Rev Fish Biol Fisheries (2012) 22:377–408
DOI 10.1007/s11160-011-9240-8

REVIEWS

The foraging ecology of larval and juvenile fishes

A. D. Nunn · L. H. Tewson · I. G. Cowx

Received: 8 July 2011 / Accepted: 8 October 2011 / Published online: 26 October 2011

Abstract Knowledge of the foraging ecology of fishes is fundamental both to understanding the processes that function at the individual, population and community levels, and for the management and conservation of their populations and habitats. Furthermore, the factors that influence the acquisition and assimilation of food can have significant consequences for the condition, growth, survival and recruitment of fishes. The majority of marine and freshwater fish species are planktivorous at the onset of exogenous nutrition and have a limited ability to detect, capture, ingest and digest prey. Improvements in vision, development of fins and associated improvements in swimming performance, increases in gape size and development of the alimentary tract during ontogeny often lead to shifts in diet composition. Prey size, morphology, behaviour and abundance can all influence the prey selection of larval and juvenile fishes. Differences in feeding behaviour between fish species, individuals or during ontogeny can also be important, as can inter- and intraspecific interactions (competition, predation risk). Temporal (diel, seasonal, annual) and spatial (microhabitat, mesohabitat, macrohabitat, regional) variations in prey availability can have important implications for the prey selection, diet composition, growth, survival, condition and, ultimately, recruitment success of fishes. For fish populations to persist, habitat must be available in sufficient quality and quantity for the range of activities undertaken during all periods of development. Habitats that enhance the diversity, size ranges and abundance of zooplankton should ensure that sufficient food resources are available to larval and juvenile fishes.

Keywords Interspecific and intraspecific interactions · Ontogenetic shifts · Predator–prey relationships · Prey selection · Spatial variations · Temporal variations

Introduction

Foraging theory has received considerable attention across a diverse range of fauna over the last four decades (see Pyke 1984), including some classic work on fishes (e.g. Werner and Hall 1974). Knowledge of the feeding ecology of fishes is fundamental both to understanding the processes that function at the individual, population and community levels, and for the management and conservation of their populations and habitats. Furthermore, the factors that influence the acquisition and assimilation of food can have significant consequences for the condition, growth, survival and recruitment of fishes. This is of particular importance during early development, when fishes are

A. D. Nunn (✉) · L. H. Tewson · I. G. Cowx
Hull International Fisheries Institute, Department
of Biological Sciences, University of Hull,
Hull HU6 7RX, UK
e-mail: a.d.nunn@hull.ac.uk

invariably most vulnerable to predation, competition, disease and environmental perturbations (Mills and Mann 1985; Myers 1995; Houde 1997; Ondračková et al. 2002; Nunn et al. 2003, 2007a, 2010a; Longshaw et al. 2005, 2010). Indeed, important factors regulating the growth and survival of young fishes include food availability and their ability to capture and ingest food items, with a lack of suitable prey potentially causing either reduced growth or starvation, both of which influence survival (Cushing 1990; Mayer and Wahl 1997; Beaugrand et al. 2003; Dickmann et al. 2007; Burrow et al. 2011; Stige et al. 2011). Notwithstanding, the feeding ecology of young fishes, particularly larvae and 0+ juveniles, is poorly understood compared with older individuals. Indeed, there are a large number of species for which there is no information on their foraging ecology during the larval and juvenile periods. For example, there appears to be no primary literature for more than 90% of the freshwater fish species recorded in Europe and information is even more sparse for other regions, particularly for deep-water marine fishes (Kottelat and Freyhof 2007; Froese and Pauly 2011). This paper synthesises the current knowledge of the feeding ecology of larval and 0+ juvenile teleost fishes, using pertinent examples mainly from temperate latitudes in the northern and southern hemispheres, and identifies areas where further research is required.

The diets of larval and juvenile fishes

The ecology of yolk-sac feeding in fishes has been thoroughly reviewed by Kamler (2002) and is not repeated here. Moreover, the nutrition of yolk-feeding fishes is, necessarily, determined by the quantity and quality of yolk reserves, which are intrinsically linked to various maternal attributes (e.g. body size). Most researchers concur that the switch from purely endogenous to exogenous nutrition is a, if not the, key event in the survival of fishes. The majority of marine and freshwater fish species are planktivorous at the onset of exogenous feeding, and many exhibit mixed feeding, with exogenous nutrition commencing before complete absorption of the yolk reserves. Zooplankton serve as a vital food resource for the larvae of most fish species (Tables 1, 2; limited to European species for brevity). Rotifers are frequent prey of the majority of cyprinids, especially in the early larval period, with copepods, cladocerans, insects and phytoplankton also important in the diet (Table 1; Fig. 1a). By contrast, most centrarchids and percids prey upon cladocerans, copepods and insect larvae, while salmonids mainly consume cladocerans and copepods (in lentic environments) or insect larvae (in lotic environments), and the diets of clupeid, gadid, gobiid and osmerid larvae are characterised mainly by various developmental stages of copepods (eggs, nauplii, copepodites, adults) (Tables 1, 2; Fig. 1a). Protozoans may also be important prey for fish larvae, especially in marine ecosystems (Montagnes et al. 2010).

The feeding diversity of juvenile fishes is generally greater than during the larval period, and there is often an increase in the importance of species-specific dietary traits (Tables 1, 2). The majority of juvenile cyprinids consume cladocerans, copepods and insect larvae, with aufwuchs (the periphyton and associated microfauna that grow on underwater surfaces) and adult dipterans also important in some species, while centrarchids and percids prey mainly upon cladocerans, copepods, insect larvae, isopods, amphipods and fishes (Table 1; Fig. 1b). The diets of juvenile salmonids are invariably dominated by larval, pupal or adult insects, although cladocerans and copepods are important in coregonids, while clupeids, gadids and osmerids consume copepods, isopods, amphipods, mysids, euphausiids, decapods and fishes (Tables 1, 2; Fig. 1b).

Even fish species that are piscivorous (e.g. European seabass (*Dicentrarchus labrax* (L.), Moronidae), northern pike (*Esox lucius* L., Esocidae)), herbivorous (e.g. common nase (*Chondrostoma nasus* (L.), Cyprinidae), butterfish (*Odax pullus* (Forster), Odacidae)) or detritivorous (e.g. thin-lipped grey mullet (*Liza ramada* (Risso), Mugilidae), fathead minnow (*Pimephales promelas* Rafinesque, Cyprinidae)) as juveniles or adults may initially be zooplanktivorous (Ferrari and Chieregato 1981; Aprahamian and Barr 1985; Clements and Choat 1993; Bry et al. 1995; Reckendorfer et al. 2001; Herwig and Zimmer 2007). Notable exceptions include fishes inhabiting the upper, fast-flowing reaches of rivers, where plankton is usually rare, such as many salmonid species. In such habitats, diets are invariably dominated by insects and crustaceans captured from the river bed, drift or water surface (Allen 1941; Frost 1950; Wańkowski and Thorpe 1979; Williams 1981; Zimmerman and

Table 1 The diets of the larvae and juveniles of key fish species in European fresh waters

Family *Species*	Vernacular name	Larvae	Juveniles	Selected references
Balitoridae				
Barbatula barbatula	Stone loach	Chydoridae, Cyclopoida (nauplii, adults), Chironomidae (larvae)	Chironomidae (larvae), Simuliidae (larvae), Ephemeroptera (larvae), Ostracoda, Trichoptera (larvae), Oligochaeta, Chydoridae, Cyclopoida	Hyslop (1982), Welton et al. (1983)
Centrarchidae				
Lepomis gibbosus	Pumpkinseed	Bosminidae, Cyclopoida, Daphniidae, Leptodoridae	Daphniidae, Cyclopoida, Amphipoda, Chironomidae (larvae), Ephemeroptera (larvae), Gastropoda, Trichoptera (larvae), Hemiptera, Mysidacea, Corophiidae	Wolfram-Wais et al. (1999), Declerck et al. (2002), Rezsu and Specziár (2007)
Micropterus dolomieu	Smallmouth bass	Daphniidae, Cyclopoida, Chironomidae (larvae), Trichoptera (larvae), Ephemeroptera (larvae)	Daphniidae, Cyclopoida, Chironomidae (larvae), Trichoptera (larvae, adults), Ephemeroptera (larvae), Amphipoda, Isopoda, fishes	George and Hadley (1979), Easton et al. (1996)
Micropterus salmoides	Largemouth bass	Daphniidae, Cyclopoida	Cladocera, Amphipoda, Ephemeroptera (larvae), Chironomidae (larvae), fishes	Hamilton and Powles (1979), García-Berthou (2002)
Clupeidae				
Alosa fallax	Twaite shad	Chironomidae (larvae, pupae), Chydoridae, Cyclopoida, Ephemeroptera (larvae), Simuliidae (larvae), Diptera (larvae)	Chironomidae (larvae, pupae, adults), Chydoridae, Cyclopoida, Ephemeroptera (larvae), Simuliidae (larvae), Trichoptera (larvae), Diptera (larvae), fishes	Aprahamian (1989), Nunn et al. (2008a)
Cottidae				
Cottus gobio	European bullhead		Chironomidae (larvae), Ephemeroptera (larvae), Simuliidae (larvae), Trichoptera (larvae), Gastropoda, Asellidae	Hyslop (1982), Welton et al. (1983), Nunn et al. (2007a)
Cyprinidae				
Abramis brama	Common bream	Rotifera, Diatoma, Chydoridae, Bosminidae, Daphniidae, Chironomidae (larvae), Cyclopoida (nauplii, adults)	Daphniidae, Chydoridae, Bosminidae, Chironomidae (larvae), Cyclopoida, aufwuchs	Garner (1996a), Mehner et al. (1997), Matěna (1998), Vašek et al. (2006), Nunn et al. (2007a)
Alburnoides bipunctatus	Spirlin		Bacillariophyta	Treer et al. (2006)
Alburnus alburnus	Bleak	Rotifera, Bosminidae, Chydoridae, Cyclopoida (nauplii, adults), Bacillariophyta, Chironomidae (larvae)	Rotifera, Bosminidae, Chydoridae, Cyclopoida (nauplii), Chironomidae (larvae)	Schiemer et al. (1989), Garner (1996a), Nunn et al. (2007a)

Table 1 continued

Family *Species*	Vernacular name	Larvae	Juveniles	Selected references
Aspius aspius	Asp	Rotifera, Copepoda (nauplii, copepodites, adults), Cladocera, Chironomidae (adults)	Chironomidae (adults)	Specziár and Rezsu (2009)
Barbus barbus	Barbel	Chironomidae (larvae), Ephemeroptera (larvae), Chydoridae, Cyclopoida (nauplii, adults), Rotifera	Chironomidae (larvae), Ephemeroptera (larvae), Chydoridae, Cyclopoida (nauplii, adults), Rotifera	Bischoff and Freyhof (1999), Copp et al. (2005), Nunn et al. (2007a)
Carassius carassius	Crucian carp	Daphniidae, Bosminidae, Chydoridae, Copepoda, Chironomidae (larvae)	Daphniidae, Bosminidae, Chydoridae, Copepoda, Chironomidae (larvae)	Penttinen and Holopainen (1992)
Chondrostoma nasus	Common nase	Rotifera, Chironomidae (larvae, adults), Aphidina, Thysanoptera	Aufwuchs, detritus	Reckendorfer et al. (2001)
Cyprinus carpio	Common carp	Daphniidae, Chydoridae, Ostracoda, Corixidae, Cyclopoida (nauplii, adults), Chironomidae (larvae)	Daphniidae, Chydoridae, Ostracoda, Hemiptera, Chironomidae (larvae), Cyclopoida, Oligochaeta, Gastropoda, Trichoptera (larvae)	Vilizzi (1998), Nunn et al. (2007b)
Gobio gobio	Gudgeon	Chydoridae, Chironomidae (larvae), Cyclopoida (nauplii, adults)	Chironomidae (larvae), Ephemeroptera (larvae), Trichoptera (larvae), Chydoridae, aufwuchs, Cyclopoida, Ostracoda	Garner (1996a), Copp et al. (2005), Nunn et al. (2007a)
Leucaspius delineatus	Sunbleak	Aufwuchs, Rotifera, Bosminidae, Daphniidae, Chironomidae (larvae), Chydoridae, Cyclopoida	Bosminidae, Daphniidae, Chironomidae (larvae), Chydoridae, Cyclopoida, aufwuchs	Gozlan et al. (2003), Pinder et al. (2005)
Leuciscus leuciscus	Common dace	Rotifera, Bosminidae, Chydoridae, Cyclopoida (nauplii, adults), Bacillariophyta, Chironomidae (larvae, pupae, adults), Diptera (adults), Polyphemidae	Diptera (adults), Chironomidae (larvae, pupae, adults), aufwuchs, Cyanophyta, detritus	Mills et al. (1985), Weatherley (1987), Nunn et al. (2007a)
Phoxinus phoxinus	European minnow	Rotifera, Chironomidae (larvae), Chydoridae, Cyclopoida (nauplii, adults), Bosminidae, Hydracarina	Cyclopoida (copepodites, adults), Chironomidae (larvae), Trichoptera (larvae), Bosminidae, Rotifera, Chydoridae	Frost (1943), Nunn et al. (2007a)
Pseudorasbora parva	Topmouth gudgeon	Rotifera, Bosminidae	Bosminidae, Chydoridae, Chironomidae (larvae, pupae), Trichoptera (larvae)	Wolfram-Wais et al. (1999), Declerck et al. (2002)
Rutilus rutilus	Roach	Rotifera, Bacillariophyta, Bosminidae, Chydoridae, Daphniidae, Cyclopoida (nauplii, adults), Chironomidae (larvae, pupae), aufwuchs	Daphniidae, Bosminidae, Chironomidae (larvae, pupae), Cyclopoida, aufwuchs, detritus, cyanobacteria	Weatherley (1987), Garner (1996a), Mann et al. (1997), Mehner et al. (1997), Kamjunke et al. (2002), Vašek et al. (2006), Nunn et al. (2007a, 2008b)

Table 1 continued

Family *Species*	Vernacular name	Larvae	Juveniles	Selected references
Scardinius erythrophthalmus	Rudd	Rotifera, Bacillariophyta, Bosminidae, Chydoridae, Daphniidae, Copepoda (nauplii), Chironomidae (larvae)	Bosminidae, Chydoridae, Daphniidae, Chironomidae (larvae), Cyclopoida	Kennedy and Fitzmaurice (1974), Mark et al. (1987)
Squalius cephalus	Chub	Rotifera, Chlorophyta, Bacillariophyta, Chydoridae, Daphniidae, Bosminidae, Polyphemidae, Chironomidae (larvae), Diptera (adults), Cyclopoida (nauplii, adults)	Chironomidae (larvae, adults), Diptera (adults), aufwuchs, Cyclopoida	Mark et al. (1987), Garner (1996a), Nunn et al. (2007a)
Tinca tinca	Tench	Rotifera, Protozoa, Bacillariophyta, Bosminidae, Chydoridae, Ostracoda, Daphniidae, Cyclopoida, Chironomidae (larvae), Ephemeroptera (larvae)	Rotifera, Bosminidae, Chydoridae, Ostracoda, Daphniidae, Cyclopoida, Chironomidae (larvae), Ephemeroptera (larvae)	Kennedy and Fitzmaurice (1970), Copp and Mann (1993)
Esocidae				
Esox lucius	Northern pike	Rotifera, Bosminidae, Chydoridae, Daphniidae, Cyclopoida, Chironomidae (larvae, pupae), Asellidae, Gammaridae	Fishes, Daphniidae, Cyclopoida, Chironomidae (larvae, pupae), Asellidae, Gammaridae	Bry et al. (1995), Žiliukiene and Ziliukas (2006)
Gadidae				
Lota lota	Burbot	Rotifera, Cyclopoida (nauplii, adults), Daphniidae, Polyphemidae, Sididae, Calanoida (nauplii, adults)	Cyclopoida, Daphniidae, Polyphemidae, Sididae, Calanoida, Amphipoda, Ephemeroptera (larvae), Chironomidae (larvae), fishes	Ghan and Sprules (1993), Wang and Appenzeller (1998)
Gasterosteidae				
Gasterosteus aculeatus	Three-spined stickleback	Rotifera, Cyclopoida (nauplii, adults), Chironomidae (larvae), Chydoridae, Daphniidae, Bosminidae	Bosminidae, Chydoridae, Chironomidae (larvae, pupae), Cyclopoida, Oligochaeta, Asellidae, Gammaridae	Hynes (1950), Copp and Kováč (2003), Nunn et al. (2007a)
Pungitius pungitius	Ninespine stickleback	Chydoridae, Daphniidae, Cyclopoida, Chironomidae (larvae)	Chydoridae, Daphniidae, Cyclopoida, Chironomidae (larvae, pupae), Gammaridae, Asellidae	Hynes (1950), Copp and Kováč (2003)
Osmeridae				
Osmerus eperlanus	European smelt	Bacillariophyta, Rotifera, Copepoda (nauplii), Daphniidae	Bosminidae, Daphniidae, Polyphemidae, Leptodoridae, Cyclopoida, Calanoida, Chaoboridae (larvae), Mysidacea	Naesje et al. (1987), Jachner (1991)
Percidae				
Gymnocephalus cernua	Ruffe	Rotifera, Cyclopoida (nauplii, adults), Daphniidae, Bosminidae, Chydoridae, Chironomidae (larvae)	Daphniidae, Chironomidae (larvae), Ephemeroptera (larvae), Trichoptera (larvae), Hirudinea, Cyclopoida	Matěna (1998), Ogle et al. (2004), Rezsu and Specziár (2007)

Table 1 continued

Family *Species*	Vernacular name	Larvae	Juveniles	Selected references
Perca fluviatilis	Eurasian perch	Rotifera, Bosminidae, Chydoridae, Daphniidae, Polyphemidae, Leptodoridae, Cyclopoida (nauplii, adults)	Daphniidae, Bosminidae, Chydoridae, Leptodoridae, Cyclopoida, Chironomidae (larvae), Ephemeroptera (larvae), fishes	Guma'a (1978), Matěna (1995), Mehner et al. (1997), Vašek et al. (2006), Nunn et al. (2007a), Rezsu and Specziár (2007)
Sander lucioperca	Pikeperch	Cyclopoida (nauplii, adults), Daphniidae, Bosminidae, Chydoridae	Daphniidae, Cyclopoida, Leptodoridae, fishes	Mehner et al. (1997), Matěna (1998), Nunn et al. (2007a)
Salmonidae				
Coregonus albula	Vendace	Rotifera, Bosminidae, Chydoridae, Daphniidae, Cyclopoida (nauplii, copepodites, adults), Calanoida		Karjalainen (1991), Sutela and Huusko (1997)
Coregonus autumnalis	Arctic cisco	Copepoda (nauplii, copepodites, adults)	Daphniidae, Chironomidae (larvae, pupae), Cyclopoida, Polyphemidae, Ostracoda	Dąbrowski et al. (1984), Wilson (1984)
Coregonus lavaretus	European whitefish	Cyclopoida (nauplii, copepodites, adults), Daphniidae		Cretenoy and Gerdeaux (1997), Anneville et al. (2007)
Salmo salar	Atlantic salmon	Chironomidae (larvae, pupae, adults), Plecoptera (larvae), Trichoptera (adults), Ephemeroptera (larvae), Coleoptera (larvae)	Diptera (pupae, adults), Chironomidae (larvae, pupae, adults), Gammaridae, Ephemeroptera (larvae), Trichoptera (larvae), Coleoptera (larvae)	Allen (1941), Frost (1950), Williams (1981), Keeley and Grant (1997)
Salmo trutta	Brown trout	Diptera (larvae), Chironomidae (larvae), Ephemeroptera (larvae), Simuliidae (larvae), Trichoptera (larvae)	Chironomidae (larvae), Ephemeroptera (larvae), Plecoptera (larvae), Trichoptera (larvae), Simuliidae (larvae)	Frost (1950), Zimmerman and Mosegaard (1992), Rincón and Lobón-Cerviá (1999), Sánchez-Hernández et al. (2011)
Salvelinus alpinus	Arctic char	Chironomidae (larvae), Harpacticoida	Chironomidae (larvae, pupae), Copepoda, Bosminidae, Chydoridae, Ostracoda, Mysidacea	Moore and Moore (1974), Sparholt (1985)
Thymallus thymallus	Grayling	Chironomidae (larvae, pupae, adults)	Chironomidae (larvae, pupae), Simuliidae (larvae), Ephemeroptera (larvae)	Scott (1985), Sempeski et al. (1995)
Siluridae				
Silurus glanis	Wels catfish	Copepoda, Cladocera, Chironomidae, Oligochaeta, Amphipoda	Chironomidae, Hemiptera, Diptera, Coleoptera, Mysidacea, Daphniidae, Odonata, Gammaridae, Gastropoda, fishes	Bruyenko (1971), Bekbergenov and Sagitov (1984), Stolyarov (1985), Orlova and Popova (1987), all cited in Copp et al. (2009)

It is probable that other food sources are used that reflect biogeographical factors and availability

Table 2 The diets of the larvae and juveniles of key fish species in European inshore marine and transitional waters

Family *Species*	Vernacular name	Larvae	Juveniles	Selected references
Clupeidae				
Alosa fallax	Twaite shad		Calanoida, Harpacticoida, Isopoda, Mysidacea, fishes	Aprahamian (1989), Oesmann and Thiel (2001), Nunn et al. (2008a)
Clupea harengus	Atlantic herring	Bosminidae, Podonidae, Calanoida (eggs, nauplii, copepodites, adults), Gastropoda (larvae), Cyclopoida, Rotifera	Calanoida, Euphausiacea	Arrhenius (1996), Thiel et al. (1996), Pedersen and Fossheim (2008)
Engraulis encrasicholus	European anchovy	Calanoida (eggs, nauplii, copepodites, adults), Cyclopoida (eggs, nauplii, copepodites, adults)		Conway et al. (1998), Tudela et al. (2002)
Sardina pilchardus	European pilchard	Copepoda (eggs, nauplii, copepodites), Tintinnida		Fernandez and Gonzalez-Quiros (2006)
Sprattus sprattus	European sprat	Bosminidae, Podonidae, Calanoida (eggs, nauplii, copepodites, adults), Cyclopoida	Bosminidae, Podonidae, Calanoida (nauplii, copepodites, adults)	Arrhenius (1996), Thiel et al. (1996), Voss et al. (2003), Dickmann et al. (2007)
Gadidae				
Gadus morhua	Atlantic cod	Calanoida (eggs, nauplii, copepodites, adults), Cyclopoida (eggs, nauplii, copepodites, adults), Euphausiacea (nauplii)	Calanoida (copepodites, adults), Cyclopoida, Euphausiacea, Mysidacea, Decapoda (zooea, adults), Harpacticoida, Amphipoda, Gastropoda, fishes	Bromley et al. (1997), Voss et al. (2003), Pedersen and Fossheim (2008), Rowlands et al. (2008), Shaw et al. (2008), Demain et al. (2011)
Melanogrammus aeglefinus	Haddock	Calanoida (nauplii, adults), Cyclopoida	Calanoida, Amphipoda, Decapoda (larvae), fishes	Bromley et al. (1997), Rowlands et al. (2008), Demain et al. (2011)
Merlangius merlangus	Whiting	Calanoida (nauplii, copepodites, adults), Cyclopoida	Calanoida (copepodites, adults), Euphausiacea, Mysidacea, Amphipoda, fishes	Bromley et al. (1997), Rowlands et al. (2008), Shaw et al. (2008), Demain et al. (2011)
Pollachius virens	Saithe		Calanoida, Decapoda (larvae, adults), Amphipoda, Euphausiacea, Polychaeta, fishes	Bromley et al. (1997), Hojgaard (1999)
Trisopterus esmarkii	Norway pout		Calanoida, Euphausiacea	Bromley et al. (1997)
Trisopterus luscus	Pouting	Calanoida, Mysidacea	Mysidacea, Amphipoda, Decapoda, fishes	Hostens and Mees (1999), França et al. (2004)
Trisopterus minutus	Poor cod		Mysidacea, Decapoda, Euphausiacea	Politou and Papaconstantinou (1994)
Gobiidae				
Pomatoschistus microps	Common goby	Calanoida (eggs, nauplii, copepodites, adults), Harpacticoida, Chydoridae, Mysidacea	Calanoida, Mysidacea, Amphipoda, Isopoda, Polychaeta, Bivalvia	Thiel et al. (1996), Leitao et al. (2006)

Table 2 continued

Family *Species*	Vernacular name	Larvae	Juveniles	Selected references
Pomatoschistus minutus	Sand goby	Rotifera, Calanoida (nauplii, copepodites, adults)	Calanoida, Mysidacea, Amphipoda, Polychaeta, Decapoda	Thiel et al. (1996), Hostens and Mees (1999), Leitao et al. (2006)
Moronidae				
Dicentrarchus labrax	European seabass	Calanoida, Mysidacea	Calanoida (nauplii, adults), Mysidacea, Gammaridae, Corophiidae, Harpacticoida, Cirripedia (nauplii), Polychaeta, Decapoda (larvae), fishes	Ferrari and Chieregato (1981), Aprahamian and Barr (1985), Hostens and Mees (1999), Fonseca et al. (2011)
Mugilidae				
Liza aurata	Golden grey mullet		Calanoida (nauplii, adults), Cirripedia (nauplii), Polychaeta, Harpacticoida, Amphipoda, aufwuchs	Ferrari and Chieregato (1981)
Liza ramada	Thin-lipped grey mullet		Calanoida (nauplii, adults), Cirripedia (nauplii), Polychaeta, Harpacticoida, Amphipoda, Insecta (adults), aufwuchs	Ferrari and Chieregato (1981)
Mugil cephalus	Flathead grey mullet		Bacillariophyta, Chlorophyta, Cyanophyta, detritus, Copepoda, Polychaeta	Blaber and Whitfield (1977), Eggold and Motta (1992)
Osmeridae				
Mallotus villosus	Capelin	Tintinnida, Calanoida (nauplii, copepodites, adults), Cyclopoida (nauplii, copepodites, adults), Bivalvia, Bacillariophyta	Calanoida, Cyclopoida, Euphausiacea, Amphipoda, Appendicularia	Courtois and Dodson (1986), Pedersen and Fossheim (2008)
Osmerus eperlanus	European smelt	Calanoida (eggs, nauplii, copepodites, adults), Mysidacea, Amphipoda		Thiel et al. (1996)
Pleuronectidae				
Limanda limanda	Common dab		Mollusca, Polychaeta, Amphipoda, Bivalvia, Harpacticoida	Wyche and Shackley (1986), Hostens and Mees (1999)
Platichthys flesus	European flounder	Harpacticoida, Cyclopoida, Calanoida	Harpacticoida, Polychaeta, Oligochaeta, Cyclopoida, Calanoida, Amphipoda, Mysidacea, Chironomidae (larvae, pupae), Ephemeroptera (larvae), fishes	Aarnio et al. (1996), Thiel et al. (1996), Andersen et al. (2005), Grønkjaer et al. (2007)
Pleuronectes platessa	European plaice		Mysidacea, Polychaeta, Amphipoda, Cumacea	Wyche and Shackley (1986), Hostens and Mees (1999)
Scombridae				
Scomber scombrus	Atlantic mackerel	Phytoplankton, Calanoida (eggs, nauplii, copepodites), crustacean faecal pellets, fishes, Cladocera		Peterson and Ausubel (1984), Conway et al. (1999)

Table 2 continued

Family *Species*	Vernacular name	Larvae	Juveniles	Selected references
Scophthalmidae				
Psetta maxima	Turbot		Amphipoda, Mysidacea, fishes	Last (1979), Aarnio et al. (1996)
Scophthalmus rhombus	Brill		Polychaeta, Amphipoda, Isopoda, Decapoda, Mysidacea	Wyche and Shackley (1986)
Soleidae				
Solea solea	Common sole		Amphipoda, Polychaeta	Hostens and Mees (1999), Cabral (2000)
Sparidae				
Sparus auratus	Gilthead seabream		Calanoida (nauplii, adults), Cirripedia (nauplii), Polychaeta, Harpacticoida, Amphipoda, Mysidacea, fishes	Ferrari and Chieregato (1981)

It is probable that other food sources are used that reflect biogeographical factors and availability

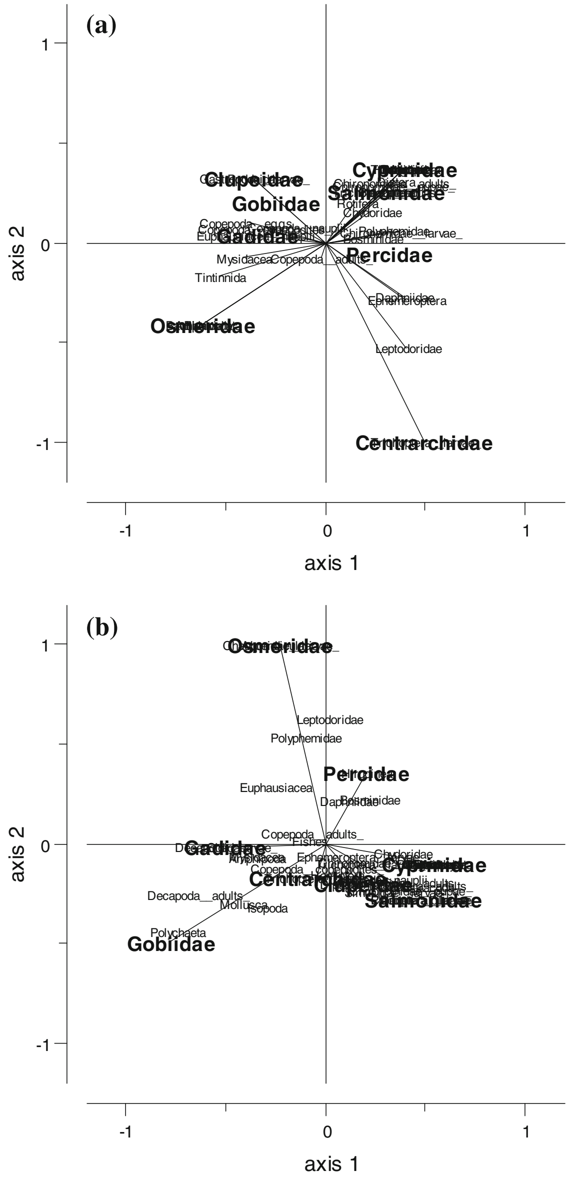

Fig. 1 Correspondence analysis plots comparing the diet composition of **a** larval and **b** juvenile marine and freshwater fishes (from Tables 1, 2)

Mosegaard 1992; Keeley and Grant 1997; Rincón and Lobón-Cerviá 1999). Calanoid copepods, mysids, euphausiids and decapods tend to be more abundant in the diets of marine than of freshwater species, largely because they are usually most abundant or only present in marine environments, whereas rotifers, cyclopoid copepods, cladocerans and insects are most important in the diets of freshwater species (Table 3). The larvae and juveniles of fishes inhabiting tidal

Table 3 Similarity percentages (SIMPER) analysis (Clarke and Warwick 2001) of the mean abundances of key prey taxa and their contributions (%) to dissimilarities in the diets of freshwater and marine larval and juvenile fishes (from Tables 1, 2)

Taxa	Larvae		%	Taxa	Juveniles		%
	Freshwater	Marine			Freshwater	Marine	
Copepoda (copepodites)	12.28	87.50	10.86	Chironomidae (larvae)	77.50	4.17	8.73
Daphniidae	71.21	0.00	10.76	Amphipoda	24.00	75.00	7.38
Copepoda (eggs)	0.00	56.25	8.19	Ephemeroptera (larvae)	55.75	4.17	6.04
Chironomidae (larvae)	52.83	0.00	7.81	Mysidacea	17.33	66.67	5.95
Copepoda (nauplii)	51.34	93.75	7.41	Trichoptera (larvae)	39.67	0.00	4.67
Bosminidae	54.09	12.50	6.85	Daphniidae	46.08	20.83	4.58
Chydoridae	48.88	12.50	6.45	Polychaeta	0.00	37.50	4.47
Rotifera	40.55	18.75	5.20	Fishes	33.33	25.00	4.29
Mysidacea	0.00	31.25	4.68	Euphausiacea	6.67	37.50	4.22
Ephemeroptera	18.60	0.00	3.10	Decapoda (adults)	0.00	33.33	3.99
Leptodoridae	16.67	0.00	2.58	Chydoridae	31.08	0.00	3.82
Tintinnida	0.00	18.75	2.55	Bosminidae	28.58	16.67	3.26
Copepoda (adults)	84.60	93.75	2.52	Chironomidae (pupae)	26.42	0.00	3.19
Chironomidae (adults)	11.83	0.00	1.81	Leptodoridae	13.33	16.67	2.80
Mean dissimilarity			66.87	Mean dissimilarity			71.19

rivers or upper estuaries (e.g. twaite shad (*Alosa fallax* (Lacépède), Clupeidae), Atlantic herring (*Clupea harengus* L., Clupeidae), European smelt (*Osmerus eperlanus* (L.), Osmeridae), European flounder (*Platichthys flesus* (L.), Pleuronectidae), common goby (*Pomatoschistus microps* (Krøyer), Gobiidae), three-spined stickleback (*Gasterosteus aculeatus* L., Gasterosteidae)) frequently have diets containing both marine and freshwater taxa (Beaumont and Mann 1984; Aprahamian 1989; Weatherley 1989; Thiel et al. 1996; Nunn et al. 2008a). Fishes can also be important prey, especially during the juvenile period and in species with large mouths (e.g. gadids, percids, centrarchids; Tables 1, 2, 3; Mittelbach and Persson 1998).

Prey selection

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 (Lazzaro 1987). 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 larval and juvenile fishes (Ghan and Sprules 1993; Anderson 1994). Prey selection is thus 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 (Pyke 1984).

A key factor in prey selection is the relative availability ($\approx$ search time) of particular prey. Townsend et al. (1986), for example, observed that juvenile roach (*Rutilus rutilus* (L.), Cyprinidae) switched from planktonic to non-planktonic cladocerans with a decline in the availability of planktonic prey, and similar responses have been observed for other fish species, including common bream (*Abramis brama* (L.), Cyprinidae) (Persson and Brönmark 2002a), Eurasian perch (*Perca fluviatilis* L., Percidae) (Persson and Greenberg 1990), yellow perch (*Perca flavescens* (Mitchill), Percidae) (Wu and Culver 1992), silver perch (*Bidyanus bidyanus* (Mitchell), Terapontidae) (Warburton et al. 1998), walleye (*Sander vitreus* (Mitchill), Percidae) (Hoxmeier et al. 2004), European flounder (Aarnio et al. 1996) and redfish (*Sebastes* spp., Sebastidae) (Anderson 1994), as well as for roach switching from zooplankton to aufwuchs (Garner 1996a; Mann et al. 1997; Vašek et al. 2006; Nunn et al. 2007b) and for Eurasian perch, pikeperch (*Sander luciperca* (L.), Percidae) and walleye becoming piscivorous (Mehner et al. 1996; Galarowicz et al. 2006). Indeed, Hoogenboezem et al. (1992) used zooplankton density to predict a switch between particulate and filter feeding in common bream. Conversely, switches in prey selection may not occur if zooplankton densities remain high.

The diets of larval and juvenile fishes can include both an increase in prey size and changes in prey species as they grow and develop (Ghan and Sprules 1993; Arrhenius 1996; Dickmann et al. 2007; Nunn et al. 2007b, c). Gape has often been identified as a key morphological trait limiting the prey size of fish that swallow prey whole (e.g. Lazzaro 1987; DeVries et al. 1998; Mehner et al. 1998; Sabatés and Saiz 2000). The small gape of larval and juvenile fishes limits their prey size, yet within constraints set by gape, food eaten influences growth and, ultimately, survival (Bremigan and Stein 1994). Indeed, Mayer and Wahl (1997) demonstrated that young walleye fed selectively and that, for at least some size classes, the selected prey increased growth or survival. Similarly, the switch of some species to piscivory is related to the relative sizes of the predator and their potential prey, and may have a direct positive effect on growth and survival, with piscivorous individuals being larger and in superior nutritional condition than non-piscivorous individuals at the end of the first year of life (Buijse and Houthuijzen 1992; Mehner et al. 1996; Bromley et al. 1997; Frankiewicz et al. 1999; Brabrand 2001; Pelham et al. 2001; Persson and Brönmark 2002b; Klemetsen et al. 2003; Galarowicz et al. 2006; Urbatzka et al. 2008). For example, Olson (1996) observed that rapid growth while feeding on invertebrates allowed 0+ largemouth bass (*Micropterus salmoides* (Lacépède), Centrarchidae) to gain a size advantage over 0+ bluegill (*Lepomis macrochirus* Rafinesque, Centrarchidae), facilitating a shift to piscivory. By contrast, slow growth while feeding on invertebrates reduced the size advantage of largemouth bass over bluegill and delayed or even prevented the shift to piscivory in the first year of life.

Fishes do not necessarily consume the largest prey possible, with Scott (1987) calculating that juvenile roach and common dace (*Leuciscus leuciscus* (L.), Cyprinidae) favour prey approximately 60% of their maximum gape, probably related to the increases in handling times associated with large prey (Wanzenböck 1995). Furthermore, there can be substantial interspecific variations, with Scharf et al. (2000) observing that the prey of 18 fish species off the north-east coast of the USA ranged from 10 to >50% of their body size. Gape size is less restrictive for larval and juvenile fishes that do not swallow prey whole or those, such as some cannibalistic species, that are able to partially ingest large prey (sometimes larger than themselves) and then regurgitate the remains (Baras 1999; Baras et al. 2000). Another factor influencing prey selection is the change in the effective profitability of particular types and sizes of prey in relation to fish satiation (Fig. 2; Turesson et al. 2006). For instance, three-spined stickleback have been shown to select specific sizes of prey until the stomach is full, whereafter smaller prey are selected (Gill and Hart 1998). Similarly, juvenile roach have been observed to initially feed upon large *Daphnia* sp. before switching to smaller individuals, with the switch occurring sooner in small than in large fish (Mikheev and Wanzenböck 1999).

Certain taxa may be consistently selected over others, irrespective of size, suggesting that taxa-specific characteristics are also important in the prey selection process. Nunn et al. (2007c), for example,

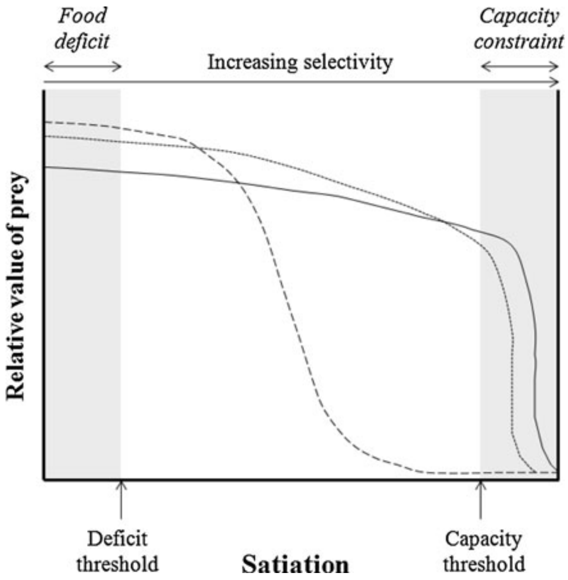

Fig. 2 Changes in the relative value of three sizes (small (*solid line*), optimum (*stippled line*), large (*dashed line*)) of prey with respect to fish satiation and motivation to feed. Changes in selectivity occur where the prey value lines intersect (modified from Gill 2003)

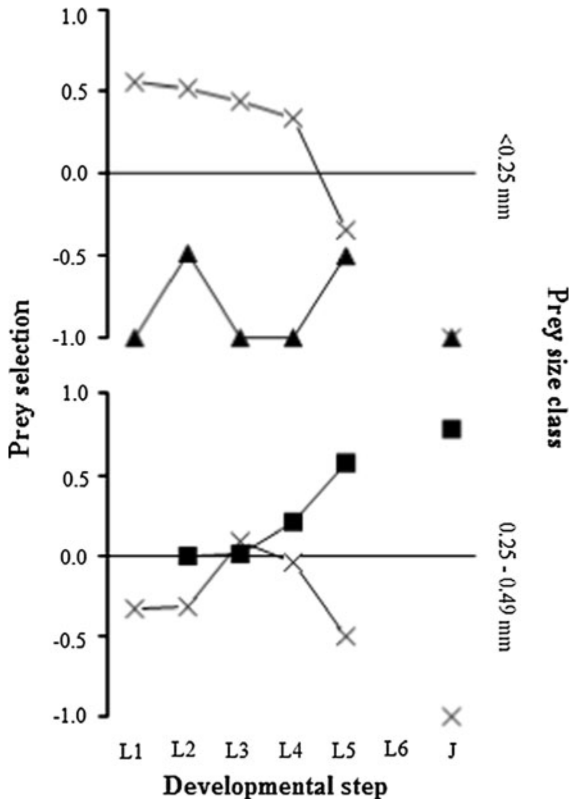

Fig. 3 Selection by seven developmental steps (six larval, one juvenile) of 0+ common dace for two size classes of rotifers (*cross*), copepod nauplii (*triangle*) and non-planktonic crustaceans (mostly Chydoridae; *square*) in the River Trent, England. The selection index ranges from −1 to +1, with negative values indicating avoidance, positive values indicating selection, and 0 representing no preference (modified from Nunn et al. 2007c)

observed that the young larvae of a number of cyprinid species selected rotifers over similar-sized copepod nauplii (Fig. 3), and Gliwicz et al. (2004) found that European smelt favoured elongated- (*Daphnia* spp., *Diaphanosoma* spp.) over compact-bodied (*Bosmina* spp., *Chydorus* spp.) cladocerans. Ghan and Sprules (1993) observed a similar phenomenon in young burbot (*Lota lota* (L.), Gadidae) larvae, with the globular rotifer *Asplanchna* sp. selected over spined rotifers and copepod nauplii, perhaps because of 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, the extensive consumption of cladocerans by many freshwater fishes during the late larval and early juvenile periods is probably because of their ease of capture compared to copepods, with the latter being faster moving than cladocerans and able to detect the shock waves of approaching fishes (Winfield et al. 1983), although visibility may also be important (Mayer and Wahl 1997). The larvae of a number of marine fish species have been found to select the nauplii and copepodites of calanoid copepods over those of cyclopoid copepods, probably as calanoids swim more consistently and predictably than cyclopoids (Pepin and Penney 1997), and redfish larvae have been observed to select *Calanus* sp. eggs and nauplii over *Oithona* spp. copepodites, even though the latter were within the preferred size range (Anderson 1994). Furthermore, fishes may select egg-bearing over non-egg-bearing zooplankters, or even females with the largest clutches, probably because the opaque eggs increase their visibility (Winfield and Townsend 1983; Ghan and Sprules 1993; Gliwicz et al. 2004). Piscivorous individuals may also select particular species over others, most likely related to interspecific differences in prey morphology and the costs associated with their capture and ingestion (Nilsson and Brönmark 2000; Borcherding 2006).

Ontogenetic shifts

There are two opposing schools-of-thought regarding the development of fishes. Subscribers to the theory of saltatory ontogeny (Balon 1979) assert that 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. By contrast, ‘gradualists’ contest that development occurs steadily, with no dramatic shifts in form and function. A comprehensive review of the debate is presented by Peňáz (2001). Irrespective of the process, the changes that occur during ontogeny, whether gradual or step-wise, often coincide with shifts in the diets of young fishes (Clements and Choat 1993; Vilizzi 1998; García-Berthou 2002; King 2005; Tonkin et al. 2006; Nunn et al. 2007b, 2008a). With respect to foraging ability, two of the key attributes are those pertaining to enhanced swimming performance, namely development of the fins, and improved vision (Lazzaro 1987; Schiemer et al. 1989). Once fins are fully developed,

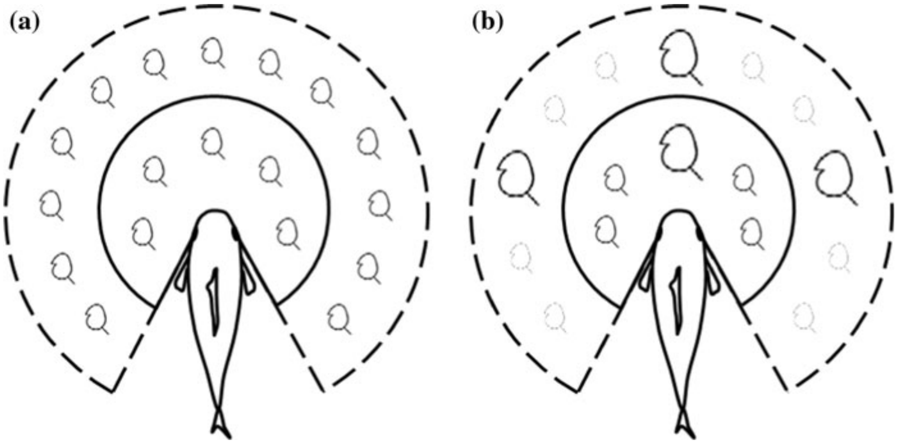

Fig. 4 Differences in **a** the visual field volume of larval (*solid line*) and juvenile (*dashed line*) fishes, and **b** the reaction distance (the distance over which fish can see their prey) for small (*solid line*) and large (*dashed line*) prey. The faint small prey are beyond the visual field (for small prey), so the densities of small and large prey would be assessed as equal even though the real densities differ three-fold (modified from Gliwicz 2001)

associated improvements in swimming performance allow a diversification of diet spectra, effectively increasing prey-capture efficiency. Similarly, improved vision increases the search volumes of larval and juvenile fishes (Fig. 4), effectively increasing prey availability (Wanzenböck and Scheimer 1989; Miller et al. 1993; Carvalho et al. 2002).

Newly hatched individuals of many fish species prey mainly upon small zooplankters and phytoplankton, partly because of their inability to handle larger prey (Whiteside et al. 1985; Krebs and Turingan 2003). In addition, larvae of the majority of fish species initially have poorly developed alimentary tracts, typically characterised by short length, narrow width, simple structure, weak digestive enzymes and, thus, limited digestive capacity (Kolkovski 2001; Makrakis et al. 2005). As the larvae develop, so their alimentary tracts develop, frequently characterised by an increase in length and width, differentiation of the gut into distinct regions and the production of potent digestive enzymes (Hofer and Uddin 1985; Junger et al. 1989). Development of the alimentary canal, concurrent with other changes in morphology, function and behaviour (Balon 1979; Werner and Gilliam 1984; Peňáz 2001), frequently coincides with shifts in the diet composition of young fishes.

A general sequence of shifts in resource use often occurs in the weeks after hatching. Moreover, distinct shifts in diet may occur that coincide with key intervals in ontogeny. Nunn et al. (2007b) differentiated two main ontogenetic shifts in the diets of a number of cyprinid and percid fishes in the lower River Trent, England, corresponding with the transition from apterolarvae (‘finfold’ larvae) to pterolarvae (‘finformed’ larvae), and from the larval to the juvenile period, probably linked to improvements in swimming performance and vision increasing the efficiency of prey capture. Similarly, King (2005) observed major dietary shifts in the larval, juvenile and adult periods of a number of floodplain fishes in Australia, and Clements and Choat (1993) reported differences in the diets of juvenile and adult butterfish off the coast of New Zealand. Such changes frequently coincide with shifts in habitat use or behaviour with development. Sunbleak (*Leucaspius delineatus* (Heckel), Cyprinidae), for example, exhibit a clear shift in diet at the transition from the larval to the juvenile period after moving from shallow river margins into open, deeper water (Pinder et al. 2005), and common carp (*Cyprinus carpio* L., Cyprinidae) switch from a planktonic to a benthic feeding mode at the onset of the juvenile period (Vilizzi 1998). Similarly, Demain et al. (2011) observed that juvenile Atlantic cod (*Gadus morhua* L., Gadidae) and haddock (*Melanogrammus aeglefinus* L., Gadidae) switched from mostly pelagic to benthic prey with a shift from shallow to deeper water. Ontogenetic shifts in the diets of smooth blenny (*Lipophrys pholis* (L.), Blenniidae) and Spanish toothcarp (*Aphanius iberus* (Valenciennes), Cyprinodontidae) have also been linked to changes in microhabitat use (Monteiro et al. 2005; Alcaraz and García-Berthou 2007).

Two of the best-studied and most widely distributed freshwater fish species in Europe are the roach and Eurasian perch. Roach larvae initially feed on pelagic rotifers, copepod nauplii and phytoplankton, with microcrustaceans and early instar chironomid larvae also eaten occasionally (Mark et al. 1987; Weatherley 1987; Matěna 1995; Garner 1996a; Mann et al. 1997; Nunn et al. 2007b). Cladocerans (e.g. Bosminidae, Chydoridae, Daphniidae), copepods and periphytic invertebrates increase in importance in the diet as the larvae develop, although phytoplankton may be important if the abundance of other prey is low (Weatherley 1987). As 0+ juveniles, roach feed primarily upon zooplankton before switching to either benthic invertebrates or aufwuchs (Garner 1996a; Mann et al. 1997; Vašek et al. 2006; Nunn et al. 2007b, 2008b). Rotifers and copepod nauplii are the initial food items of perch larvae (Spanovskaya and Grygorash 1977; Mehner et al. 1997), with ciliates and algae also eaten occasionally (Guma'a 1978). Small cladocerans are eaten as the larvae increase in size, while *Daphnia* spp. become important after perch reach 10–15 mm, and *Leptodora* sp. and *Bythotrephes* spp. are consumed 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; Kratochvíl et al. 2008), and are sometimes favoured over cladocerans (Guma'a 1978). In still waters, juvenile perch consume mainly planktonic cladocerans, especially *Daphnia* spp., *Bosmina* spp. and *Leptodora* sp., and copepods (Spanovskaya and Grygorash 1977; Vašek et al. 2006; Kratochvíl et al. 2008). By contrast, phytophilic and benthic invertebrates appear to be more important in rivers (Nunn et al. 2007b). In addition, some 0+ juvenile perch may become piscivorous and even cannibalistic (Brabrand 1995, 2001; Mehner et al. 1996; Mélard et al. 1996; van Densen et al. 1996; Borcherding et al. 2000; Beeck et al. 2002; Urbatzka et al. 2008).

The Atlantic cod is one of the most-studied fish species in the marine environment, and numerous investigations have demonstrated that cod larvae feed mainly on copepods (see Heath and Lough 2007). Small copepod nauplii are usually the main prey of the youngest cod larvae, with larger nauplii, copepodites and adult copepods (particularly *Calanus* spp., *Paracalanus* spp., *Pseudocalanus* spp., *Temora* spp., *Acartia* spp. and *Oithona* spp.) increasing in importance as the fish grow and develop (Voss et al. 2003; Rowlands et al. 2008). Juvenile cod feed upon a wide range of macroplankton, particularly copepods and euphausiids, and may also consume benthic invertebrates and fishes (Bromley et al. 1997; Pedersen and Fossheim 2008). Similarly, the diets of Atlantic herring larvae are dominated by zooplankton, particularly cladocerans (e.g. *Bosmina* sp., *Pleopsis* sp.) and copepods (e.g. *Eurytemora* sp., *Acartia* spp.), with copepods and euphausiids the main prey of 0+ juveniles (Arrhenius 1996; Pedersen and Fossheim 2008).

Diel variations

Larval and juvenile fishes may exhibit diel variations in behaviour (Gliwicz and Jachner 1992; Bromley et al. 1997; MacKenzie et al. 1999; Copp et al. 2005; Gliwicz et al. 2006; Nunn et al. 2010b). Mills et al. (1985), for example, observed that common dace larvae consumed up to four times more prey during daylight than at night, whereas Weatherley (1987) found that peak gut fullness occurred at night, while juvenile Eurasian perch, roach, chub (*Squalius* (syn. *Leuciscus*) *cephalus* (L.), Cyprinidae) and gizzard shad (*Dorosoma cepedianum* (L.), Clupeidae) are mostly diurnal and common bream are nocturnal (Winfield and Townsend 1988; Garner 1996b; Shepherd and Mills 1996; Okun et al. 2005; Kratochvíl et al. 2008). Alternatively, some species, such as haddock, adopt a crepuscular feeding regime, with activity being greatest in the morning and/or evening (MacKenzie et al. 1999). Notwithstanding, there may be ontogenetic shifts in diel feeding activity. For example, Bromley et al. (1997) observed that peak feeding activity in small juvenile Atlantic cod was from 12.00 to 20.00, whereas larger individuals foraged mainly from 00.00 to 08.00, with small and larger individuals, respectively, consuming invertebrates and fishes. There may also be diel variations in diet composition. Juvenile roach and chub, for instance, have been observed to consume fewer planktonic prey at night than in daylight, whereas aufwuchs increased in importance at night, suggesting a possible diel shift between particulate and benthic feeding modes (Garner 1996b). Similarly, although the diets of juvenile barbel (*Barbus barbus* (L.), Cyprinidae) and gudgeon (*Gobio gobio* (L.), Cyprinidae) are often dominated by chironomid larvae, the selection of some prey, such as simuliid larvae, may increase at night (Copp et al. 2005). Significantly, resource use may be substantially greater over the diel cycle than during daylight or darkness alone, suggesting that estimates of niche breadth based solely upon diurnal (or nocturnal) studies are potentially inaccurate (Copp 2008).

Diel shifts in diet composition are often linked to changes in habitat use. Nunn et al. (2010b), for example, observed that juvenile European bullhead (*Cottus gobio* L., Cottidae), stone loach (*Barbatula barbatula* (L.), Balitoridae) and gudgeon were mostly nocturnal, whereas European minnow (*Phoxinus phoxinus* (L.), Cyprinidae) and three-spined stickleback were mainly diurnal, possibly associated with directed movements to foraging habitats. Indeed, juvenile European hake (*Merluccius merluccius* (L.), Gadidae) inhabit the pelagial at night and the demersal during the day, which is reflected by diel qualitative and quantitative changes in prey consumption (Bozzano et al. 2005). Similarly, in deep lakes, larval and juvenile European smelt, Eurasian perch and roach often migrate into the epilimnion at dusk and the hypolimnion (smelt) or littoral (perch and roach) at dawn (Gliwicz and Jachner 1992). Another key factor influencing habitat use is the risk of predation, with diurnal species seeking refuge from predators at night and moving to profitable foraging habitats during daylight, while the opposite behaviour is characteristic of nocturnal species. Jacobsen and Berg (1998), for example, found that, under predation risk, there was significant diel variation in habitat use by juvenile Eurasian perch, suggesting a migration from open-water habitats at night into macrophytes in daylight. Similarly, shallow river margins are important night-time refuges from predation for small fishes (Baras and Nindaba 1999; Copp and Jurajda 1999), and it is possible that predator-induced shifts in habitat use may lead to diel changes in diet composition. Changes in habitat use by potential prey can also lead to diel variations in diet composition. In deep waterbodies, for example, many zooplankton species exhibit diel vertical migrations between the hypolimnion and epilimnion, seeking refuge in deep water from fish predation during daylight and grazing upon phytoplankton near the water surface at night (Gliwicz 1986). By contrast, zooplankton sometimes undertake horizontal migrations in shallow waterbodies (Lauridsen et al. 1996), which can also affect the prey availability to, and predation efficiency of, larval and juvenile fishes.

Seasonal variations

Populations of many zooplankton species vary on a seasonal basis, frequently related to fluctuations in food availability, predation pressure and environmental conditions (Sommer et al. 1986; Soetaert and Van Rijswijk 1993). 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 (Sommer et al. 1986). Seasonal successions in composition, abundance and biomass therefore occur in zooplankton communities, and comparable fluctuations are also a feature of many benthic or periphytic invertebrate communities, as well as phytoplankton, periphyton and macrophyte communities (Colebrook 1979; Angermeier 1982; Marker and Collett 1997a, b).

Seasonal fluctuations in prey abundance can influence the diet composition of 0+ fishes. This is particularly the case for juvenile fishes, which generally experience more than one season in their first year of life, whereas the larvae of most species experience only one season (exceptions are species that adopt multiple/fractional or protracted spawning strategies: Lowerre-Barbieri et al. 1998; Begg and Marteinsdottir 2000; Fuiman et al. 2005; Nunn et al. 2007d). Variations in the prey of juvenile European flounder in the Baltic Sea were related to seasonal changes in prey abundance, with macrofauna (oligochaetes, amphipods, chironomids) dominating the diet in spring and meiofauna (copepods) dominating in summer and autumn (Aarnio et al. 1996). Similarly, seasonal changes in the diet of pumpkinseed (*Lepomis gibbosus* (L.), Centrarchidae) have been linked to resource availability, with fish eggs and plant debris consumed in spring and summer and zooplankton eaten in the autumn (García-Berthou and Moreno-Amich 2000), while the diet of butterfish can be influenced by changes in algal composition (Clements and Choat 1993). Seasonal variations in diet composition imply that many fish species are able to feed opportunistically. Indeed, Townsend et al. (1986) observed that juvenile roach fed predominantly on planktonic cladocerans in spring and summer but non-planktonic cladocerans for the remainder of the year, with the switch coinciding with low availabilities of planktonic prey, and Anderson (1994) noted that the consumption of *Oithona* spp. copepodites by juvenile redfish increased as *Calanus finmarchicus* (Gunnerus) nauplii, the preferred prey, declined in abundance.

Dietary switches linked to seasonal variations in prey abundance have been reported for a range of 0+ fishes (e.g. Allen 1941; Persson 1983; Persson and Greenberg 1990; Wu and Culver 1992; Aarnio et al. 1996; Mehner et al. 1996; Mann et al. 1997; Warburton et al. 1998; Galarowicz et al. 2006) and may have implications for their growth and survival, especially if forced to switch to poor-quality food resources. At temperate latitudes, overwinter survival of many juvenile fish species is positively related to condition (a function of fish length), with smaller individuals less likely to survive than larger conspecifics, and numerous studies have reported a reduction in condition over the winter due to the utilisation of lipid reserves (see Hurst 2007). Food ration also has an influence on survival, with feeding fish more likely to surviving than starved individuals (Pangle et al. 2004). The extensive consumption of aufwuchs by many juvenile fishes in the autumn and winter is probably linked to a low availability of suitable animal prey (Nunn et al. 2008b). Indeed, while zooplankton populations in temperate fresh waters are invariably low throughout the autumn and winter (Sommer et al. 1986; Nunn et al. 2007e), aufwuchs is frequently still abundant after zooplankton populations have declined (Marker and Collett 1997b). Furthermore, although the juveniles of some species consume aufwuchs in mid- to late summer, the switch may be delayed or not occur if sufficient invertebrates are available (Weatherley 1987; Garner 1996a; Mann et al. 1997; Nunn et al. 2007b). As aufwuchs is considered a poor food resource because of its low digestibility and nutritive value (Bowen 1979; Persson 1983; Lemke and Bowen 1998), the combination of reduced feeding activity and poor food quality could have implications for the overwinter survival of juvenile fishes, particularly in areas or years that experience long or severe winters. This may also be an issue for other poor-quality food resources.

Annual variations

Larval and juvenile fishes can be highly susceptible to fluctuations in prey availability, with interannual variations in zooplankton abundance having potentially important consequences for their growth and survival (Mills and Forney 1988; Mayer and Wahl 1997; Dickmann et al. 2007; Burrow et al. 2011; Stige et al. 2011). The feeding success and growth of Arctic cod (*Boreogadus saida* (Lepechin), Gadidae) and sand lance (*Ammodytes* spp., Ammodytidae) larvae, for example, have been positively correlated with inter-annual differences in the density of copepod nauplii (Fortier et al. 1995). Furthermore, fluctuations in zooplankton dynamics have been implicated with long-term changes in Atlantic cod recruitment in the North Sea (Beaugrand et al. 2003). Indeed, the match/mismatch hypothesis (Cushing 1990) postulates that the survival of fish larvae will be highest in years 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) (Fig. 5), and a number of empirical studies of both marine (e.g. Atlantic cod, Arctic cod, sand lance) and freshwater (e.g. striped bass (*Morone saxatilis* (Walbaum), Moronidae)) fish species appear to support the theory (Fortier et al. 1995; Gotceitas et al. 1996; Chick and van den Avyle 1999). Food must therefore be available to larval and juvenile fishes in sufficient quantity, and of the correct

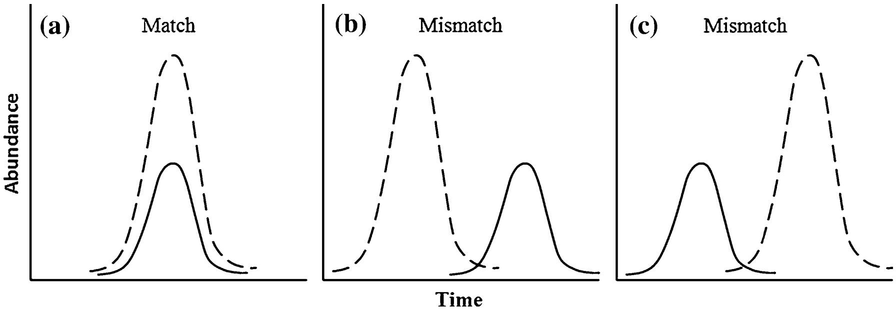

Fig. 5 The match/mismatch hypothesis (Cushing 1990), where **a** depicts a ‘match’ scenario and **b** and **c** depict ‘mismatch’ scenarios. The *curves* represent the abundance of fish larvae (*solid line*) and prey (*dashed line*)

size, with a lack of appropriately sized prey potentially causing either reduced growth or starvation (Beaugrand et al. 2003; Graeb et al. 2004; Dickmann et al. 2007).

Numerous studies have reported interannual differences in zooplankton composition and abundance. Bass et al. (1997), for example, found that maximum rotifer densities in a regulated lowland river were usually around 2,000–3,000 L^{-1}, but observed a peak of over 15,000 L^{-1} in one year, and comparable interannual variations have been reported for a range of other taxa, both in marine and fresh waters (e.g. George and Taylor 1995; Reid et al. 1998; Hays et al. 2005; Lees et al. 2006). The factors causing interannual differences in zooplankton composition and abundance are generally the same as for seasonal variations, namely food availability, predation pressure and environmental conditions. Hydrological regime is a key factor governing interannual variations in riverine plankton populations, with abundance and biomass generally lowest in years with high river discharge (Bass et al. 1997; Marker and Collett 1997a). The coincidence of elevated river discharges with the larval period may thus negatively influence fish growth and survival either directly (through discharge-induced mortality) or indirectly (through reduced growth at lower water temperatures, discharge-associated increases in energy expenditure or reduced food availability) (Nunn et al. 2003, 2007a, 2010a). Conversely, a number of studies have demonstrated a negative influence of drought on benthic invertebrate populations, which may also affect the foraging ecology of larval and juvenile fishes, especially salmonids (e.g. Extence 1981; Cowx et al. 1984; Wood and Armitage 2004; Wood et al. 2010). Interannual differences in the composition and abundance of marine and lacustrine freshwater plankton have been linked to a range of complex and interacting factors, including regional changes in climate and local weather anomalies, making it difficult to identify the most important factors (George and Taylor 1995; Reid et al. 1998; Hays et al. 2005; Lees et al. 2006).

Interannual differences in the diet composition of larval and juvenile fishes have been related to variations in prey abundance. Variations in the diet of Murray cod (*Maccullochella peelii peelii* (Mitchell), Percichthyidae) larvae have been observed between years of high and low river discharge, with chironomid larvae dominating the diet when discharge was high and macrothricid cladocerans dominating when discharge was low (Kaminskas and Humphries 2009). Similarly, redfish larvae consumed a lower quantity and quality of prey in warm than in cool springs, probably because of a mismatch in the timing of fish hatching and the development of their preferred prey (Anderson 1994). Moreover, the availability of preferred, but not necessarily all, prey may influence fish growth, condition and survival. The growth and survival of small (<12 mm) yellow perch larvae, for example, was found to be greatest when feeding on adult copepods and nauplii, whereas adult copepods and small cladocerans were more important for larger larvae (Graeb et al. 2004), and the condition of redfish larvae was higher for individuals feeding on *C. finmarchicus* than for those feeding on *Oithona* spp. (Anderson 1994). The abundance, timing, duration and geographical distribution of marine plankton populations in particular can vary substantially on an annual basis, whereas the spawning periods of most fish species are less variable, meaning that there is a high risk of a mismatch in the timing of fish hatching and plankton blooms (Cushing 1990).

Spatial variations

The habitats used by fishes can have an important influence on prey availability and, therefore, their diet composition. The diets of marine and freshwater fishes differ largely because the majority of prey taxa are confined to either marine or freshwater environments, although the larvae and juveniles of euryhaline species may consume both marine and freshwater prey (Beaumont and Mann 1984; Aprahamian 1989; Weatherley 1989; Thiel et al. 1996; Nunn et al. 2008a). Mysids, euphausiids, tunicates, cirripedians, cumaceans, decapods and polychaetes tend to be more abundant in marine than in freshwater environments, whereas rotifers, cladocerans, oligochaetes and insects are most important in fresh water. Notwithstanding, there may be variations in diet composition within marine and freshwater ecosystems.

The distributions of plankton are intrinsically linked to the movement of water, from microscale turbulence to oceanic currents, although a range physicochemical factors, such as temperature, dissolved oxygen concentration and salinity, are also influential. In addition, zooplankton may undertake diel migrations between the epilimnion and hypolimnion or the littoral and pelagial, and often form swarms, resulting in a contagious distribution. Heath and Lough (2007) observed latitudinal patterns in the diet composition of Atlantic cod larvae, with fish at the northern edge of the species' range consuming mainly *C. finmarchicus*, whereas those at the southern edge preyed upon *Paracalanus* spp. and *Pseudocalanus* spp. Furthermore, the diet composition and feeding activity of Atlantic cod and blue whiting (*Micromesistius poutassou* (Risso), Gadidae) larvae have been found to vary between water masses (e.g. warm vs. cool temperatures, high vs. low salinities) at a regional scale, and the direction and strength of the wind can also be important (McLaren et al. 1997; Hillgruber and Kloppmann 1999). Indeed, shifts in the diet composition of juvenile Arctic char (*Salvelinus alpinus* (L.), Salmonidae) have been observed to coincide with wind-induced changes in the distribution of zooplankton in Loch Ness, Scotland (Winfield et al. 2002).

The dominance of rotifers in the diets of many riverine fish larvae can be explained by their small size, poor mobility, ubiquity and high abundance compared with other zooplankton (Bass et al. 1997; Viroux 1997; Nunn et al. 2007e). 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; maximum rotifer densities in the regulated Great Ouse, England, were usually 2,000–3,000 L^{-1}, whereas copepods (<125 L^{-1}) and cladocerans (<10 L^{-1}) were recorded at consistently lower densities (Bass et al. 1997). The diets of old larvae and juvenile fishes in riverine environments thus tend to be dominated by non-planktonic invertebrates, such as benthic crustaceans and insect larvae, or aufwuchs. By contrast, areas of reduced flow facilitate plankton development because of increased water-residence times. For example, the mean density of daphnids in the main channel of the lower River Trent was 0.03 L^{-1} compared with 76 L^{-1} in a connected pond (maximum >900 L^{-1}) (Nunn et al. 2007e), and comparable results have been obtained elsewhere and for other taxa (e.g. Bass et al. 1997; Spaink et al. 1998; Tans et al. 1998). Areas such as backwaters and oxbow lakes thus provide superior feeding opportunities for planktivorous fishes compared with main river channels. Indeed, whereas rotifers and aufwuchs, respectively, were the main prey of 'finformed' larvae and juvenile roach in the main channel of the lower River Trent, cladocerans and cyclopoid copepods were dominant in a connected pond (Nunn et al. 2007b). Similarly, plankton densities are generally higher in river margins than in mid-channel because of increased water retention near the shore (Reckendorfer et al. 1999; Schiemer et al. 2001).

There may also be variations in diet composition at smaller spatial scales, both in marine and freshwater ecosystems. Significant differences in the diets of 0+ roach, chub, bleak (*Alburnus alburnus* (L.), Cyprinidae), common bream and gudgeon were observed between habitats in a lowland river (Garner 1998), and spatial variations in prey consumption have been documented in coastal populations of 0+ European flounder (Andersen et al. 2005; Grønkjaer et al. 2007). Similarly, the diets of eastern blue groper (*Achoerodus viridis* (Steindachner), Labridae) larvae in seagrass beds were dominated by tanaids, whereas fish from rocky reefs consumed harpacticoid copepods (Gillanders 1995), and newly hatched brook trout (*Salvelinus fontinalis* (Mitchill), Salmonidae) ate more dipteran larvae but fewer crustaceans and insect pupae/adults in fast- than in slow-flowing habitats (McLaughlin and Grant 1994). One of the key factors influencing the composition of benthic communities is sediment particle size, whereas physical structures are more important for epifauna and zooplankton. Aquatic macrophytes and macroalgae are particularly important for many larval and juvenile fishes as they provide refuge from predators and water currents, and habitat for phytophilic and planktonic invertebrates (Garner et al. 1996; Nagelkerken et al. 2000; Grenouillet et al. 2001a). Indeed, macrophytes invariably support larger numbers of invertebrates, greater ranges of body size and greater numbers of species than open water (Whiteside et al. 1985), and species composition and abundance may differ between macrophyte forms (e.g. submerged, emergent, floating-leaved) or species (Cyr and Downing 1988; Grenouillet et al. 2001a).

The habitats used by fishes can also have an important influence on their foraging efficiency. For example, Winfield (1986) demonstrated that the foraging efficiencies of juvenile roach and rudd (*Scardinius erythrophthalmus* (L.), Cyprinidae) decreased with increasing habitat complexity, largely because swimming speeds were lower in complex habitats, and Diehl (1988) found that prey consumption by Eurasian perch, common bream and roach was reduced in complex habitats. Furthermore, Diehl and Eklöv (1995) observed that perch in vegetated habitats had slow growth, partly because the physical complexity of submerged macrophytes reduced their foraging efficiency.

Inter- and intraspecific interactions

Interspecific interactions can have important implications for the growth, survival and recruitment success of fishes. Competitive effects occur when behavioural interactions cause an unequal distribution of a resource that is directly or indirectly related to growth, survival or recruitment (Wootton 1990). For example, fishes may alter their diets, and have lower growth rates, in the presence of competing species. Persson and Greenberg (1990) demonstrated that roach had a negative impact on the growth of juvenile Eurasian perch, with individual growth rates of perch decreasing with increasing roach density, which was related to competition for food resources; in the absence of roach, perch fed mainly upon planktonic cladocerans, whereas in the presence of roach they consumed copepods and macroinvertebrates. Similarly, Amundsen and Gabler (2008) found empirical evidence for food limitation and competition between juvenile Atlantic salmon (*Salmo salar* L., Salmonidae) and Alpine bullhead (*Cottus poecilopus* Heckel, Cottidae), resulting in reduced food acquisition and growth rates in salmon, and Scharf et al. (2009) observed that, when prey was limited, bluefish (*Pomatomus saltatrix* (L.), Pomatomidae) out-competed striped bass. Furthermore, Ward et al. (2002) demonstrated that chub preferred conspecific over heterospecific shoals, which was probably driven by interspecific competition with European minnow and the oddity effect. It should be noted, however, that the relative competitive abilities of fishes may vary between habitats (Winfield 1986; Diehl 1988).

Dietary overlap, which can be indicative of competition, is often greatest in the early larval period, probably as fishes are less morphologically and behaviourally differentiated than later in ontogeny (Garner 1996a). Indeed, a number of studies have found a high degree of overlap in the diets of young fish larvae in marine and fresh waters. The diets of many young cyprinid larvae, for example, are dominated by rotifers, while young clupeid, gadid and osmerid larvae prey mainly upon copepods (Garner 1996a; Thiel et al. 1996; Bromley et al. 1997; Nunn et al. 2007b; Pedersen and Fossheim 2008). Notwithstanding, overlap can also be substantial in the juvenile period. For example, the diets of juvenile Eurasian perch, pikeperch, ruffe (*Gymnocephalus cernua* (L.), Percidae), roach and common bream overlapped significantly in a lowland reservoir, suggesting strong interspecific competition for resources (Matěna 1998), and juvenile Atlantic cod and whiting (*Merlangius merlangus* (L.), Gadidae) have been reported to compete for zooplankton in the North Sea (Shaw et al. 2008).

Although the diets of the larvae of many species are similar, they do not necessarily compete for resources. Early spawning species, for example, may already be juveniles by the time late-spawning species hatch: the larvae of early- and late-spawning species, therefore, are unlikely to compete for resources. Similarly, the larvae of rheophilic fish species rarely occur in the same habitats as limnophilic larvae, and competition between benthic and pelagic species is likely to be limited. Moreover, dietary overlap does not necessarily imply competition, as competition only occurs when demand for a resource exceeds the immediate supply (Zaret and Rand 1971; Wootton 1990). Overlap is often greatest among young larvae feeding upon the most abundant food resources (Garner 1996a; Thiel et al. 1996; Bromley et al. 1997; Nunn et al. 2007b; Pedersen and Fossheim 2008), leading some authors to suggest that competition is more likely to affect older larvae or juveniles consuming less abundant prey (Cowan et al. 2000). Indeed, resource partitioning is a characteristic feature of many juvenile fish assemblages, often coinciding with an increase in the importance of species-specific prey selection, with competition most likely among ecologically similar species or trophic guilds (Mark et al. 1987; Matěna 1995; Garner 1996a; Demain et al. 2011).

Intraspecific interactions can also be important and, indeed, are inevitable as conspecifics invariably occupy identical niches (Ward et al. 2006). A number of studies have demonstrated a negative relationship between the density and growth of larval and juvenile fishes (e.g. Byström and García-Berthou 1999; Romare 2000), and the high densities of fishes inhabiting many nursery areas may increase the effects of intraspecific (and interspecific) interactions on feeding behaviour, which could have implications for the growth and survival of fishes. Grenouillet et al. (2001b), for example, stated that the survival of roach in the first year of life was density-dependent, and that intraspecific competition could negatively affect recruitment, while Cryer et al. (1986) and Perrow and Irvine (1992) demonstrated that the suppression of prey populations by juvenile roach can have a negative impact on their growth. Similarly, Welker et al. (1994) suggested that the growth and survival of gizzard shad larvae and the growth of bluegill larvae were affected by the availability of zooplankton, which may become limiting when densities of larvae are high. Conversely, assuming resources are not limiting, high densities may allow fish to increase their foraging rates, as shoals increase the probability of patchily distributed food being located (Pitcher 1986). At the individual level, the impacts of intraspecific interactions are governed by a range of complex and interacting factors, including social status and hunger (Pitcher 1986; Gotceitas and Godin 1991; Krause 1994). A thorough review of intraspecific food competition in fishes is provided by Ward et al. (2006).

Predation risk, both inter- and intraspecific, can also influence the foraging behaviour of larval and juvenile fishes. For example, food consumption by juvenile Eurasian perch is often reduced in the presence of piscivorous northern pike, and there may be an increase in the relative importance of small prey (Mikheev et al. 2006; Wanzenböck et al. 2006). In addition, juvenile perch may increase their use of complex refuge habitats in the presence of piscivores, which invariably reduces their foraging efficiency (Diehl and Eklöv 1995). Comparable results have been obtained for a number of other fish species (see Pitcher 1986; Winfield 1986; Metcalfe et al. 1987; Gotceitas and Godin 1991; Fuiman and Magurran 1994; Bean and Winfield 1995). Although such behaviours may allow fishes to forage even in risky situations, there are inherent implications for the energy intake, nutritional condition, growth and survival of larval and juvenile fishes, with individuals exposed to severe or continuous predation pressure likely to ingest fewer and smaller prey than those able to forage in relative safety (Fuiman and Magurran 1994; Diehl and Eklöv 1995).

Predator–prey relationships

It has long been recognised that planktivorous fishes are a major factor influencing the species and size composition of zooplankton communities (e.g. Hrbáček et al. 1961; Brooks and Dodson 1965; Cushing 1983; Lazzaro 1987). Phenomena frequently attributed to heavy fish predation include suppressed zooplankton biomass, small individual size of plankters, and reduced representation of vulnerable (typically larger) species. Large-bodied zooplankters are more efficient grazers of phytoplankton than are smaller-bodied species and, in the absence of severe predation, dominate the zooplankton (Brooks and Dodson 1965). Zooplanktivorous fishes may, therefore, cause changes in ecosystem functioning by increasing predation on zooplankton, thereby reducing grazing of phytoplankton and causing a reduction in water clarity. This has also been observed for larval and juvenile fishes (Cushing 1983; Bollens 1988; Mills and Forney 1988; Munk and Nielsen 1994; Kurmayer and Wanzenböck 1996; Mehner and Winfield 1997; Mehner and Thiel 1999). Similarly, selection of large zooplankton species and individuals can cause shifts in the species composition of zooplankton communities, as well as reductions in the mean size of individuals of large species and in the assemblage as a whole (Cryer et al. 1986; Romare et al. 1999). In particular, larval and juvenile fishes have the potential to suppress populations of large zooplankton species (Cushing 1983; Bollens 1988; Munk and Nielsen 1994; Mehner and Thiel 1999). Cryer et al. (1986), for example, observed that in summers when 0+ roach were abundant, zooplankton was sparse and dominated by copepods and rotifers, with cladocerans present in only low densities. Moreover, a number of studies (e.g. Cryer et al. 1986; Dettmers and Wahl 1999; Cowan et al. 2000) have suggested a causal link between fish recruitment and zooplankton dynamics, with abundant 0+ fishes sometimes showing poor growth as a result of depression of their prey populations.

Conversely, piscivory can influence the species and size composition of larval and juvenile fish communities. Brabrand (2001), for example, noted that piscivorous 0+ Eurasian perch significantly affected the size distributions of 0+ roach cohorts, because smaller individuals were predated more frequently than larger conspecifics. Furthermore, Beeck et al. (2002) speculated that piscivory by large 0+ Eurasian perch may have contributed to the complete disappearance of smaller individuals and 0+ common bream from a eutrophic lake by the end of the summer. Similarly, Bromley et al. (1997) stated that 0+ gadids can be subjected to substantial levels of piscivory (including cannibalism), potentially of sufficient magnitude to affect recruitment, and Buckel et al. (1999) suggested that predation by 0+ bluefish could have a substantial impact on the recruitment of striped bass. In addition, consumption of zooplanktivorous fishes by piscivorous larvae and juveniles may reduce predation pressure on zooplankton, potentially leading to increased grazing pressure on phytoplankton. Indeed, piscivory by larval and juvenile fishes may prevent the increases in 0+ fish abundance that often occur following depletion of adult fish stocks, which is important to ensure the long-term success of biomanipulation experiments (Beeck et al. 2002).

Apart from the direct affects of fish predation on zooplankton demography, indirect impacts can also occur through shifts in life history (e.g. changes in birth rates, fecundity, size and age at maturity, a switch from parthenogenetic to sexual reproduction, diapause), morphology (e.g. cyclomorphosis) or behaviour (e.g. diel vertical and horizontal migration) (Hanazato et al. 2001; Lass and Spaak 2003), all of which may have implications for ecosystem functioning. In addition, such phenomena may mask the impacts of fish predation. Gliwicz (2001), for example, found that the species-specific density levels of particular zooplankton did not depend upon reproduction rate, since neither increased birth rates nor reproductive effort coincided with an increase in population density; a clear indication that larger numbers of prey were being consumed by fishes at the time of increased reproduction. Furthermore, fish may select ephippial or egg-bearing zooplankters, due to their increased visibility compared with non-ephippial and non-egg-bearing individuals, and thereby influence zooplankton recruitment potential. For example, Gliwicz et al. (2004) revealed strong selection by European smelt for later instars and females of *Daphnia* spp. and *Bosmina* sp. with greater clutches, and similar behaviour has been reported in burbot (Ghan and Sprules 1993).

Management implications

For fish populations to persist, habitat must be available in sufficient quality and quantity for the range of activities undertaken during all periods of development. Implicit with this statement is that fish must be able to move between areas of habitat according to ontogenetic or temporal requirements. When this is not the case a bottleneck can occur, and fish population/community size and structure may be restricted. As such, knowledge of the ecology of larval and juvenile fishes has important implications for fisheries management, especially considering their vulnerability to predation, competition, disease and environmental perturbations.

Adult fish stocks are, directly or indirectly, limited by the quality and quantity of habitat and food available to larval and juvenile fishes. Floodplain waterbodies can enhance the recruitment of riverine fish populations through the provision of spawning and nursery habitats, refuge from floods, and higher water temperatures and, importantly, availability of planktonic food resources compared with main river channels. In addition, zooplankton populations often persist longer in floodplain waterbodies than in main river channels, and may be important sources of drifting material, which can colonise main river channels (Bass et al. 1997). Thus, connection of relict channels and man-made waterbodies to rivers has the potential to augment riverine fish populations and communities where natural river-floodplain connectivity has been lost (Grift et al. 2003; Nunn et al. 2007e). Similarly, managed realignment has the potential to enhance fish recruitment in the marine environment by increasing the availability of intertidal habitats, such as mudflats and salt marshes (Dixon et al. 1998; Colclough et al. 2005). It is important, however, that a high diversity of habitats is available to cater for the requirements of all life stages of a range of fish species. Habitats that enhance the diversity, size ranges and abundance of prey should ensure that sufficient food resources are available to larval and juvenile fishes.

It is critical that habitats are complex in structure, to enable segregation of species and minimise the potential for competition, predation and the spread of parasites and diseases. This is particularly important when implementing rehabilitation schemes in engineered ecosystems, where habitats have been modified and invariably simplified. Rehabilitation measures should be designed not just to provide refuge and nursery habitats for fishes, but also to enhance their food base. In general, floodplain waterbodies should be shallow, have complex shorelines with a high variability of flow velocities, and be located close to known spawning areas of key fish species. In addition, such waterbodies should ideally support submerged and emergent macrophytes, and a range in the degree of connectivity with main river channels is desirable (Grift et al. 2003; Bolland et al. 2012). Similarly, managed realignment sites should be designed to encourage the development of mudflats and salt marshes. Indeed, such areas are dynamic and naturally accrete and become colonised by vegetation (French 2006; Garbutt et al. 2006; Mazik et al. 2007). Accretion may increase the amount of habitat available to some fish species (e.g. flatfishes) and also facilitate the development of creeks, which provide areas of deeper water for large-bodied fishes, as well as habitat for small fishes at low water. Establishment of salt marsh further improves habitat complexity, which should increase the importance of managed realignment sites to fishes (Dixon et al. 1998; Colclough et al. 2005). Such habitats frequently support substantial zooplankton populations, thus improving the chances of survival and recruitment of fishes into the adult populations.

The foraging ecology of larval and juvenile fishes also has ramifications for husbandry protocols and stocking densities in aquaculture facilities. There is effectively a trade-off between stocking density and fish growth and survival. Whereas stocking at high densities may produce large numbers of fish, stocking at lower densities may produce larger fish. Thus, it is critical that the correct densities and species of fish are used in aquaculture facilities, and that adequate food is available: if certain fish species affect the growth or condition of other species, they could reduce survival in facilities and once released into the wild, thus reducing stocking success. Priming aquaculture facilities to provide fish larvae with abundant prey, and timing stock-out to coincide with peak zooplankton densities, should maximise survival and growth rates. Rearing fishes in single-species enclosures will eliminate the possibility for interspecific competition during the larval and juvenile periods, although there is still the potential for intraspecific competition to occur. If it is not possible to rear fishes in single-species enclosures, selecting fishes of contrasting behaviour (e.g. benthic and open-water feeders) should minimise any interspecific interactions.

Conclusions and recommendations

Zooplankton serve as a vital food resource for the larvae of most fish species. Even fish species that are piscivorous, herbivorous or detritivorous as juveniles or adults may initially be zooplanktivorous. Notable exceptions include fishes inhabiting the upper, fast-flowing reaches of rivers, where plankton is usually rare. Feeding diversity generally increases during the juvenile period, when there is often an increase in the importance of species-specific dietary traits. There are a large number of species, however, for which there is no information on their foraging ecology during the larval and juvenile periods. Indeed, primary literature was found for only 34 (35%) of the 96 freshwater fish species and 28 (8%) of the 369 marine fish species recorded in the UK, and information is even more sparse for other regions (Froese and Pauly 2011). For example, there appears to be no information for 93% of the 579 freshwater fish species recorded in Europe (Kottelat and Freyhof 2007), and there is also a paucity of knowledge on the foraging ecology of deep-water marine fishes. It is, therefore, recommended that further research is conducted in an attempt to address some of the gaps in the knowledge of the foraging ecology of larval and juvenile fishes.

A range of factors influence the foraging ecology of larval and juvenile fishes, including the ontogeny, morphology, behaviour, availability of potential food items, local habitat complexity and hunger of the fish (Fig. 6). Ontogeny influences the ability of fish to detect, capture, ingest and digest prey. For example, many young larvae have poor vision, which limits their prey-detection capacity. In addition, young larvae are poor swimmers and have small gape size, which limits their prey-capture efficiency and the size of prey that can be ingested. Furthermore, the young larvae of many fish species have poorly developed alimentary tracts and, thus, limited digestive capacity. Once fins are fully developed, associated improvements in swimming performance allow a broadening and diversification of diet spectra, effectively increasing their efficiency and capacity to capture and ingest prey. Similarly, improved vision increases the search volumes of 0+ fishes, effectively increasing prey availability, and development of the alimentary tract and the production of potent digestive enzymes increases digestive capacity. Differences in feeding behaviour (e.g. diurnal vs. nocturnal, filter vs. particulate feeding, vision vs. olfaction) between species, individuals or during ontogeny can also be important.

Prey size, morphology, behaviour and abundance can all influence the prey selection and diet

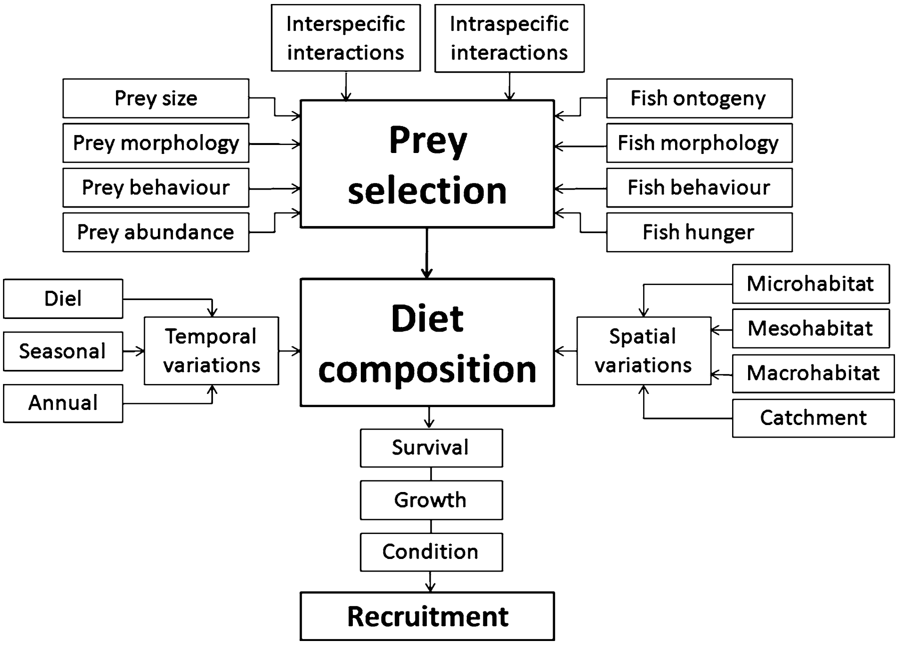

Fig. 6 The complexity of factors (simplified) influencing the prey selection and diet composition of larval and juvenile fishes

composition of larval and juvenile fishes (Fig. 6). 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. Prey selection is thus determined by the relative profitabilities of particular types and sizes of prey, with maximum profit conferred by prey types and sizes that provide the maximum energy gain per unit handling time. The energetic content of a given prey type increases with prey size. However, certain prey may be consistently selected over others, irrespective of size, suggesting that taxa- as well as size-specific characteristics are important in the prey selection process. For example, cladocerans are common prey of many 0+ freshwater fishes because they are easier to capture than copepods, even though the latter are often numerically abundant and of greater calorific value. Similarly, the larvae of many marine fish species select calanoid over cyclopoid copepods, probably as calanoids swim more consistently and predictably than cyclopoids. It is recommended that further studies and experiments are conducted to establish the relative importance of taxa- and size-specific characteristics in prey selection by larval and juvenile fishes at various stages of development. Such research should consider potential selection for specific components of prey populations, such as egg-bearing or ephippial females, as well as piscivory (including cannibalism). This level of analysis could reveal areas of inter- or intraspecific dietary overlap/competition or, alternatively, resource partitioning. It may also be possible to obtain field evidence of switching, and possibly species-specific threshold densities when fishes change their feeding behaviour.

Temporal and spatial variations in prey availability can have important implications for the prey selection, diet composition, growth, survival, condition and, ultimately, recruitment success of fishes (Fig. 6). Food availability may vary for a number of reasons, including diel, seasonal, annual, microhabitat, mesohabitat, macrohabitat and regional differences in prey abundance. It is recommended that research is conducted to investigate ontogenetic and seasonal changes in diel feeding behaviour. In addition, further research into interannual variations in diet composition and prey availability may allow a causal link between larval and juvenile fish growth and food resources, and possibly threshold densities of key prey taxa, to be identified. Although it is recognised that habitats differ in the composition, abundance and size ranges of potential prey, there is little evidence for an influence of habitat on the species- and development-specific condition of larval and juvenile fishes. Studies of the relative contribution of particular habitats to the diets (e.g. using stable isotope analysis, in combination with traditional diet analyses and estimates of prey availability; Fry 2002) and nutritional condition (e.g. using RNA-DNA ratio analysis; Caldarone et al. 2006) of specific developmental steps of particular fish species may allow key habitats in terms of both food resources and nutritional condition, respectively, to be identified. Such knowledge has fundamental and applied implications and, indeed, is essential if the habitat requirements of all life stages and species of fish are to be met by rehabilitation schemes.

Inter- and intraspecific interactions can also have an important influence on the prey selection and diet composition of larval and juvenile fishes, either through dietary overlap/competition, resource partitioning or predation risk (Fig. 6). It is recommended that experiments are conducted using a range of fish densities and different combinations and ratios of species. This could demonstrate the influence of interspecific interactions on the diet composition and prey selection of different fish species, and identify the densities at which interspecific, and intraspecific, interactions manifest in differences in growth, condition and survival rates. 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. Conducting experiments at various densities may also permit species-specific optimal stocking densities to be identified, potentially allowing an increase in production in aquaculture facilities. The effects of density and interspecific interactions, as well as food quantity and quality, on the nutritional condition of fishes could be assessed using RNA-DNA ratio analysis.

Larval and juvenile fishes have the potential to influence the density, species and size composition of prey communities, either directly or indirectly. It is recommended that further studies are initiated to investigate the predator–prey relationships of larval and juvenile fishes, and the cascading impacts on primary production and ecosystem functioning. These could include studies of zooplankton demography to assess the impacts of fish predation or presence on the fecundity, birth and death rates, size and age at maturity, reproductive strategy, morphology and behaviour of key zooplankton groups, as well as piscivory (including cannibalism). The outcomes of such studies will further our understanding of predator–prey relationships and may be of use in the context of biomanipulation and habitat rehabilitation.

Acknowledgments This paper was funded partly by Environment Agency Science Project No. SC060048/SR. The paper benefitted greatly from the constructive comments of two anonymous reviewers.

References

Aarnio K, Bonsdorff E, Rosenback N (1996) Food and feeding habits of juvenile flounder *Platichthys flesus* (L.), and turbot *Scophthalmus maximus* L. in the Åland archipelago northern Baltic Sea. J Sea Res 36:311–320

Alcaraz C, García-Berthou E (2007) Food of an endangered cyprinodont (*Aphanius iberus*): ontogenetic diet shift and prey electivity. Environ Biol Fish 78:193–207

Allen KR (1941) Studies on the biology of the early stages of the salmon (*Salmo salar*). J Anim Ecol 10:47–76

Amundsen PA, Gabler HM (2008) Food consumption and growth of Atlantic salmon *Salmo salar* parr in sub-arctic rivers: empirical support for food limitation and competition. J Fish Biol 73:250–261

Andersen BS, Carli JD, Gronkjaer P, Stottrup JG (2005) Feeding ecology and growth of age 0 year *Platichthys flesus* (L.) in a vegetated and a bare sand habitat in a nutrient rich fjord. J Fish Biol 66:531–552

Anderson JT (1994) Feeding ecology and condition of larval and pelagic juvenile redfish *Sebastes* spp. Mar Ecol Prog Ser 104:211–226

Angermeier PL (1982) Resource seasonality and fish diets in an Illinois stream. Environ Biol Fish 7:251–264

Anneville O, Laine L, Benker S, Ponticelli A, Gerdeaux D (2007) Food habits and ontogenetic changes in the diet of whitefish larvae in Lake Annecy. Bull Franç Pêche Piscic 387:21–33

Aprahamian MW (1989) The diet of juvenile and adult twaite shad *Alosa fallax fallax* (Lacépède) from the rivers Severn and Wye (Britain). Hydrobiologia 179:173–182

Aprahamian MW, Barr CD (1985) The growth, abundance and diet of 0-group sea bass, *Dicentrarchus labrax*, from the Severn Estuary. J Mar Biol Assoc UK 65:169–180

Arrhenius F (1996) Diet composition and food selectivity of 0-group herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* (L.)) in the northern Baltic Sea. ICES J Mar Sci 53:701–712

Balon EK (1979) The theory of saltation and its applicability to the ontogeny of fishes: steps and thresholds. Environ Biol Fish 4:97–101

Baras E (1999) Sibling cannibalism among juvenile vundu under controlled conditions. I. Cannibalistic behaviour, prey selection and prey size selectivity. J Fish Biol 54: 82–105

Baras E, Nindaba J (1999) Seasonal and diel utilisation of inshore microhabitats by larvae and juveniles of *Leuciscus cephalus* and *Leuciscus leuciscus*. Environ Biol Fish 56:183–197

Baras E, Ndao M, Maxi MYJ, Jeandrain D, Thorne JP, Vandewalle P, Mélard C (2000) Sibling cannibalism in dorada under experimental conditions. I. Ontogeny, dynamics, bioenergetics of cannibalism and prey size selectivity. J Fish Biol 57:1001–1020

Bass JAB, Pinder LCV, Leach DV (1997) Temporal and spatial variation in zooplankton populations in the River Great Ouse: an ephemeral food resource for larval and juvenile fish. Regul Riv 13:245–258

Bean CW, Winfield IJ (1995) Habitat use and activity patterns of roach (*Rutilus rutilus* (L.)), rudd (*Scardinius erythrophthalmus* (L.)), perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) in the laboratory: the role of predation threat and structural complexity. Ecol Freshw Fish 4:37–46

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661–664

Beaumont WRC, Mann RHK (1984) The age, growth and diet of a fresh-water population of the flounder, *Platichthys flesus* (L.), in southern England. J Fish Biol 25:607–616

Beeck P, Tauber S, Kiel S, Borcherding J (2002) 0+ perch predation on 0+ bream: a case study in a eutrophic gravel pit lake. Freshw Biol 47:2359–2369

Begg GA, Marteinsdottir G (2000) Spawning origins of pelagic juvenile cod *Gadus morhua* inferred from spatially explicit age distributions: potential influences on year-class strength and recruitment. Mar Ecol Prog Ser 202:193–217

Bischoff A, Freyhof J (1999) Seasonal shifts in day-time resource use of 0+ barbel, *Barbus barbus*. Environ Biol Fish 56:199–212

Blaber SJM, Whitfield AK (1977) Feeding ecology of juvenile mullet (Mugilidae) in south-east African estuaries. Biol J Linn Soc 9:277–284

Bolland JD, Nunn AD, Lucas MC, Cowx IG (2012) The importance of variable lateral connectivity between man-made floodplain waterbodies and river channels. River Res Appl (in press). doi:10.1002/rra.1498

Bollens SM (1988) A model of the predatory impact of larval marine fish on the population dynamics of their zooplankton prey. J Plankton Res 10:887–906

Borcherding J (2006) Prey or predator: 0+ perch (*Perca fluviatilis*) in the trade-off between food and shelter. Environ Biol Fish 77:87–96

Borcherding J, Maw SK, Tauber S (2000) Growth of 0+ perch (*Perca fluviatilis*) predating on 0+ bream (*Abramis brama*). Ecol Freshw Fish 9:236–241

Bowen SH (1979) A nutritional constraint in detritivory by fishes: the stunted population of *Sarotherodon mossambicus* in Lake Sibaya, South Africa. Ecol Monogr 49: 17–31

Bozzano A, Sarda F, Rios J (2005) Vertical distribution and feeding patterns of the juvenile European hake, *Merluccius merluccius* in the NW Mediterranean. Fish Res 73:29–36

Brabrand Å (1995) Intra-cohort cannibalism among larval stages of perch (*Perca fluviatilis*). Ecol Freshw Fish 4:70–76

Brabrand Å (2001) Piscivory in larval perch (*Perca fluviatilis*): mechanisms structuring larval roach (*Rutilus rutilus*) cohorts. Ecol Freshw Fish 10:97–104

Bremigan MT, Stein RA (1994) Gape-dependent larval foraging and zooplankton size: implications for fish recruitment across systems. Can J Fish Aquat Sci 51:913–922

Bromley PJ, Watson T, Hislop JRG (1997) Diel feeding patterns and the development of food webs in pelagic 0-group cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), whiting (*Merlangius merlangus* L.), saithe (*Pollachius virens* L.), and Norway pout (*Trisopterus esmarkii* Nilsson) in the northern North Sea. ICES J Mar Sci 54:846–853

Brooks JL, Dodson SI (1965) Predation, body size, and composition of plankton. Science 150:28–37

Bry C, Bonamy F, Manelphe J, Duranthon B (1995) Early life characteristics of pike, *Esox lucius*, in rearing ponds: temporal survival pattern and ontogenetic diet shifts. J Fish Biol 46:99–113

Buckel JA, Conover DO, Steinberg ND, McKown KA (1999) Impact of age-0 bluefish (*Pomatomus saltatrix*) predation on age-0 fishes in the Hudson River estuary: evidence for density dependent loss of juvenile striped bass (*Morone saxatilis*). Can J Fish Aquat Sci 56:275–287

Buijse AD, Houthuijzen RP (1992) Piscivory, growth, and size-selective mortality of age 0 pikeperch (*Stizostedion lucioperca*). Can J Fish Aquat Sci 49:894–902

Burrow JF, Horwood JW, Pitchford JW (2011) The importance of variable timing and abundance of prey for fish larval recruitment. J Plankton Res 33:1153–1162

Byström P, García-Berthou E (1999) Density dependent growth and size specific competitive interactions in young fish. Oikos 86:217–232

Cabral HN (2000) Comparative feeding ecology of sympatric *Solea solea* and *S. senegalensis*, within the nursery areas of the Tagus Estuary, Portugal. J Fish Biol 57:1550–1562

Caldarone EM, Clemmesen CM, Berdalet E, Miller TJ, Folkvord A, Holt GJ, Olivar MP, Suthers IM (2006) Intercalibration of four spectrofluorometric protocols for measuring RNA/DNA ratios in larval and juvenile fish. Limnol Oceanogr Meth 4:153–163

Carvalho PSM, Noltie TB, Tillitt DE (2002) Ontogenetic improvement of visual function in the medaka *Oryzias latipes* based on an optomotor testing system for larval and adult fish. Anim Behav 64:1–10

Chick JH, van den Avyle MJ (1999) Zooplankton variability and larval striped bass foraging: evaluating potential match/mismatch regulation. Ecol Appl 9:320–334

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth

Clements KD, Choat JH (1993) Influence of season, ontogeny and tide on the diet of the temperate marine herbivorous fish *Odax pullus* (Odacidae). Mar Biol 117:213–220

Colclough S, Fonseca L, Astley T, Thomas K, Watts W (2005) Fish utilisation of managed realignments. Fish Manag Ecol 12:351–360

Colebrook JM (1979) Continuous plankton records: seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea. Mar Biol 51:23–32

Conway DVP, Coombs SH, Smith C (1998) Feeding of anchovy *Engraulis encrasicolus* larvae in the northwestern Adriatic Sea in response to changing hydrobiological conditions. Mar Ecol Prog Ser 175:35–49

Conway DVP, Coombs SH, Lindley JA, Llewellyn CA (1999) Diet of mackerel (*Scomber scombrus*) larvae at the shelf-edge to the south-west of the British Isles and the incidence of piscivory and coprophagy. Vie Milieu 49: 213–220

Copp GH (2008) Putting multi-dimensionality back into niche: diel vs. day-only niche breadth separation in stream fishes. Fund Appl Limnol 170:273–280

Copp GH, Jurajda P (1999) Size-structured diel use of river banks by fish. Aquat Sci 61:75–91

Copp GH, Kováč V (2003) Sympatry between threespine *Gasterosteus aculeatus* and ninespine *Pungitius pungitius* sticklebacks in English lowland streams. Ann Zool Fenn 40:341–355

Copp GH, Mann RHK (1993) Comparative growth and diet of tench *Tinca tinca* (L.) larvae and juveniles from river floodplain biotopes in France and England. Ecol Freshw Fish 2:58–66

Copp GH, Spathari S, Turmel M (2005) Consistency of diel behaviour and interactions of stream fishes and invertebrates during summer. River Res Appl 21:75–90

Copp GH, Britton JR, Cucherousset J, García-Berthou E, Kirk R, Peeler E, Stakėnas S (2009) Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. Fish Fish 10:252–282

Courtois R, Dodson JJ (1986) Diet and principal factors influencing the feeding of the larvae of capelin (*Mallotus villosus*), of smelt (*Osmerus mordax*) and of herring (*Clupea harengus harengus*) in a partially mixed estuary. Can J Fish Aquat Sci 43:968–979

Cowan JH, Rose KA, DeVries DR (2000) Is density-dependent growth in young-of-the-year fishes a question of critical weight? Rev Fish Biol Fisher 10:61–89

Cowx IG, Young WO, Hellawell JM (1984) The influence of drought on the fish and invertebrate populations of an upland stream in Wales. Freshw Biol 14:165–177

Cretenoy L, Gerdeaux D (1997) Growth and feeding of coregonid larvae (*Coregonus lavaretus*) in Lake Annecy during March and April 1996. Bull Franç Pêche Piscic 346: 519–526

Cryer M, Peirson G, Townsend CR (1986) Reciprocal interactions between roach *Rutilus rutilus* (L.) and zooplankton in a small lake: prey dynamics and fish growth and recruitment. Limnol Oceanogr 31:1022–1038

Cushing DH (1983) Are fish larvae too dilute to affect the density of their prey? J Plankton Res 5:847–854

Cushing DH (1990) Plankton production and year-class strength in fish populations–an update of the match mismatch hypothesis. Adv Mar Biol 26:249–293

Cyr H, Downing JA (1988) The abundance of phytophilous invertebrates on different species of submerged macrophytes. Freshwater Biol 20:365–374

Dąbrowski K, Murawska E, Terlecki J, Wielgosz S (1984) Studies on the feeding of *Coregonus pollan* (Thompson) alevins and fry in Lough Neagh. Int Rev Ges Hydrobiol 69:529–540

Declerck S, Louette G, De Bie T, De Meester L (2002) Patterns of diet overlap between populations of non-indigenous and native fishes in shallow ponds. J Fish Biol 61:1182–1197

Demain DK, Gallego A, Jaworski A, Priede IG, Jones EG (2011) Diet and feeding niches of juvenile *Gadus morhua*, *Melanogrammus aeglefinus* and *Merlangius merlangus* during the settlement transition in the northern North Sea. J Fish Biol 79:89–111

Dettmers JM, Wahl DH (1999) Evidence for zooplankton compensation and reduced fish growth in response to increased juvenile fish density. Hydrobiologia 400:115–121

DeVries DR, Bremigan MT, Stein RA (1998) Prey selection by larval fishes as influenced by available zooplankton and gape limitation. T Am Fish Soc 127:1040–1050

Dickmann M, Mollmann C, Voss R (2007) Feeding ecology of central Baltic sprat *Sprattus sprattus* larvae in relation to zooplankton dynamics: implications for survival. Mar Ecol Prog Ser 342:277–289

Diehl S (1988) Foraging efficiency of three freshwater fishes: effects of structural complexity and light. Oikos 53: 207–214

Diehl S, Eklöv P (1995) Effects of piscivore-mediated habitat use on resources, diet, and growth of perch. Ecology 76:1712–1726

Dixon AM, Leggett DJ, Weight RC (1998) Habitat creation opportunities for landward coastal re-alignment: Essex case studies. J CIWEM 12:107–112

Easton RS, Orth DJ, Voshell JR (1996) Spatial and annual variation in the diets of juvenile smallmouth bass, *Micropterus dolomieu*. Environ Biol Fish 46:383–392

Eggold BT, Motta PJ (1992) Ontogenic dietary shifts and morphological correlates in striped mullet, *Mugil cephalus*. Environ Biol Fish 34:139–158

Extence CA (1981) The effect of drought on benthic invertebrate communities in a lowland river. Hydrobiologia 83:217–224

Fernandez IM, Gonzalez-Quiros R (2006) Analysis of feeding of *Sardina pilchardus* (Walbaum, 1792) larval stages in the central Cantabrian Sea. Sci Mar 70:131–139

Ferrari I, Chieregato AR (1981) Feeding-habits of juvenile stages of *Sparus auratus* L., *Dicentrarchus labrax* L. and Mugilidae in a brackish embayment of the Po River Delta. Aquaculture 25:243–257

Fonseca L, Colclough S, Hughes RG (2011) Variations in the feeding of 0-group bass *Dicentrarchus labrax* (L.) in managed realignment areas and saltmarshes in SE England. Hydrobiologia 672:15–31

Fortier L, Ponton D, Gilbert M (1995) The match mismatch hypothesis and the feeding success of fish larvae in ice-covered southeastern Hudson Bay. Mar Ecol Prog Ser 120:11–27

França S, Vinagre C, Costa MJ, Cabral HN (2004) Use of the coastal areas adjacent to the Douro estuary as a nursery area for pouting, *Trisopterus luscus* Linnaeus, 1758. J Appl Ichthyol 20:99–104

Frankiewicz P, Dąbrowski K, Martyniak A, Zalewski M (1999) Cannibalism as a regulatory force of pikeperch, *Stizostedion lucioperca* (L.), population dynamics in the lowland Sulejow reservoir (Central Poland). Hydrobiologia 408(409):47–55

French PW (2006) Managed realignment—the developing story of a comparatively new approach to soft engineering. Estuar Coast Shelf Sci 67:409–423

Froese R, Pauly D (eds) (2011) FishBase. World Wide Web electronic publication. http://www.fishbase.org, version (02/2011). Accessed 10 March 2011

Frost WE (1943) The natural history of the minnow, *Phoxinus phoxinus*. J Anim Ecol 12:139–162

Frost WE (1950) The growth and food of young salmon (*Salmo salar*) and trout (*S. trutta*) in the River Forss, Caithness. J Anim Ecol 19:147–158

Fry B (2002) Stable isotopic indicators of habitat use by Mississippi River fish. J N Am Benthol Soc 21:676–685

Fuiman L, Magurran AE (1994) Development of predator defenses in fishes. Rev Fish Biol Fisher 4:145–183

Fuiman LA, Cowan JH Jr, Smith ME, O'Neal JP (2005) Behavior and recruitment success in fish larvae: variation with growth rate and the batch effect. Can J Fish Aquat Sci 62:1337–1349

Galarowicz TL, Adams JA, Wahl DH (2006) The influence of prey availability on ontogenetic diet shifts of a juvenile piscivore. Can J Fish Aquat Sci 63:1722–1733

Garbutt RA, Reading CJ, Wolters M, Gray AJ, Rothery P (2006) Monitoring the development of intertidal habitats on former agricultural land after the managed realignment of coastal defences at Tollesbury, Essex, UK. Mar Pollut Bull 53:155–164

García-Berthou E (2002) Ontogenetic diet shifts and interrupted piscivory in introduced largemouth bass (*Micropterus salmoides*). Int Rev Hydrobiol 87:353–363

García-Berthou E, Moreno-Amich R (2000) Food of introduced pumpkinseed sunfish: ontogenetic diet shift and seasonal variation. J Fish Biol 57:29–40

Garner P (1996a) Microhabitat use and diet of 0+ cyprinid fishes in a lentic, regulated reach of the River Great Ouse, England. J Fish Biol 48:367–382

Garner P (1996b) Diel patterns in the feeding and habitat use behaviour of 0-group fishes in a regulated river: the River Great Ouse, England. Ecol Freshw Fish 5:175–182

Garner P (1998) Variation in the feeding of 0+ cyprinid fish in a regulated river: mesohabitat scale effects. Folia Zool 47: 61–64

Garner P, Bass JAB, Collett GD (1996) The effects of weed cutting upon the biota of a large regulated river. Aquat Conserv 6:21–29

George EL, Hadley WF (1979) Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieui*) young of the year. T Am Fish Soc 108:253–261

George DG, Taylor AH (1995) UK lake plankton and the Gulf stream. Nature 378:139

Ghan D, Sprules WG (1993) Diet, prey selection, and growth of larval and juvenile burbot *Lota lota* (L.). J Fish Biol 42:47–64

Gill AB (2003) The dynamics of prey choice in fish: the importance of prey size and satiation. J Fish Biol 63(Suppl A):105–116

Gill AB, Hart PJB (1998) Stomach capacity as a directing factor in prey size selection of three-spined stickleback. J Fish Biol 53:897–900

Gillanders BM (1995) Feeding ecology of the temperate marine fish *Achoerodus viridis* (Labridae): size, seasonal and site-specific differences. Mar Freshw Res 46:1009–1020

Gliwicz ZM (1986) Predation and the evolution of vertical migration in zooplankton. Nature 320:746–748

Gliwicz ZM (2001) Species-specific population-density thresholds in cladocerans? Hydrobiologia 442:291–300

Gliwicz ZM, Jachner A (1992) Diel migrations of juvenile fish: a ghost of predation past or present? Arch Hydrobiol 124:385–430

Gliwicz ZM, Jawiński A, Pawłowicz M (2004) Cladoceran densities, day-to-day variability in food selection by smelt, and the birth-rate-compensation hypothesis. Hydrobiologia 526:171–186

Gliwicz ZM, Slon J, Szynkarczyk I (2006) Trading safety for food: evidence from gut contents in roach and bleak captured at different distances offshore from their daytime littoral refuge. Freshw Biol 51:823–839

Gotceitas V, Godin JGJ (1991) Foraging under the risk of predation in juvenile Atlantic salmon (*Salmo salar* L.): effects of social status and hunger. Behav Ecol Sociobiol 29: 255–261

Gotceitas V, Puvanendran V, Leader LL, Brown JA (1996) An experimental investigation of the 'match mismatch' hypothesis using larval Atlantic cod. Mar Ecol Prog Ser 130:29–37

Gozlan RE, Pinder AC, Durand S, Bass J (2003) Could the small size of sunbleak, *Leucaspius delineatus* (Pisces, Cyprinidae) be an ecological advantage in invading British waterbodies? Folia Zool 52:99–108

Graeb BDS, Dettmers JM, Wahl DH, Cáceres CE (2004) Fish size and prey availability affect growth, survival, prey selection, and foraging behavior of larval yellow perch. Trans Am Fish Soc 133:504–514

Grenouillet G, Pont D, Olivier JM (2001a) Linking zooplankton and juvenile fish assemblages in a large lowland river: influence of submerged macrophytes. Arch Hydrobiol 151:383–404

Grenouillet G, Hugueny B, Carrel GA, Olivier JM, Pont D (2001b) Large-scale synchrony and inter-annual variability in roach recruitment in the Rhône River: the relative role of climatic factors and density-dependent processes. Freshw Biol 46:11–26

Grift RE, Buijse AD, van Densen WLT, Machiels MAM, Kranenbarg J, Klein Breteler JGP, Backx JJGM (2003) Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. River Res Appl 19:353–374

Grønkjaer P, Carl JD, Rasmussen TH, Hansen KW (2007) Effect of habitat shifts on feeding behaviour and growth of 0 year-group flounder *Platichthys flesus* (L.) transferred between macroalgae and bare sand habitats. J Fish Biol 70:1587–1605

Guma'a SA (1978) The food and feeding habits of young perch, *Perca fluviatilis*, in Windermere. Freshw Biol 8:177–187

Hamilton JG, Powles PM (1979) Feeding-habits and growth of young-of-the-year largemouth bass (*Micropterus salmoides*) near its northern limit, Nogies Creek, Ontario. Can J Zool 57:1431–1437

Hanazato T, Fueki K, Yoshimoto M (2001) Fish-induced life-history shifts in the cladocerans *Daphnia* and *Simocephalus*: are they positive or negative responses? J Plankton Res 23:945–951

Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. Trends Ecol Evol 20:337–344

Heath MR, Lough RG (2007) A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (*Gadus morhua*). Fish Oceanogr 16:169–185

Herwig BR, Zimmer KD (2007) Population ecology and prey consumption by fathead minnows in prairie wetlands: importance of detritus and larval fish. Ecol Freshw Fish 16:282–294

Hillgruber N, Kloppmann M (1999) Distribution and feeding of blue whiting *Micromesistius poutassou* larvae in relation to different water masses in the Porcupine Bank area, west of Ireland. Mar Ecol Prog Ser 187:213–225

Hofer R, Uddin N (1985) Digestive processes during the development of roach, *Rutilus rutilus* (L.). J Fish Biol 26:683–689

Hojgaard DP (1999) Food and parasitic nematodes of saithe, *Pollachius virens* (L.), from the Faroe Islands. Sarsia 84:473–478

Hoogenboezem W, Lammens E, Vanvugt Y, Osse JWM (1992) A model for switching between particulate-feeding and filter-feeding in the common bream, *Abramis brama*. Environ Biol Fish 33:13–21

Hostens K, Mees J (1999) The mysid-feeding guild of demersal fishes in the brackish zone of the Westerschelde estuary. J Fish Biol 55:704–719

Houde ED (1997) Patterns and trends in larval-stage growth and mortality of teleost fish. J Fish Biol 51(Suppl A):52–83

Hoxmeier RJH, Wahl DH, Hooe ML, Pierce CL (2004) Growth and survival of larval walleyes in response to prey availability. Trans Am Fish Soc 133:45–54

Hrbáček J, Dvorakova M, Korínek V, Prochàzkóva L (1961) Demonstration of the effect of fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verh Int Verein Theor Angew Limnol 14:192–195

Hurst TP (2007) Causes and consequences of winter mortality in fishes. J Fish Biol 71:315–345

Hynes HBN (1950) The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. J Anim Ecol 19:36–58

Hyslop EJ (1982) The feeding-habits of 0+ stone loach, *Noemacheilus barbatulus* (L.), and bullhead, *Cottus gobio* L. J Fish Biol 21:187–196

Jachner A (1991) Food and habitat partitioning among juveniles of three fish species in the pelagial of a mesotrophic lake. Hydrobiologia 226:81–89

Jacobsen L, Berg S (1998) Diel variation in habitat use by planktivores in field enclosure experiments: the effect of submerged macrophytes and predation. J Fish Biol 53: 1207–1219

Junger H, Kotrschal K, Goldschmid A (1989) Comparative morphology and ecomorphology of the gut in European cyprinids (Telostei). J Fish Biol 34:315–326

Kaminskas S, Humphries P (2009) Diet of Murray cod (*Maccullochella peelii peelii*) (Mitchell) larvae in an Australian lowland river in low flow and high flow years. Hydrobiologia 636:449–461

Kamjunke N, Schmidt K, Pflugmacher S, Mehner T (2002) Consumption of cyanobacteria by roach (*Rutilus rutilus*): useful or harmful to the fish? Freshw Biol 47: 243–250

Kamler E (2002) Ontogeny of yolk-feeding fish: an ecological perspective. Rev Fish Biol Fisher 12:79–103

Karjalainen J (1991) Survival, growth and feeding of vendace, *Coregonus albula* (L.), larvae in net enclosures. J Fish Biol 38:905–919

Keeley ER, Grant JWA (1997) Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 54:1894–1902

Kennedy M, Fitzmaurice P (1970) The biology of the tench, *Tinca tinca* (L.), in Irish waters. Proc R Irish Acad 69B:31–84

Kennedy M, Fitzmaurice P (1974) Biology of the rudd, *Scardinius erythrophthalmus* (L.) in Irish waters. Proc R Irish Acad 74B:245–303

King AJ (2005) Ontogenetic dietary shifts of fishes in an Australian floodplain river. Mar Freshw Res 56:215–225

Klemetsen A, Amundsen PA, Dempson JB, Jonsson B, Jonsson N, O'Connell MF, Mortensen E (2003) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecol Freshw Fish 12:1–59

Kolkovski S (2001) Digestive enzymes in fish larvae and juveniles—implications and applications to formulated diets. Aquaculture 200(Special Issue):181–201

Kottelat M, Freyhof J (2007) Handbook of European freshwater fishes. Publications Kottelat, Cornol

Kratochvíl M, Peterka J, Kubečka J, Matěna J, Vašek M, Vaníčková I, Čech M, Seďa J (2008) Diet of larvae and juvenile perch, *Perca fluviatilis* performing diel vertical migrations in a deep reservoir. Folia Zool 57:313–323

Krause J (1994) The influence of food competition and predation risk on size-assortative shoaling in juvenile chub (*Leuciscus cephalus*). Ethology 96:105–116

Krebs JM, Turingan RG (2003) Intraspecific variation in gape-prey size relationships and feeding success during early ontogeny in red drum, *Sciaenops ocellatus*. Environ Biol Fish 66:75–84

Kurmayer R, Wanzenböck J (1996) Top-down effects of underyearling fish on a phytoplankton community. Freshw Biol 36:599–609

Lass S, Spaak P (2003) Chemically induced anti-predator defences in plankton: a review. Hydrobiologia 491: 221–239

Last JM (1979) Food of larval turbot *Scophthalmus maximus* L. from the west central North Sea. J Cons 38:308–313

Lauridsen TL, Pedersen LJ, Jeppesen E, Sondergaard M (1996) The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. J Plankton Res 18:2283–2294

Lazzaro X (1987) A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. Hydrobiologia 146:97–167

Lees K, Pitois S, Scott C, Frid C, Mackinson S (2006) Characterizing regime shifts in the marine environment. Fish Fish 7:104–127

Leitao R, Martinho E, Neto JM, Cabral H, Marques JC, Pardal MA (2006) Feeding ecology, population structure and distribution of *Pomatoschistus microps* (Krøyer, 1838) and *Pomatoschistus minutus* (Pallas, 1770) in a temperate estuary, Portugal. Estuar Coast Shelf S 66:231–239

Lemke MJ, Bowen SH (1998) The nutritional value of organic detrital aggregate in the diet of fathead minnows. Freshw Biol 39:447–453

Longshaw M, Frear PA, Feist SW (2005) Descriptions, development and pathogenicity of myxozoan (Myxozoa: Myxosporea) parasites of juvenile cyprinids (Pisces: Cyprinidae). J Fish Dis 28:489–508

Longshaw M, Frear PA, Nunn AD, Cowx IG, Feist SW (2010) The influence of parasitism on fish population success. Fish Manag Ecol 17:426–434

Lowerre-Barbieri SK, Lowerre JM, Barbieri LR (1998) Multiple spawning and the dynamics of fish populations: inferences from an individual-based simulation model. Can J Fish Aquat Sci 55:2244–2254

MacKenzie BR, Ueberschar B, Basford D, Heath M, Gallego A (1999) Diel variability of feeding activity in haddock (*Melanogrammus aeglefinus*) larvae in the East Shetland area, North Sea. Mar Biol 135:361–368

Makrakis MC, Nakatani K, Bialetzki A, Sanches PV, Baumgartner G, Gomes LC (2005) Ontogenetic shifts in digestive tract morphology and diet of fish larvae of the Itaipu Reservoir, Brazil. Environ Biol Fish 72:99–107

Mann RHK, Bass JAB, Leach D, Pinder AC (1997) Temporal and spatial variations in the diet of 0 group roach (*Rutilus rutilus*) larvae and juveniles in the River Great Ouse in relation to prey availability. Regul Riv 13:287–294

Mark W, Hofer R, Wieser W (1987) Diet spectra and resource partitioning in the larvae and juveniles of three species and six cohorts of cyprinids from a subalpine lake. Oecologia 71:388–396

Marker AFH, Collett GD (1997a) Spatial and temporal characteristics of algae in the River Great Ouse. I. Phytoplankton. Regul Riv 13:219–233

Marker AFH, Collett GD (1997b) Spatial and temporal characteristics of algae in the River Great Ouse. II. The epiphytic algal flora. Regul Riv 13:235–244

Matěna J (1995) The role of ecotones as feeding grounds for fish fry in a Bohemian water supply reservoir. Hydrobiologia 303:31–38

Matěna J (1998) Diet spectra and competition between juvenile fish in the pelagic zone of a deep stratified reservoir during the first year of life. Int Rev Hydrobiol 83:577–584

Mayer CM, Wahl DH (1997) The relationship between prey selectivity and growth and survival in a larval fish. Can J Fish Aquat Sci 54:1504–1512

Mazik K, Smith JE, Leighton A, Elliott M (2007) Physical and biological development of a newly breached managed realignment site, Humber estuary, UK. Mar Pollut Bull 55:564–578

McLaren IA, Avendaňo P, Taggart CT, Lochmann SE (1997) Feeding by larval cod in different water masses on Western Bank, Scotian Shelf. Fish Oceanogr 6:250–265

McLaughlin RL, Grant JWA (1994) Morphological and behavioral differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow-running vs fast-running water. Environ Biol Fish 39:289–300

Mehner T, Thiel R (1999) A review of predation impact by 0+ fish on zooplankton in fresh and brackish waters of the temperate northern hemisphere. Environ Biol Fish 56: 169–181

Mehner T, Winfield IJ (eds) (1997) Trophic interactions of age-0 fish and zooplankton in temperate waters. Arch Hydrobiol Special Issue Adv Limnol 49:1–152

Mehner T, Schultz H, Bauer D, Herbst R, Voigt H, Benndorf J (1996) Intraguild predation and cannibalism in age-0 perch (*Perca fluviatilis*) and age-0 zander (*Stizostedion lucioperca*): interactions with zooplankton succession, prey fish availability and temperature. Ann Zool Fenn 33:353–361

Mehner T, Plewa M, Hülsmann S, Voigt H, Benndorf J (1997) Age-0 fish predation on daphnids—spatial and temporal variability in the top-down manipulated Bautzen reservoir, Germany. Arch Hydrobiol Special Issue Adv Limnol 49:13–25

Mehner T, Plewa M, Hülsmann S, Worischka S (1998) Gape-size dependent feeding of age-0 perch (*Perca fluviatilis*) and age-0 zander (*Stizostedion lucioperca*) on *Daphnia galeata*. Arch Hydrobiol 142:191–207

Mélard C, Baras E, Mary L, Kestemont P (1996) Relationships between stocking density, growth, cannibalism and survival rate in intensively cultured larvae and juveniles of perch (*Perca fluviatilis*). Ann Zool Fenn 33:643–651

Metcalfe NB, Huntingford FA, Thorpe JE (1987) Predation risk impairs diet selection in juvenile salmon. Anim Behav 35:931–933

Mikheev VN, Wanzenböck J (1999) Satiation-dependent, intra-cohort variations in prey size selection of young roach (*Rutilus rutilus*). Oecologia 121:499–505

Mikheev VN, Wanzenböck J, Pasternak AF (2006) Effects of predator-induced visual and olfactory cues on 0+ perch (*Perca fluviatilis* L.) foraging behaviour. Ecol Freshw Fish 15:111–117

Miller TJ, Crowder LB, Rice JA (1993) Ontogenic changes in behavioral and histological measures of visual acuity in three species of fish. Environ Biol Fish 37:1–8

Mills EL, Forney JL (1988) Trophic dynamics and development of freshwater pelagic food webs. In: Carpenter SR (ed) Complex interactions in lake communities. Springer, New York, pp 11–30

Mills CA, Mann RHK (1985) Environmentally-induced fluctuations in year class strength and their implications for management. J Fish Biol 27(Suppl A):209–226

Mills CA, Beaumont WRC, Clarke RT (1985) Sources of variation in the feeding of larval dace *Leuciscus leuciscus* in an English river. Trans Am Fish Soc 114:519–524

Mittelbach GG, Persson L (1998) The ontogeny of piscivory and its ecological consequences. Can J Fish Aquat Sci 55: 1454–1465

Montagnes DJS, Dower JF, Figueiredo GM (2010) The protozooplankton-ichthyoplankton trophic link: an overlooked aspect of aquatic food webs. J Eukaryot Microbiol 57:223–228

Monteiro NM, Quinteira SM, Silva K, Vieira MN, Almada VC (2005) Diet preference reflects the ontogenetic shift in microhabitat use in *Lipophrys pholis*. J Fish Biol 67: 102–113

Moore JW, Moore IA (1974) Food and growth of Arctic char, *Salvelinus alpinus* (L.), in the Cumberland Sound area of Baffin Island. J Fish Biol 6:79–92

Munk P, Nielsen TG (1994) Trophodynamics of the plankton community at Dogger Bank: predatory impact by larval fish. J Plankton Res 16:1225–1245

Myers RA (1995) Recruitment of marine fish: the relative roles of density-dependent and density-independent mortality in the egg, larval, and juvenile stages. Mar Ecol Prog Ser 128:308–309

Naesje TF, Jonsson B, Klyve L, Sandlund OT (1987) Food and growth of age-0 smelts, *Osmerus eperlanus*, in a Norwegian fjord lake. J Fish Biol 30:119–126

Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, van't Hof T, den Hartog C (2000) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuar Coast Shelf 51:31–44

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

Nunn AD, Cowx IG, Frear PA, Harvey JP (2003) Is water temperature an adequate predictor of recruitment success in cyprinid fish populations in lowland rivers? Freshw Biol 48:579–588

Nunn AD, Harvey JP, Britton JR, Frear PA, Cowx IG (2007a) Fish, climate and the Gulf Stream: the influence of abiotic factors on the recruitment success of cyprinid fishes in lowland rivers. Freshw Biol 52:1576–1586

Nunn AD, Harvey JP, Cowx IG (2007b) The food and feeding relationships of larval and 0+ year juvenile fishes in lowland rivers and connected waterbodies. I. Ontogenetic shifts and interspecific diet similarity. J Fish Biol 70: 726–742

Nunn AD, Harvey JP, Cowx IG (2007c) The food and feeding relationships of larval and 0+ year juvenile fishes in lowland rivers and connected waterbodies. II. Prey selection and the influence of gape. J Fish Biol 70:743–757

Nunn AD, Harvey JP, Cowx IG (2007d) Variations in the spawning periodicity of eight fish species in three English lowland rivers over a 6 year period, inferred from 0+ year fish length distributions. J Fish Biol 70:1254–1267

Nunn AD, Harvey JP, Cowx IG (2007e) Benefits to 0+ fishes of connecting man-made waterbodies to the lower River Trent, England. River Res Appl 23:361–376

Nunn AD, Noble RAA, Harvey JP, Cowx IG (2008a) The diets and parasites of larval and 0+ juvenile twaite shad in the lower reaches and estuaries of the rivers Wye, Usk and Towy, UK. Hydrobiologia 614:209–218

Nunn AD, Harvey JP, Cowx IG (2008b) Winter diet and condition of two 0+ year cyprinid fish species in the lower River Trent, England. J Fish Biol 72:1529–1533

Nunn AD, Frear PA, Lee M, Cowx IG (2010a) Is there evidence for a shift in fish growth and recruitment success linked to climate change? J Fish Biol 77:1780–1792

Nunn AD, Copp GH, Vilizzi L, Carter MG (2010b) Seasonal and diel patterns in the migrations of fishes between a river and a floodplain tributary. Ecol Freshw Fish 19:153–162

Oesmann S, Thiel R (2001) Feeding of juvenile twaite shad (*Alosa fallax* Lacépède, 1803) in the Elbe estuary. Bull Franç Pêche Piscic 362(363):785–800

Ogle DH, Ray BA, Brown WP (2004) Diet of larval ruffe (*Gymnocephalus cernuus*) in the St. Louis River Harbor, Lake Superior. J Great Lakes Res 30:287–292

Okun N, Mendonca R, Mehner T (2005) Diel shifts in community composition and feeding of juvenile fishes in the pelagic area of a large shallow lake. Limnologica 35:70–77

Olson MH (1996) Ontogenetic niche shifts in largemouth bass: vulnerability and consequences for first-year growth. Ecology 77:179–190

Ondračková M, Jurajda P, Gelnar M (2002) The distribution of *Posthodiplostomum cuticola* metacercariae in young-of-the-year cyprinid fishes. J Fish Biol 60:1355–1357

Pangle KL, Sutton TM, Kinnunen RE, Hoff MH (2004) Overwinter survival of juvenile lake herring in relation to body size, physiological condition, energy stores, and food ration. Trans Am Fish Soc 133:1235–1246

Pedersen T, Fossheim M (2008) Diet of 0-group stages of capelin (*Mallotus villosus*), herring (*Clupea harengus*) and cod (*Gadus morhua*) during spring and summer in the Barents Sea. Mar Biol 153:1037–1046

Pelham ME, Pierce CL, Larscheid JG (2001) Diet dynamics of the juvenile piscivorous fish community in Spirit Lake, Iowa, USA, 1997–1998. Ecol Freshw Fish 10:198–211

Peňáz M (2001) A general framework of fish ontogeny: a review of the ongoing debate. Folia Zool 50:241–256

Penttinen OP, Holopainen IJ (1992) Seasonal feeding activity and ontogenetic dietary shifts in crucian carp, *Carassius carassius*. Environ Biol Fish 33:215–221

Pepin P, Penney RW (1997) Patterns of prey size and taxonomic composition in larval fish: are there general size-dependent models? J Fish Biol 51(Suppl A):84–100

Perrow MR, Irvine K (1992) The relationship between cladoceran body size and the growth of underyearling roach (*Rutilus rutilus* (L.)) in two shallow lowland lakes: a mechanism for density-dependent reductions in growth. Hydrobiologia 241:155–161

Persson L (1983) Food consumption and the significance of detritus and algae to intraspecific competition in roach *Rutilus rutilus* in a shallow eutrophic lake. Oikos 41: 118–125

Persson A, Brönmark C (2002a) Foraging capacities and effects of competitive release on ontogenetic diet shift in bream, *Abramis brama*. Oikos 97:271–281

Persson A, Brönmark C (2002b) Foraging capacity and resource synchronization in an ontogenetic diet switcher, pikeperch (*Stizostedion lucioperca*). Ecology 83:3014–3022

Persson L, Greenberg LA (1990) Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)-roach (*Rutilus rutilus*) interaction. Ecology 71:44–56

Peterson WT, Ausubel SJ (1984) Diets and selective feeding by larvae of Atlantic mackerel *Scomber scombrus* on zooplankton. Mar Ecol Prog Ser 17:65–75

Pinder AC, Gozlan RE, Beyer K, Bass JAB (2005) Ontogenetic induced shifts in the ecology of sunbleak *Leucaspius delineatus* during early development. J Fish Biol 67:205–217

Pitcher TJ (ed) (1986) The behaviour of teleost fishes. Croom Helm, London

Politou CY, Papaconstantinou C (1994) Feeding ecology of Mediterranean poor cod, *Trisopterus minutus capelanus* (Lacepede), from the eastern coast of Greece. Fish Res 19:269–292

Pyke GH (1984) Optimal foraging theory: a critical review. Annu Rev Ecol Evol S 15:523–575

Reckendorfer W, Keckeis H, Winkler G, Schiemer F (1999) Zooplankton abundance in the River Danube, Austria: the significance of inshore retention. Freshw Biol 41:583–591

Reckendorfer W, Keckeis H, Tiitu V, Winkler G, Zornig H, Schiemer F (2001) Diet shifts on 0+ nase, *Chondrostoma nasus*: size-specific differences and the effect of food availability. Arch Hydrobiol Suppl 135(Large Rivers v.12):425–440

Reid PC, Planque B, Edwards M (1998) Is observed variability in the long-term results of the Continuous Plankton

Recorder survey a response to climate change? Fish Oceanogr 7:282–288

Rezsu E, Specziár A (2007) Ontogenetic diet profiles and size-dependent diet partitioning of ruffe *Gymnocephalus cernuus*, perch *Perca fluviatilis* and pumpkinseed *Lepomis gibbosus* in Lake Balaton. Ecol Freshw Fish 15:339–349

Rincón PA, Lobón-Cerviá J (1999) Prey-size selection by brown trout (*Salmo trutta* L.) in a stream in northern Spain. Can J Zool 77:755–765

Romare P (2000) Growth of larval and juvenile perch: the importance of diet and fish density. J Fish Biol 56:876–889

Romare P, Bergman E, Hansson LA (1999) The impact of larval and juvenile fish on zooplankton and algal dynamics. Limnol Oceanogr 44:1655–1666

Rowlands WL, Dickey-Collas M, Geffen AJ, Nash RDM (2008) Diet overlap and prey selection through metamorphosis in Irish Sea cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*). Can J Fish Aquat Sci 65:1297–1306

Sabatés A, Saiz E (2000) Intra- and interspecific variability in prey size and niche breadth of myctophiform fish larvae. Mar Ecol Prog Ser 201:261–271

Sánchez-Hernández J, Vieira-Lanero R, Servia MJ, Cobo F (2011) First feeding diet of young brown trout fry in a temperate area: disentangling constraints and food selection. Hydrobiologia 663:109–119

Scharf FS, Juanes F, Rountree RA (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and the effects of ontogeny and body size on trophic niche breadth. Mar Ecol Prog Ser 208:229–248

Scharf FS, Buckel JA, Juanes F (2009) Contrasting patterns of resource utilization between juvenile estuarine predators: the influence of relative prey size and foraging ability on the ontogeny of piscivory. Can J Fish Aquat Sci 66: 790–801

Schiemer F, Keckeis H, Wanzenböck J (1989) Foraging in cyprinids during early development. Pol Arch Hydrobiol 36:467–474

Schiemer F, Keckeis H, Reckendorfer W, Winkler G (2001) The 'inshore retention concept' and its significance for large rivers. Arch Hydrobiol Suppl 135(Large Rivers v.12): 509–516

Scott A (1985) Distribution, growth, and feeding of postemergent grayling *Thymallus thymallus* in an English river. Trans Am Fish Soc 114:525–531

Scott A (1987) Prey selection by juvenile cyprinids from running water. Freshw Biol 17:129–142

Sempeski P, Gaudin P, Persat H, Grolet O (1995) Diet selection in early-life stages of grayling (*Thymallus thymallus*). Arch Hydrobiol 132:437–452

Shaw M, Diekmann R, van der Kooij J, Milligan S, Bromley P, Righton D (2008) Assessment of the diets of cod *Gadus morhua* and whiting *Merlangius merlangus* juveniles in a frontal region close to the Norwegian trench: co-existence or competition? J Fish Biol 73:1612–1634

Shepherd WC, Mills EL (1996) Diel feeding, daily food intake, and *Daphnia* consumption by age-0 gizzard shad in Oneida Lake, New York. Trans Am Fish Soc 125:411–421

Soetaert K, Van Rijswijk P (1993) Spatial and temporal patterns of the zooplankton in the Westerschelde estuary. Mar Ecol Prog Ser 97:47–59

Sommer U, Gliwicz ZM, Lampert W, Duncan A (1986) The plankton ecology group model of seasonal succession of planktonic events in fresh waters. Arch Hydrobiol 106: 433–472

Spaink P, Ietswaart T, Roijackers R (1998) Plankton dynamics in a dead arm of the River Waal: a comparison with the main channel. J Plankton Res 20:1997–2007

Spanovskaya VD, Grygorash VA (1977) Development and food of age-0 Eurasian perch (*Perca fluviatilis*) in reservoirs near Moscow, USSR. J Fish Res Board Can 34:1551–1558

Sparholt H (1985) The population, survival, growth, reproduction and food of Arctic charr, *Salvelinus alpinus* (L.), in four unexploited lakes in Greenland. J Fish Biol 26: 313–330

Specziár A, Rezsu ET (2009) Feeding guilds and food resource partitioning in a lake fish assemblage: an ontogenetic approach. J Fish Biol 75:247–267

Stige LC, Ottersen G, Hjermann DØ, Dalpadado P, Jensen LK, Stenseth NC (2011) Environmental toxicology: population modeling of cod larvae shows high sensitivity to loss of zooplankton prey. Mar Pollut Bull 62:395–398

Sutela T, Huusko A (1997) Food consumption of vendace *Coregonus albula* larvae in Lake Lentua, Finland. J Fish Biol 51:939–951

Tans M, Mathoux L, Grandjean T, Kestemont P (1998) Temporal variation and spatial heterogeneity of zooplankton food availability in backwaters and the main channel of the River Meuse (Belgium). Int J Limnol 34:49–55

Thiel R, Mehner T, Kopcke B, Kafemann R (1996) Diet niche relationships among early life stages of fish in German estuaries. Mar Freshw Res 47:123–136

Tonkin ZD, Humphries P, Pridmore PA (2006) Ontogeny of feeding in two native and one alien fish species from the Murray-Darling Basin, Australia. Environ Biol Fish 76:303–315

Townsend CR, Winfield IJ, Peirson G, Cryer M (1986) The response of young roach *Rutilus rutilus* to seasonal changes in abundance of microcrustacean prey: a field demonstration of switching. Oikos 46:372–378

Treer T, Piria M, Aničič I, Safner R, Tomljanović T (2006) Diet and growth of spirlin, *Alburnoides bipunctatus* in the barbel zone of the Sava River. Folia Zool 55:97–106

Tudela S, Palomera I, Quilez G (2002) Feeding of anchovy *Engraulis encrasicolus* larvae in the north-west Mediterranean. J Mar Biol Assoc UK 82:349–350

Turesson H, Brönmark C, Wolf A (2006) Satiation effects in piscivore prey size selection. Ecol Freshw Fish 15: 78–85

Urbatzka R, Beeck P, van der Velde G, Borcherding J (2008) Alternative use of food resources causes intra-cohort variation in the size distribution of young-of-the-year perch (*Perca fluviatilis*). Ecol Freshw Fish 17:475–480

van Densen WLT, Ligtvoet W, Roozen RWM (1996) Intra-cohort variation in the individual size of juvenile pike-perch, *Stizostedion lucioperca*, and perch, *Perca fluviatilis*, in relation to the size spectrum of their food items. Ann Zool Fenn 33:495–506

Vašek M, Kubečka J, Matěna J, Sedǎ J (2006) Distribution and diet of 0+ fish within a canyon-shaped European reservoir in late summer. Int Rev Hydrobiol 91:178–194

Vilizzi L (1998) Observations on ontogenetic shifts in the diet of 0+ carp, *Cyprinus carpio* L., from the River Murray, Australia. Folia Zool 47:225–229

Viroux L (1997) Zooplankton development in two large lowland rivers, the Moselle (France) and the Meuse (Belgium), in 1993. J Plankton Res 19:1743–1762

Voss R, Koster FW, Dickmann M (2003) Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fish Res 63:97–111

Wang N, Appenzeller A (1998) Abundance, depth distribution, diet composition and growth of perch (*Perca fluviatilis*) and burbot (*Lota lota*) larvae and juveniles in the pelagic zone of Lake Constance. Ecol Freshw Fish 7:176–183

Wańkowski JWJ, Thorpe JE (1979) Spatial distribution and feeding in Atlantic salmon, *Salmo salar* L. juveniles. J Fish Biol 14:239–247

Wanzenböck J (1995) Changing handling times during feeding and consequences for prey size selection of 0+ zooplanktivorous fish. Oecologia 104:372–378

Wanzenböck J, Scheimer F (1989) Prey detection in cyprinids during early development. Can J Fish Aquat Sci 46: 995–1001

Wanzenböck J, Mikheev VN, Pasternak AF (2006) Modification of 0+ perch foraging behaviour by indirect cues of predation risk. Ecol Freshw Fish 15:118–124

Warburton K, Retif S, Hume D (1998) Generalists as sequential specialists: diets and prey switching in juvenile silver perch. Environ Biol Fish 51:445–454

Ward AJW, Axford S, Krause J (2002) Mixed-species shoaling in fish: the sensory mechanisms and costs of shoal choice. Behav Ecol Sociobiol 52:182–187

Ward AJW, Webster MM, Hart PJB (2006) Intraspecific food competition in fishes. Fish Fish 7:231–261

Weatherley NS (1987) The diet and growth of 0-group dace, *Leuciscus leuciscus* (L.), and roach, *Rutilus rutilus* (L.), in a lowland river. J Fish Biol 30:237–247

Weatherley NS (1989) The diet and growth of 0-group flounder, *Platichthys flesus* (L.), in the River Dee, North Wales. Hydrobiologia 178:193–198

Welker MT, Pierce CL, Wahl DH (1994) Growth and survival of larval fishes: roles of competition and zooplankton abundance. Trans Am Fish Soc 123:703–717

Welton JS, Mills CA, Rendle EL (1983) Food and habitat partitioning in two small benthic fishes, *Noemacheilus barbatulus* (L.) and *Cottus gobio* L. Arch Hydrobiol 97: 434–454

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Evol S 15:393–425

Werner EE, Hall DJ (1974) Optimal foraging and the size selection of prey by bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042–1052

Whiteside MC, Doolittle WL, Swindoll CM (1985) Zooplankton as food resources for larval fish. Verh Int Verein Theor Angew Limnol 22:2523–2526

Williams DD (1981) The first diets of postemergent brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) alevins in a Quebec river. Can J Fish Aquat Sci 38:765–771

Wilson JPF (1984) The food of the pollan, *Coregonus autumnalis pollan* Thompson, in Lough Neagh, Northern Ireland. J Fish Biol 24:253–261

Winfield IJ (1986) The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophthalmus*, and perch, *Perca fluviatilis*. J Fish Biol 29(Suppl A):37–48

Winfield IJ, Townsend CR (1983) The cost of copepod reproduction–increased susceptibility to fish predation. Oecologia 60:406–411

Winfield IJ, Townsend CR (1988) Factors affecting prey selection by young bream *Abramis brama* and roach *Rutilus rutilus*: insights provided by parallel studies in laboratory and field. Environ Biol Fish 21:279–292

Winfield IJ, Peirson G, Cryer M, Townsend CR (1983) The behavioural basis of prey selection by underyearling bream (*Abramis brama* (L.)) and roach (*Rutilus rutilus* (L.)). Freshw Biol 13:139–149

Winfield IJ, Bean CW, Hewitt DP (2002) The relationship between spatial distribution and diet of Arctic charr, *Salvelinus alpinus*, in Loch Ness, UK. Environ Biol Fish 64:63–73

Wolfram-Wais A, Wolfram G, Auer B, Mikschi E, Hain A (1999) Feeding habits of two introduced fish species (*Lepomis gibbosus*, *Pseudorasbora parva*) in Neusiedler See (Austria), with special reference to chironomid larvae (Diptera: Chironomidae). Hydrobiologia 408:123–129

Wood PJ, Armitage PD (2004) The response of the macroinvertebrate community to low-flow variability and supraseasonal drought within a groundwater dominated river. Arch Hydrobiol 161:1–20

Wood PJ, Boulton AJ, Little S, Stubbington R (2010) Is the hyporheic zone a refugium for macroinvertebrates during severe low flow conditions? Fund Appl Limnol 176: 377–390

Wootton RJ (1990) Ecology of teleost fishes. Chapman and Hall, London

Wu L, Culver DA (1992) Ontogenetic diet shift in Lake Erie age-0 yellow perch (*Perca flavescens*): a size-related response to zooplankton density. Can J Fish Aquat Sci 49:1932–1937

Wyche CJ, Shackley SE (1986) The feeding ecology of *Pleuronectes platessa* L., *Limanda limanda* (L.) and *Scophthalmus rhombus* (L.) in Carmarthen Bay, South Wales, UK. J Fish Biol 29:303–311

Zaret TM, Rand AS (1971) Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:336–342

Žiliukienė V, Ziliukas V (2006) Feeding of early larval pike *Esox lucius* L. reared in illuminated cages. Aquaculture 258:378–387

Zimmerman C, Mosegaard H (1992) Initial feeding in migratory brown trout (*Salmo trutta* L.) alevins. J Fish Biol 40:647–650