased growth and survival rates (A.C. Henshaw, pers. comm.). Furthermore, the fishes are currently reared in single-species ponds for the whole of the first year of life, thereby eliminating the possibility for interspecific competition during the larval and 0+ juvenile periods, although there is the potential for interspecific competition to occur in mixed-species ponds in the second year of life. However, the current policy of stocking 1+ fish of contrasting behaviour (e.g. benthic and open-water feeders) together should minimise any interspecific interactions.

River management is increasingly turning from hard-engineering solutions to ecologically based restoration projects to improve degraded river systems (Palmer *et al*., 2005), especially since the implementation of the WFD. River Basin Management Plans, which are a catchment based approach to river rehabilitation within the Environment Agency, need to be based on a good understanding of the factors influencing the river system, therefore, research into the feeding ecology of fishes (temporal, spatial and interspecific interactions) and their subsequent recruitment to adulthood is an important resource for river rehabilitation schemes to be successful. Improving and increasing the number of off-channel refuges such as marinas or man-made connections/back channels may provide important refuge areas for larval and juvenile fishes to grow before moving out into the main river. These areas provide refuge from flow as well as offering a more diverse range of macrophytes and consequently zooplankton populations needed throughout the development of 0+ fishes (Nunn *et al*., 2007a, b & c; Nunn *et al*., 2012). However, there is a constant battle with flood defence, which requires a more hard engineering approach by removing instream vegetation, dredging channels and building hard flood defence walls. These departments (fisheries and flood defence) need to work together to enable sustainable fish populations to be established as well as providing flood defence, improved habitat and conserving riverine ecosystems as a whole.

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