# Intraspecific food competition in fishes

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## Abstract

Intraspecific food competition exerts powerful selective forces on all animals; successful foragers thrive relative to weaker conspecifics. Understanding competition is therefore fundamental both to ecological insight and to conservation efforts. Fish are adaptable and tractable experimental organisms, offering excellent model systems for studies on competition, and they lend themselves to two approaches: (i) studies of short-term competition, which quantify the components of behavioural interactions; (ii) studies of long-term interactions, in which the indeterminate nature of fish growth makes it possible to measure rates directly and correlate them with competitive success. The nature and the intensity of competition vary according to resource characteristics and distributions in time and space, the ecological context, and the relative competitive abilities of the foragers. Second-order effects, such as winner and loser consequences, add to the complexity and frustrated early attempts to develop realistic models of intraspecific competition. Recently, however, considerable advances have been made in both laboratory and field studies on fishes adding to our understanding of these interacting effects. At the same time, the application of individual-based modelling offers the prospect of progress towards greater realism and accuracy in predicting competitive outcomes. This review draws together a wide and disparate literature on intraspecific competition in fishes to facilitate the work of both empiricists and theoreticians towards these important goals.

In the short term, competing individuals may adopt different behavioural strategies and feeding patterns or establish dominance hierarchies and feeding territories. In the longer term, competition can drive character displacement and the formation of species pairs and fish provide some of the most compelling examples of these processes in evolutionary biology. The challenge for the future is to further develop our understanding of the relationship between the competitive environment and the responses of fishes, particularly with closer co-operation between empiricists and theoreticians, and to apply this knowledge to aquaculture and to better management of exploited fish stocks.

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## Introduction

Intraspecific food competition may be generally defined as the attempt by two or more conspecifics to feed on a critical and limited food resource. Such competition may be intense and is largely unavoidable because, with a few exceptions, conspecifics occupy the same niche. Intraspecific competition exerts powerful selective forces and is central to the biology of a species, playing a vital role in limiting populations, eliminating unfit genes and driving evolution.

Fish make excellent models for the study of competition for three main reasons: (i) their tractability as experimental animals; (ii) the direct effects of competitive success in fish may be measured in terms of fecundity and increases in body length, which is rare amongst vertebrates; and (iii) the size of many species of fish and their short-generation times allow an insight into larger-scale processes in free-living populations. These and other factors have enabled researchers to examine many different areas of competition in fish both from short-term and long-term perspectives and this has resulted in a substantial literature. It was the aim of this review article to provide an overview of the various areas within this literature and to link them by their common theme of intraspecific competition.

We consider, first, how a number of factors, including food characteristics and distribution, individual competitive ability, strategic behaviour and the broader ecological context of the competitive interaction influence intraspecific competitive outcomes, and second, the ecological and evolu-tionary impact of intraspecific competition. We will provide a brief overview of classic theoretical work before reviewing the modelling and empirical approaches to predicting the outcomes and ecological effects of intraspecific food competition. For the purpose of this review we have had to apply our judgement in categorizing certain areas, for example, we separate relative competitive ability, which is a measure in the context of the local population, from dominance, which implies greater complexity in terms of social interactions. Intraspecific food competition is an extremely varied and disparate field; our intention, therefore, is to provide an overview of the topic in the hope of stimulating other fish biologists to produce more comprehensive, up-to-date reviews of each of our main subject headings.

## Types of competition

Interference can be said to occur when by increasing its own feeding rate, an individual decreases that of another. This might come about in one of three different ways by: (i) exploitation competition; (ii) scramble competition; or (iii) contest competition. In the case of exploitation competition, there is usually no direct interaction between competitors, instead one individual exploits and depletes a food patch before a second individual arrives. In scramble competition, each foraging individual can detect its competitors and attempts to be the first to obtain a food item. Contest competition is similar to scramble competition except that it involves direct aggression between the competitors.

## Resource distribution and characteristics and the ideal free distribution

The type of competition is determined largely by the distribution of the food resource in time and space (Milinski and Parker 1991). If food items are distributed quite evenly then competitive interactions are less likely than if they are clumped. As resource distributions become more heterogeneous, so do the distributions of those animals that require that resource, increasing the probability that direct interactions and competition will occur. As competitors aggregate at a food patch, they deplete the resources by exploitation and may begin to compete over single prey items, initiating scramble or contest conditions. When this occurs, competitors are likely to select the most profitable food items first in order to maximize their net energy intake rate, as predicted by optimal diet theory. If competition reduces an individual's rate of feeding below a critical level, it may decide to leave and attempt to locate another patch and the distribution of individuals in the local population will theoretically mirror the resource landscape.

Fretwell and Lucas (1970) proposed the theory of ideal free distribution (IFD) to describe the habitat selection patterns of animals and their relationships to available resources. Individuals are 'free' in that there is no cost to moving between patches and have an 'ideal' awareness of patch profitabilities. In the simplest model all competitors are equal. A number of studies have shown that foragers distribute between patches according to the number of prey items supplied, known as the 'input-matching rule' (see Tregenza 1995).

A number of modifications of the classical model have been made to add a greater degree of realism. The most simple models of IFD assume a continuous supply of food to a patch. A more common situation in the real world is that competitors deplete a patch as they feed, so that the profitability of a patch is not fixed over time, requiring competitors to frequently reassess patch choice (Kacelnik et al. 1992). Studies by Mittelbach (1981) and Werner et al. (1983) demonstrated that bluegill sunfish (*Lepomis macrochirus*) were able to accurately assess fluctuating patch profitability and switch when required to maximize feeding rates. In addition, allocating a weighting to each competitor in the model recognizes that competitive ability varies between individuals (Parker and Sutherland 1992; see also Hugie and Grand 1998). The negative influence of interference between competitors on feeding rates at a patch has also been built into various models (Ruxton et al. 1992; van der Meer and Ens 1997).

The costs associated with a given patch may also vary. For example, Tyler and Gilliam (1995) investigated food patch choice by blacknose dace (*Rhinichthys atratulus*) in streams where flow rates, and hence energetic costs, varied between patches. The model predicted observed habitat use patterns when these costs were built in. Predation risk is another cost which may vary between patches. A number of studies have investigated the extent to which fish are prepared to tradeoff risk against patch profitability. Abrahams and Dill (1989) examined this principle using guppies (*Poecilia reticulata*) comparing first, the distribution of guppies between equally profitable patches where one patch had a predator in close proximity, and second, the increase in the profitability of the risky patch required to even out the distribution of guppies between the sites. Gilliam (1982) proposed a simple model to predict habitat use under a predation risk where fitness is maximized when the ratio of mortality rate to growth rate is minimized. This model was tested in a subsequent study on creek chub (*Semotilus atromaculatus*) which found that fish were able to evaluate the risks and rewards of a patch and make a habitat choice accordingly (Gilliam and Fraser 1987).

The simplicity of the IFD is at once both the reason for its success and its greatest limitation. It provides a framework for making basic predictions about the distribution of competitors in a habitat yet cannot replicate the complexity of the real world (although see Earn and Johnstone 1997). The progression of individual-based modelling approaches offers perhaps our best chance of fully understanding the distribution of unequal competitors under different resource distribution and competition conditions (Jackson et al. 2004).

## Predicting the outcome: phenotypes and competitive ability

### Competitors with different phenotypes

Competition for scarce resources rarely results in equal shares for all. Phenotypic variation in competitive situations often further affects the distribution of food rewards between competitors. Where, as in most cases, species have discrete breeding seasons, the population may be made up of multiple cohorts. Interactions between these cohorts play a

major role in the overall population dynamics of the species (Mittelbach 1981, 1983; Persson 1985). Inter-cohort competition in fishes is characteristically asymmetric: the effects of large fish on small fish are different from the effects of small fish on large (Connell 1983; Schoener 1983) (see Table 1). Large fish tend to forage more efficiently than small fishes, although smaller fishes have lower metabolic requirements (Hamrin and Persson 1986). Webster (2004) studied inter-cohort interactions in the fairy basslet (*Gramma loreto*), specifically the fate of newly settled juveniles as a function of the density of adult conspecifics. Juvenile mortality was positively correlated with adult density, possibly as a result of being forced to accept positions at the rear of aggregations which are associated with lower feeding rates and where attacks by predators are concentrated. Inter-cohort competition among vendace (*Coregonus albula*) produces regular oscillations in the population structure. Year-class strengths fluctuate as a function of food availability and the intensity of inter-cohort competition. Juvenile survival is negatively correlated with the size of the adult population as the latter heavily deplete zooplankton, the common food resource (Sandlund *et al.* 1991).

Variation in size is an important predictor of competitive ability both within and between cohorts (see Table 1). Large fish are more effective foragers than small fish, possessing higher visual acuity (Walton *et al.* 1994) and being faster swimmers (Beamish 1978), both of which may enable them to prevail in scramble situations and to outcompete smaller fish where there is direct competition over single prey items (Ward and Krause 2001; Szabo 2002). Milinski (1982) showed that the fastest swimming stickleback in a group captured the most prey items. Post *et al.* (1999) reported that both competitive ability and survivorship were closely related to body length in rainbow trout. A number of papers have studied the implications of body length differences for food competition among coral reef fishes, for example, the feeding rate of large humbug damselfish (*Dascyllus aruanus*) is higher than that of their smaller conspecifics (Forrester 1991). Whiteman and Cote (2004) found the same pattern in cleaning gobies (*Elacatinus prochilos*): larger, competitively dominant individuals achieved the highest feeding rates. Results of studies on the effects of size differences on competitive ability are prone to cause and effect arguments, however: are fish good competitors because they are large, or

large because they are good competitors? A study by Huntingford *et al.* (1990) on Atlantic salmon concluded that greater body size was an effect of dominance rather than a cause and that metabolic rate was a more effective predictor. A number of studies have since considered in more detail the physiological components of dominance (see Sloman and Armstrong 2002 for a review) and we return to this theme in a subsequent section.

A number of investigators have studied resource competition between different trophic morphs in the laboratory. Schluter (1993) compared the feeding performance of benthic and pelagic morphs of three-spined sticklebacks under different conditions. The benthic morphs feed more efficiently in the benthic habitat and vice versa, providing clear evidence of the importance of intraspecific competition in producing and segregating these morphs. Similar results have been obtained in other species, where each morphotype performs best in the habitat to which it is specialized (Arctic charr, *Salvelinus alpinus*: Malmquist 1992; perch, *Perca fluviatilis*: Svänback and Eklöv 2003).

Other elements of phenotypic variation appear to be less associated with competitive ability. Where individuals are matched in size there appears to be little difference between the sexes in terms of competitive ability although there is some evidence to suggest that juvenile male salmonids are more aggressive than females (Johnsson and Akerman 1998) and grow more quickly (Yamamoto 2004) which may indicate differences in competitive abilities between the sexes (but see Dittman *et al.* 1998; Johnsson *et al.* 2001).

Thorpe *et al.* (1992) reported that competitive ability in juvenile Atlantic salmon was more related to an individual's aggression than its size; however, these aggressive individuals ultimately grew more quickly than their competitive subordinates.

Finally, in addition to the phenotypic differences highlighted above, the physiology of fish may also differ between individuals. Mccarthy *et al.* (1994) reported variation among rainbow trout (*Oncorhynchus mykiss*) in terms of their protein processing efficiency; those that process most efficiently show faster growth rates for the same ration (see also Silverstein *et al.* 1999; Kolstad *et al.* 2004). As growth rate is one of the most important currencies in the early stages of a fish's life, this may level out the effects of competition for individuals that process their food most efficiently. In addition, as body length is a powerful predictor of competitive ability,

**Table 1** Competitive ability: competitors with different phenotypes.

| Reference | Scientific name | Common name | Location | Method | Outcome |
|---|---|---|---|---|---|
| Amundsen *et al.* (2001) | *Salmo salar* | Atlantic salmon | F | Stomach content analyses | Dietary overlap between three different age classes suggests inter-cohort competition for prey |
| Bozek *et al.* (1994) | *Oncorhynchus clarki pleuriticus* | Cut-throat trout | F | Stomach content analyses | Different size classes consumed different taxa and sizes of prey items; however, competition may occur between juvenile and adult fish |
| Castro and Caballero (1994) | *Diplodus sargus cadenati* | White seabream | L | Study of aggression, feeding behaviour and growth in experimental groups | A linear hierarchy in which dominant fish were more aggressive, was observed. Larger fish were seen to dominate, and to grow at greater rates |
| Gill and Hart (1996) | *Gasterosteus aculeatus* | Three-spined stickleback | L | Study of the effect of body size upon prey contest outcomes | Larger fish, with a greater gape width were seen to be more successful when contesting prey |
| Goldan *et al.* (2003) | *Sparus aurata* | Gilthead sea bream | L | Study of feeding behaviour and growth in experimental groups | Dominance hierarchies arose faster in mixed size groups. Dominant fish were more aggressive feeders and grew more rapidly |
| Greenberg *et al.* (1997) | *Salmo trutta* | Brown trout | L | Analysis of habitat and prey use by two size classes of trout | Trout displayed differences in prey and habitat preference when alone and when with individuals of a different size class |
| Hart and Salvanes (2000) | *Gadus morhua* | Cod | L | Study of individual variation in foraging competitive ability of juvenile cod | Individuals varied in their competitive ability. During winter, larger fish were seen to be better competitors, but during summer size did not affect competitive ability |
| Harvey and Nakamoto (1997) | *Oncorhynchus mykiss* | Rainbow trout | FE | Enclosure study of differences in growth rate of equal biomasses of two size classes of trout with deep and shallow treatments | Larger trout were seen to grow faster when housed with small individuals in deeper water, but more slowly in shallow water treatments suggesting an effect of both habit and intercohort competition |
| Hjelm and Persson (2001) | *Rutilus rutilus* | Roach | F | Study of the effects of inter-cohort competition | Smaller individuals were more efficient at handling zooplankton then larger ones, which exploited benthic prey in the littoral zone to a greater extent. However, both size classes grew more slowly in mixed cohort treatments, suggesting some competition |
| Jenkins *et al.* (1999) | *Salmo trutta* | Brown trout | F | Study of growth rates, survival and mortality in different size and age classes | Body length and mass of young of the year in autumn was negatively related to density; however, mortality and emigration were not |
| Keeley (2001) | *Oncorynchus mykiss* | Rainbow trout | L | Competition study in artificial channels | Smaller fish occupied poorer feeding positions and emigrated from the population when given the opportunity |
| Kristiansen (1999) | *Salmo trutta*; *Oncorhynchus mykiss* | Brown trout; rainbow trout | L | Study of heterogeneity in food resource partitioning in single species treatments | In both species larger individuals obtained a larger mean share of food over time, and were less variable in terms of proportional food consumption per individual meal |
| Mikheev and Wanzenbock (1999) | *Rutilus rutilus* | Roach | L | Study of feeding rate and behaviour of different size classes of juvenile roach | Intra-cohort variation in prey size selection was seen and was hypothesized to be related to individual social rank |
| Mol (1995) | *Hoplosternum littorale*; *Hoplosternum thoracatum*; *Callichthys callichthys* | Hassar (two species); Cascarudo | F | Stomach content analysis of three sympatric closely related species | Intraspecific inter-cohort class diet overlap was seen to be of less importance than was interspecific competition. High prey abundance may have served to minimize competition |
| Nakano *et al.* (1991) | *Oncorhynchus masou masou* | Masu salmon | F | Study of growth patterns in individuals using mark and recapture in a natural channel | Larger individuals grew more rapidly than smaller ones within pools, probably as a result of intraspecific competition within individual pools |
| Nordeide and Fossa (1992) | *Gadus morhua* | Atlantic cod | F | Stomach content analysis of prey overlap between wild and captive reared cod of the same year-class, and different year-classes of wild cod | Diet overlap, and potential for competition was seen to be greater between wild and captive reared fish of the same year-class, than between wild year-classes |
| O'Gorman *et al.* (1997) | *Alosa pseudoharengus* | Alewife | F | Investigation of factors affecting population demographics of the alewife in a system in which the pelagic community is undergoing change | Competition for zooplankton among younger cohorts was seen to affect growth of age-1 alewives |

**Table 1** Continued.

| Reference | Scientific name | Common name | Location | Method | Outcome |
|---|---|---|---|---|---|
| Pfister (2003) | *Cottus asper* | Prickly sculpin | L | Study of growth and survival of juveniles in presence of adults | Growth, survival and individual variation in growth rates of juveniles was lower in the presence of adults |
| Post *et al.* (1999) | *Oncorhynchus mykiss* | Rainbow trout | L | Study of interactions within and among size classes in experimental populations | Larger individuals outcompeted smaller conspecifics for prey |
| Rieman and Myers (1992) | *Oncorhynchus nerka* | Kokanee | F | Study of the effects of fish density and relative aquatic productivity on growth | Density-dependant limitations on growth were seen in older fish only |
| Sanderson *et al.* (1999) | *Perca flavescens* | Yellow perch | F | Study of year-class representation over several years | Older juvenile year-classes suppress younger cohorts through prey competition and cannibalism |
| Sandlund *et al.* (1991) | *Coregonus albula* | Vendace | L | Repeated sampling of population to determine demographic change over several years | Regular year-class strength oscillations were detected. These were the result of competition between young of the year and adult year classes and resulted from commercial over exploitation of adult fish |
| Szabo (2002) | *Oligocottus maculosus* | Tidepool sculpin | L and F | Laboratory and field study of body size, distribution and competitive ability | Larger fish outcompete smaller conspecifics for prey and cover, forcing them from favoured lower tide pools to those higher up the shore |
| Webster (2004) | *Gramma loreto* | Fairy basslet | F | Experimental manipulation of natural groups | Competition with adults forces juvenile fish to the rear of the shoal where prey encounters are lower and predation risk is higher |
| Zidowitz and Fock (2004) | *Zenopsis conchifer* | Silvery John Dory | F | Stomach content analyses | Larger specimens may switch from pelagic to benthic prey to avoid intraspecific competition |

efficient food processing may indirectly feedback to produce high competitive ability relative to a cohort.

## Competitors with matching phenotypes

Intraspecific competition is often cited as one of the main reasons that social fish prefer to associate with conspecifics whose phenotypes match their own (Krause and Ruxton 2002). However, even when the competitors are matched in terms of their phenotype their competitive ability may not be (Milinski 1979) (see Table 2). Some individuals may theoretically be consistently better competitors than others, in other words, they will be less susceptible to interference (Milinski and Parker 1991), usually measured as the reduction in feeding rate with increasing competitor density. Such individuals may be said to have a high competitive ability, relative to the average competitive ability of their conspecifics (Lomnicki 1980, 1988; Tyler and Rose 1994). Individuals which display a high relative competitive ability and which therefore feed more effectively under competition are often assumed to have higher fitness. However, this assumption only holds if an individual's relative competitive ability is stable over its lifetime and is consistent across different ecological contexts.

In a study on juvenile rainbow trout (*Oncorhynchus mykiss*), McCarthy (2001) reported that relative competitive ability was positively correlated with metabolic rate and that relative differences in metabolic rate between individuals remained stable, suggesting that relative competitive ability remains the same over time. Recent studies have found that an individual's boldness, its willingness to expose itself to risk (Wilson *et al.* 1994; Wilson 1998), is positively correlated with its competitive ability (three-spined sticklebacks, *Gasterosteus aculeatus*: Ward *et al.* 2004a,b; Eurasian perch, *Perca fluviatilis*: Westerberg *et al.* 2004). A further study on three-spined sticklebacks (Bell and Stamps 2004) suggests that boldness may not be a fixed trait throughout an animal's life, raising the interesting possibility that an individual's competitive ability, relative to its age cohort, may also vary over time.

The immutability of an individual's competitive ability depends on the numbers of its competitors in the local environment and their own competitive ability because it is a relative measure, rather than an absolute. Feeding group size is known to affect competitive ability (Humphries *et al.* 1999a; Ruxton 1999). However, the precise effects of an increase in

**Table 2** Competitive ability: competitors with matching phenotypes.

| Reference | Scientific name | Common name | Location | Method | Outcome |
|---|---|---|---|---|---|
| Anderson and Sabado (1999) | *Brachyistius frenatus* | Kelp perch | FE | Comparison of growth rates in sibling and non-sibling larvae groups | No differences in growth rates or variation were detected between treatments |
| Beeck et al. (2002) | *Perca fluviatilis* | Eurasian perch | F | Stomach content analyses and growth rate monitoring | Growth rates in young of the year perch were seen to vary. Faster growing individuals made an early dietary shift to piscivory, avoiding later intraspecific competition with zooplankton feeding conspecifics |
| Canario et al. (1998) | *Sparus aurata* | Gilthead seabream | L | Study of growth rates in different density treatments | Slower growth rates were observed at higher densities |
| Damsgard et al. (1997) | *Salvelinus alpinus* | Arctic charr | L | Study of factor affecting variation in food intake in hatchery reared strains of Arctic charr | Reduction in prey provision and/or water flow rate was seen to increase antagonistic interaction and variability in food intake between individuals |
| Dieterich et al. (2004) | *Perca fluviatilis; Gymnocephalus cernuus* | Eurasian perch; Ruffe | L | Study of the effects of the presence of zebra mussels (*Dreissena polymorpha*) on foraging success in mixed and single species treatments | The increased habitat complexity caused by the presence of the mussel beds led to lower foraging rates when either species competed with conspecifics |
| Hakoyama and Iguchi (2001) | *Oncorhynchus masou masou* | Masou salmon | L | Study of temporal changes in the distribution of foragers between predictable prey patches | The distribution of foragers changed from the ideal free distribution, to a despotic distribution, determined by aggression from dominant individuals. Dominance arose through differences in growth rates and the emergence of larger individuals |
| Hojesjo et al. (1998) | *Salmo trutta* | Sea trout | L | Comparison of food intake of groups of familiar and non-familiar fish | Groups comprising familiar fish were seen to have higher food intakes |
| McCarthy (2001) | *Oncorhynchus mykiss* | Rainbow trout | L | Study of the effects of metabolic rate upon competitive ability in pairs of competing fish | The partner with the higher metabolic rate was seen to be dominant in the majority of pairings |
| Metcalfe and Thomson (1995) | *Phoxinus phoxinus* | European minnow | L | Study of relative competitive abilities of size-matched fish and association preferences of intermediately ranked individuals | Individuals differed in competitive ability and intermediates showed association preferences for poorer competitors |
| Milinski (1979) | *Gasterosteus aculeatus* | Three-spined stickleback | L | Study of the distribution of fish between prey patches of differing yield | Individuals arranged themselves between prey patches according the ideal free distribution, thus maximizing prey returns and minimizing competition levels |
| Milinski (1984) | *Gasterosteus aculeatus* | Three-spined stickleback | L | Study of the feeding rates of individually tagged fish | Within groups, some individuals consistently captured and consumed more prey than did others |
| Milinski (1988) | *Gasterosteus aculeatus* | Three-spined stickleback | L | Study of the distribution of fish between prey patches of differing yield where fish are known to vary in terms of competitive ability | Individuals arranged themselves between prey patches according the ideal free distribution. Better competitors chose optimum prey patches more rapidly, feeding at a greater rate, whereas poorer competitors switched frequently |
| Olsen and Jarvi (1997) | *Salvelinus alpinus* | Arctic charr | L | Study of levels of aggression when foraging with all sibling and mixed-sibling and non-sibling groups | Aggression following periods of feeding was higher in mixed groups than in all sibling groups, suggesting kinship mediates competitive intensity |
| Partridge and DeVries (1999) | *Lepomis macrochirus* | Bluegill sunfish | F | Analyses of growth and mortality in larval bluefish | Growth and mortality are affected by larval density and intraspecific competition for zooplankton |
| Power (1984) | *Ancistrus spinosus* | Armoured catfish | F | This species feeds upon algae growing upon rocky substrates. Pools that are sun-exposed have more rapidly replenishing algae mats than do shaded areas. This study examined the distribution of fish between these faster and slower replenishing areas | Individuals arranged themselves between prey patches according the ideal free distribution, with more fish present on the more rapidly replenishing sites, thus maximizing prey returns and minimizing competition levels |

**Table 2** Continued.

| Reference | Scientific name | Common name | Location Method | Outcome |
|---|---|---|---|---|
| Resetarits (1995) | *Cottus bairdi; Cottus carolinae; Etheostoma flabellare* | Mottled sculpin; Kanawha sculpin; Fantail darter | L | Study of the effects of intra- and interspecific competition upon survival, growth and condition in the mottled sculpin | Intraspecific competition, and competition from the Kanawha sculpin had similar effects upon mottled sculpin survival and growth but the effect of competition from fantail darter was seen to be stronger |
| Ridgeway and Chapleau (1994) | *Perca flavescens* | Yellow perch | F | Investigation of factors affecting a stunted monospecific population | Intraspecific competition was considered to be a contributing factor |
| Rincon and Grossman (2001) | *Clinostomus funduloides* | Rosyside dace | L | Study of differences in intraspecific aggression and habitat use in a drift feeding fish | Individuals varied in terms of aggressive behaviour exhibited, and more aggressive individuals acquired better drift-feeding positions within the channel |
| Staffan et al. (2002) | *Perca fluviatilis* | Eurasian perch | L | Study of individual prey intake and aggression levels within experimental groups | Individual levels of food intake were seen to vary |
| Tyler (1993) | *Rhinichthys atratulus* | Blacknose dace | L | Flow-tank study of the effects of water velocity, group size, and prey arrival rate upon capture rate | Advantages gained by foraging in sites with optimal water velocity decreased as the number of competitors increased |
| Utne-Palm and Hart (2000) | *Gasterosteus aculeatus* | Three-spined stickleback | L | Study of aggression in familiar and unfamiliar pairs of fish sharing a common food resource | Levels of aggression were seen to be lower in familiar pairs |
| van Havre and Fitzgerald (1988) | *Gasterosteus aculeatus* | Three-spined stickleback | F | Observation of shoaling preferences of hungry and satiated females | Hungry individuals joined smaller shoals, trading lower levels of prey competition against increased predation risk |

the size of the feeding group on relative competitive ability are less clear. Models have proposed, variously, an increase in the disparity between the competitive abilities of two phenotypes with increasing group size (the 'phenotype scales slope' model) or general consistency in their competitive ability, relative to one another, with increasing group size (the 'phenotype scales intercept' model) (Sutherland and Parker 1985, 1992; Parker and Sutherland 1986). Empirical tests of these principles using fish have tended to conclude rather that increasing group size decreases the differences between individuals of high, and individuals of low, relative competitive ability (*Aequidens portalegrensis*: Tregenza *et al.* 1996; European minnows, *Phoxinus phoxinus*: Humphries *et al.* 1999a). One possible reason suggested by Tregenza *et al.* (1996) is a change in the competitive regime from contest competition at low densities, to scramble competition at higher densities. The complex relationship between an individual's relative competitive ability and feeding group size is as yet poorly understood and is likely to be context dependent (Humphries *et al.* 2000).

The assumption of Parker and Sutherland's (1986) model that an individual's foraging efficiency at a given resource is proportional to its relative competitive ability can lead to some counter-intuitive predictions. If a feeding group is joined by some poor competitors, for example, this will have the effect of increasing the relative competitive ability of the best competitors and will theoretically cause their intake rate to increase with group size. A modification of the model (van der Meer 1997) proposes that foraging efficiency is proportional to the group's total competitive ability which will always cause individual intake to decline with increasing group size, which is more likely to represent conditions in the real world.

In addition to fluctuations in relative competitive ability over time, it may also vary according to the ecological context. In a study on the cichlid fish, *Tilapia zillii*, Humphries *et al.* (1999b) demonstrated that the competitive ability of individuals in a single input situation was not correlated with competitive ability under dual input conditions. The type of competition changes according to the resource availability and distribution and according to the density of competitors. The relative competitive ability of an individual in a given situation may be dependent upon a particular characteristic, for example, the ability to detect prey rapidly may be important in scramble conditions whereas in a

contest situation size and/or strength are likely to aid success. The spatial distribution of resources affects competition in the pygmy sunfish, *Elassoma evergladei* (Rubenstein 1981), which switched between territorial defence of clumped resources to a situation more akin to scramble competition when the resources were more dispersed. In the medaka, *Oryzias latipes*, a clumped temporal distribution of food caused increased aggression and monopolization by comparison to a more even rate of food delivery (Bryant and Grant 1995). Where there is variation within a population in terms of behaviour and morphology, it is likely that some individuals will carry traits which allow them to prevail in some specific conditions but few will prevail in all. In some conditions, specialization may eventually lead to character displacement (see below).

Parasitism may also affect competitive ability. In a study on three-spined sticklebacks, Barber and Ruxton (1998) compared the competitive abilities of non-parasitized individuals with those that were infected with the cestode, *Schistocephalus solidus*, under different types of competitive interactions. They found that whilst there was no difference in the number of prey items taken by parasitized and by non-parasitized fish when the prey items were presented sequentially, the non-parasitized fish were more successful when there was direct competition over a single-prey item and when prey were presented in dense patches, the latter potentially because of physical limitations placed on the host's abdominal capacity by *Schistocephalus solidus*, affecting the ability to consume large numbers of prey items. Milinski (1984) described how sticklebacks infected with *Schistocephalus solidus* switched their prey preference to concentrate on smaller, lower quality prey items, possibly to militate against the effects of competition from uninfected individuals which preferred larger items (although see Cunningham *et al.* 1994). This apparent preference for lower quality food items seems to be corroborated by Tierney's (1994) stomach content analysis on a free-ranging population infected with *Schistocephalus solidus*.

Parasites can affect the competitive ability of their hosts in a variety of ways. Dace (*Leuciscus leuciscus*) infected with the eyefluke, *Diplostomum spathaceum*, are much less efficient food competitors than uninfected conspecifics, making a higher proportion of failed attacks at prey items. Reduced swimming performance, another factor which is likely to significantly affect an individual's relative compet-

itive ability, is a common result of parasitism (Barber *et al.* 2000). The extent of the effect that parasitism will have on the competitive ability of its host will depend on the parasite itself: the cost it imposes may directly affect host-feeding motivation (Giles 1987) and its manner of transmission can have implications for risk-taking behaviour in the host (Lafferty and Morris 1996). In many cases, parasites may have little or no effect on the relative competitive ability of their host, for example, Milinski (1985) has shown that sticklebacks infected with the microsporidian *Glugea* are able to compete successfully with uninfected conspecifics.

## Temporal variation in competitive ability

Competitive ability is not constant but may vary over time and for this reason, static foraging models fail to accurately predict real behaviour patterns (Hart and Gill 1993). This is because fish, like all animals, make behavioural adjustments in response to temporal differences in their internal state. Hungry fish tend to forage more actively than satiated ones and feed at a greater rate (Beukema 1968). The corollary of this with regard to the competitive environment is that as the better competitors become satiated they gradually decrease their foraging effort or switch to different prey sizes whereas weaker competitors maintain their effort. Motivation to feed may therefore be more important than competitive ability in some circumstances as a long-term predictor of an individual's rate of energy acquisition (Hart and Gill 1993; Gill 2003). The motivation to feed may also vary between different stages of an individual's life history. Migrating salmon, for example, generally cease feeding when they reach freshwater, and the time budgets of male sticklebacks alter when engaged in defending a nest, during which time they display reduced feeding motivation (Hart 1993).

## Consequences of variations in competitive ability

### Dominance hierarchies

One consequence of variation in individuals' relative competitive abilities is the formation of stable social dominance hierarchies (Huntingford and Turner 1987) (see Table 3). Dominant individuals near the top of the hierarchy obtain a disproportionate share

**Table 3** Dominance hierarchies.

| Reference | Scientific name | Common name | Location | Method | Outcome |
|---|---|---|---|---|---|
| Alanara et al. (2001) | *Salmo trutta* | Brown trout | L | Study of temporal segregation in feeding patterns | Higher ranking individuals fed at more profitable times than did subordinates |
| Carrieri and Volpato (1991) | *Oreochromis niloticus* | Nile tilapia | L | Study of hierarchy as determined by both the observed strike rates against food items and the actual ingestion rate | The correlation between strike rate and ingestion rate was low in lower hierarchical ranks. This suggests that some patterns of hierarchy may not be linear, as previously assumed |
| Carter and Davies (2004) | *Clarias gariepinus* | African catfish | L | Study of the effects of novel food upon food intake and dominance rank | Nonlinear dominance hierarchies based upon various agonistic behaviours were seen. Dominance rank and prey intake did not correlate |
| Castro and Caballero (1994) | *Diplodus sargus cadenati* | White seabream | L | Study of aggression, feeding behaviour and growth in experimental groups | A linear hierarchy in which dominant fish were more aggressive, was observed. Larger fish were seen to dominate, and to grow at greater rates |
| Goldan et al. (2003) | *Sparus aurata* | Gilthead sea bream | L | Study of feeding behaviour and growth in experimental groups | Dominance hierarchies arose faster in mixed size groups. Dominant fish were more aggressive feeders and grew more rapidly |
| Harwood et al. (2003) | *Salmo salar* | Atlantic salmon | L and F | Study of individual dominance rank of fish in laboratory trial, and subsequent growth rate 2 months after release into a natural stream | No relationship between dominance rank and growth rate was seen |
| Hollis et al. (2004) | *Trichogaster trichopterus* | Blue gourami | L | Study of the use of learned cues and sneaky tactics by socially subordinate individuals | Foraging subordinates were seen to mediate attack risk and minimize fleeing time from dominants by combining information on prey location and risk of attack, and allocating foraging effort accordingly |
| Hughes (1992) | *Thymallus arcticus* | Arctic grayling | F | Study and manipulation of the feeding positions assumed by drift-feeding fish | Larger fish occupied better drift feeding positions in the channel; following the removal of a dominant fish, the next ranking individual was seen to assume its position |
| Jenkins (1969) | *Salmo trutta* | Brown trout | F | Study of habitat use by drift feeding fish of differing dominance ranks | Dominant fish assume better feeding positions with the pool, with successively poorer individuals occupying correspondingly poorer feeding positions |
| Johnsson and Akerman (1998) | *Oncorhynchus mykiss* | Rainbow trout | L | Focal fish were given the opportunity to compete either with a dominant fish which they had previously observed in competition, or one of which they had no prior experience | When focal fish had previously observed their opponent, they either escalated competition more rapidly where they were dominant or conceding sooner where they were not, compared to when competing with a fish of which they had no prior experience |
| Kadri et al. (1996) | *Salmo salar* | Atlantic salmon | FE | Sea cage study of food partitioning between fish competing for sequential prey | Food distribution among individuals was unequal and fish of similar competitive ability engaged in scramble competition for food items |
| Kristiansen (1999) | *Salmo trutta; Oncorhynchus mykiss* | Brown trout; rainbow trout | L | Study of heterogeneity in food resource partitioning in single species treatments | In both species larger individuals obtained a larger mean share of food over time, and were less variable in terms of proportional food consumption per individual meal |
| Larson et al. (2004) | *Oncorhynchus mykiss* | Rainbow trout | L | Comparison of differences in melatonin levels in socially dominant and subordinate fish | Subordinates had higher melatonin levels, indicative of higher stress levels than did dominants or controls, although this difference was only seen at night |
| Maclean and Metcalfe (2001) | *Salmo salar* | Atlantic salmon | L | Study of the effects of dominance rank upon access to food in juveniles undergoing compensatory growth | Dominant fish commanded greater access to food resources, suggesting that social rank and the relative ability of an individual to compete for prey affects the rate of compensatory growth |

**Table 3** Continued.

| Reference | Species | Common name | L/F | Study | Findings |
|---|---|---|---|---|---|
| Mikheev and Wanzenbock (1999) | *Rutilus rutilus* | Roach | L | Study of feeding rate and behaviour of different size classes of juvenile roach | Intra-cohort variation in prey size selection was seen and was hypothesized to be related to individual social rank |
| Nakano (1995) | *Oncorhynchus masou masou* | Masu salmon | F | Study of aggression, feeding behaviour and growth in experimental groups | Size-structured linear dominance hierarchies were recognized among individuals inhabiting the same stream pools |
| O'Keefe and Benfey (1997) | *Salvelinus fontinalis; Salmo salar* | Brook trout; Atlantic salmon | L | Study of competition and dominance in different size classes between diploid and triploid fish | Diploid UNB-strain brook trout were dominated over triploid fish of the same strain when fish were small, but this difference was absent in larger fish. It was not seen in salmon of any size group. This suggests the potential for a competitive disadvantage to certain triploid salmonids in early development |
| Spina (2000) | *Oncorhynchus mykiss* | Rainbow trout | F | Experimental manipulation of natural groups with removal of older, larger fish from system | Differing habitat use patterns was seen between different age groups although no explicit effect of intraspecific was detected |
| Webster and Hixon (2000) | *Gramma loreto* | Fairy basslet | F | Experimental manipulation of natural groups | Removal of the dominant fish allows a subordinate to assume dominance and benefit from higher prey returns |
| Whiteman and Cote (2004) | *Elacatinus prochilos* | Cleaning goby | F | Experimental manipulation of natural groups | Dominance hierarchies developed, with larger fish seen to dominate, and to command prime feeding territories, with newcomers assuming lower ranks irrespective of prior dominance |

of food resources, often defending resource patches, hence dominance in social fish groups is usually correlated with an individual's feeding rate (Brown 1946; Allee *et al.* 1948). In their study on social hierarchies in yellowtail (Seriola quinqueradiata) Sakakura and Tsukamoto (1998) reported that the profile of dominance ranks within social groups consistently stabilized at 10–20% dominant individuals, 10–20% intermediates and 60–80% for subordinates. This pattern was repeated even when the group was constructed using only individuals who in other groups had hitherto been dominant. Interestingly, Sakakura and Tsukamoto reported a short-term cost to dominants in establishing their rank in the form of comparative reduced growth rates. However, during the breeding season dominant individuals may suffer as their priorities shift from acquiring and defending food resources to establishing and maintaining breeding territories (Turner 1986).

In fishes, body length is a strong predictor of an individual's position in a hierarchy. The fairy basslet (*Gramma loreto*) occupies the undersides of reef ledges and feeds on drifting plankton. Large, dominant individuals take the prime feeding sites on the outer margins of these ledges and aggressively exclude their smaller subordinate competitors (Webster and Hixon 2000). Fish body length is also strongly correlated with dominance and access to food resources in sponge-dwelling cleaning gobies (*Elacatinus prochilos*) (Whiteman and Cote 2004). Booth (1995) observed the same patterns in juvenile damselfish (*Dascyllus albisella*).

Research conducted principally on salmonids over the last 15 years or so indicates that increased body size may be the effect of dominance and not its cause (Huntingford *et al.* 1990). Instead, a range of other factors are implicated, suggesting that the origins of dominance may be more complex than previously thought (see Sloman and Armstrong 2002 for a review). In a wide-ranging study on the effects of phenotype and behaviour on dominance in coho salmon, Rhodes and Quinn (1998) found that prior residency and winning experience, rearing conditions and body size all influence dominance.

In many animal species in which dominance hierarchies have been studied, physical characteristics alone are insufficient to predict rank (see review in Beaugrand 1997). Prior residency, where an individual has experience of the competitive arena, produces a kind of home advantage. Successive studies have described the importance of this

factor in mediating the outcome of contests (swordtails, *Xiphophorus helleri*: Beaugrand *et al.* 1996; Atlantic salmon: Huntingford and deLeaniz 1997; brown trout, *Salmo trutta*: Johnsson *et al.* 1999). Parker (1974) developed the concept of an individual's 'resource-holding potential' (RHP) which takes into account not only the physical properties of an individual, but also its psychological state. A recent positive experience where an individual wins a competitive encounter seems to lead to an increase in its RHP, whereas a lost encounter does the opposite. A number of studies on fish have corroborated this phenomenon (paradise fish, *Macropodus opercularis*: Francis 1983; pumpkinseed sunfish, *Lepomis gibbiceps*: Beacham and Newman 1987; green swordtail, *X. helleri*: Beaugrand and Cotnoir 1996). A recent study by Chase *et al.* (2002) using the cichlid fish, *Metriaclima zebra*, reports that whilst the physical properties of the competitors are important in determining rank, the social interactions of the competitors, including winner effects, loser effects and bystander effects, whereby a third party watches a contest and tailors its subsequent behaviour accordingly (Johnsson and Akerman 1998; Oliveira *et al.* 1998; Silk 1999), may also be involved. The formation of dominance hierarchies is hence governed by principles of self-organization.

Theoretical approaches to these so-called winner and loser effects have shown that initial RHP values are highly correlated with dominance ranks (see Mesterton-Gibbons 1999; Beacham 2003); however, the strength of this relationship deteriorates under conditions such as low levels of variation in the RHP of the population or by overemphasis of recent winner or loser effects to the RHP (Beaugrand 1996). In other words, if all individuals are broadly similar in terms of RHP or if the system is excessively dynamic, then the ability of the RHP to predict an individual's dominance rank is reduced. In addition, Dugatkin and Earley (2004) predict that individual recognition may actually destabilize hierarchies and therefore that winner and loser effects are most influential where players are not capable of such recognition. This finding suggests the possibility that winner and loser effects may be based on physiological changes, such as elevated cortisol levels (Sloman *et al.* 2001).

In fact, physiological variations between individuals now appear to be the most accurate predictors of dominance relationships within cohorts. Metcalfe *et al.* (1995) described the relationship between standard metabolic rate (SMR) and dominance in juvenile Atlantic salmon: individuals with a high SMR were also likely to be socially dominant (see also Yamamoto *et al.* 1998). Furthermore, once SMR was controlled for, body size was unrelated to dominance. In addition to this, where an individual exhibits a high metabolic scope or range this may allow more flexibility in activity patterns, enabling fish to display energetically expensive behaviour, such as elevated aggression levels (Priede 1985). Thorpe *et al.* (1992) reported that competitive ability in juvenile Atlantic salmon was more related to an individual's aggression than its size; however, these aggressive individuals ultimately grew more quickly than their competitive subordinates. However, elevated aggression may simply be a response to the demands of the high metabolic levels associated with dominance. Furthermore, Cutts *et al.* (2002) found that dominant Atlantic salmon with high metabolic rates had low metabolic scopes.

Overli *et al.* (2004) suggest stress-coping ability as an additional predictor of social dominance. Juvenile rainbow trout that demonstrated lower cortisol levels when placed in stressful situations were more likely to be dominant (see also Sloman *et al.* 2001). The findings of these studies have implications both for our understanding of winner and loser effects and for our understanding of the physiology of boldness, for example, in Ward *et al.*'s (2003) study of stickleback where those individuals which demonstrated the least stress in a predator simulation were also competitively dominant.

## Resource defence

A full examination of the extensive literature of territoriality amongst fishes is beyond the scope of this review. We present here an overview of the subject and refer the reader to the more comprehensive work of Grant (1997).

Defence of food territories is widespread among fishes (see Table 4). According to Thresher (1984), two-thirds of coral reef fish families defend feeding territories. By contrast, there is a much lower incidence of food patch territoriality in other ecosystems; 6% of eastern Canadian marine families (Scott and Scott 1988) and 9% of Canadian freshwater families display this behaviour (Scott and Crossman 1979). The prevailing ecological conditions are likely to underlie this variability between different biomes as these essentially determine the economics of resource defence. Grant

**Table 4** Food territoriality.

| Reference | Scientific name | Common name | Location | Method | Outcome |
|---|---|---|---|---|---|
| Berg and Northcote (1985) | *Oncorynchus kisutch* | Coho salmon | L | Artificial channel study of the effects of prey provision upon juvenile feeing territory size | When prey levels were lower feeding territory sizes increased |
| Brannas *et al.* (2003) | *Salmo trutta* | Brown trout | L | Artificial channel study of the effects of food abundance upon growth and territoriality | More individuals exhibited territorial behaviour when more food was provided. Growth rates did not vary between territorial and non-territorial individuals |
| Castro and Santiago (1998) | *Diplodus sargus cadenati* | White seabream | L | Study of the effects of food location predictability upon aggressive competitive interactions | Overall aggression was greater when prey location was unpredictable and was greater in the post-feeding period |
| Dill *et al.* (1981) | *Oncorynchus kisutch* | Coho salmon | L | Study of the effects of prey provision upon juvenile feeing territory size | When prey levels were lower feeding territory sizes increased |
| Grant and Guha (1993) | *Archocentrus nigrofasciatus* | Convict cichlid | L | Laboratory study of the effects of patch size upon prey monopolization and competitive aggression | Dominant fish were seen to consume more prey and exhibited more aggression when the patch size was smaller |
| Grant *et al.* (2002) | *Archocentrus nigrofasciatus* | Convict cichlid | L | Laboratory study of levels of competitive aggression when prey provision varied from low density to excessive | Levels of competitive aggression were higher at intermediate prey levels |
| Kim *et al.* (2004) | *Archocentrus nigrofasciatus* | Convict cichlid | L | Laboratory study of the effect of patch size and predation risk upon foraging rates and aggressive behaviour | When prey patches were larger dominant fish were less able to monopolize them and more, and smaller fish were seen to feed. Perceived predation risk also led to lower levels of aggression in smaller patches |
| Robb and Grant (1998) | *Oryzias latipes* | Japanese medaka | L | Study of the effects of spatial and temporal variation in prey distribution upon aggression | Aggression was greatest when prey distribution was spatially concentrated but temporally variable |
| Savino and Kostich (2000) | *Gymnocephalus cernuus* | Ruffe | L | Laboratory study of the effect of fish density upon aggressive interaction when foraging | Aggression was lower at low and higher fish densities. The foraging rate was also low at low fish densities |
| Syarifuddin and Kramer (1996) | *Trichogaster trichopterus* | Blue gourami | L | Laboratory study of the effects of group size upon foraging aggression | The number of aggressive acts per fish was lower in smaller groups. Fish closest to the prey patch received more aggression, and in larger groups aggression was seen to increase during short periods where prey was absent |
| Weir and Grant (2004) | *Archocentrus nigrofasciatus; Carrasius auratus* | Convict cichlid; Goldfish | L | Laboratory study of food monopolization in fish which actively and aggressively compete (convict cichlid) or which compete non-aggressively, through scramble competition (goldfish) | Prey monopolization was higher in the convict cichlids when the prey resource was defendable than when it was not. In goldfish scramble competition occurred; prey monopolization did not depend upon dependability and was seen to be greater than in the cichlid |

(1997) suggests six main parameters which directly affect the cost-to-benefit ratio of resource defence, these are: competitor density, resource abundance, the spatial and temporal clumping of resources and the spatial and temporal predictability of resources. Notwithstanding this, consideration must be given to the possibility that defence of the food resources of a territory may arise secondarily and that in certain circumstances territories may be selected primarily on the basis of providing a good breeding site or refuge from predators.

Resource defence becomes more costly with increasing competitor density – an individual may have difficulty in simultaneously excluding two intruders. Juvenile sea trout (*Salmo trutta*) with large territories show reduced feeding rates where conspecific densities are high (Elliott 2002). When the utility of each prey item decreases, such as when food is superabundant, the benefits of territorial defence are low. Magnuson (1962) showed that medaka abandoned their attempts to monopolize food resources when the food supply was plentiful. Territoriality is only worthwhile when resources are clumped in space and it pays to switch to a less aggressive strategy when food is evenly distributed (Rubenstein 1981). Similarly, territoriality may be a poor strategy in situations where food resources arrive synchronously (Grant and Kramer 1992). Where resource delivery is spatially predictable, the benefits of resource monopolization are likely to increase (Grand and Grant 1994). Similarly, resource monopolization is likely to pay when resources are temporally predictable, for example, the defence of grazing areas by herbivorous reef fish may only be worthwhile when the algae are at their most nutritious, around midday and early afternoon (see Zoufal and Taborsky 1991; Zemke-White *et al.* 2002).

In addition to the traditionally understood model of a feeding territory, many species defend positions in a water current associated with a high rate of food delivery. The individuals furthest forward in the stream encounter the prey first and therefore have the first opportunity to feed, those occupying rear positions (in the 'shadow' of the vanguard) generally suffer lower food encounter rates as a result (Elliott 2002). In a study on Arctic grayling (*Thymallus arcticus*) in mountain streams, Hughes (1992) found a strong relationship between the dominance of a fish and the feeding benefits associated with its position.

Studies of territoriality in free-ranging populations demonstrate the huge benefits that accrue to territory holders and, consequently, the costs paid by those excluded. Webster and Hixon (2000) reported a 60% increase in feeding rates amongst small, subordinate fairy basslets when dominant individuals have been excluded. The importance of obtaining a feeding territory for newly emerged salmonids is exemplified by Elliott's (1990) study, who reported that brown trout (*Salmo trutta*) which failed to acquire a territory seldom survived beyond the first 2 months of life.

### Strategic behaviour

The competitive ability of an individual is determined not only by its characteristics – how large or fast it is – but also by its behaviour and the strategies that it employs. In order to reduce the costs of competition, poor competitors may behave strategically. In the simplest case, fish may simply increase their proximal feeding rate if they perceive increasing levels of interference competition, as was demonstrated by Dill and Fraser (1984) in a study on juvenile coho salmon. At the other end of the scale, poor competitors appear to show problem-solving abilities. In their study on guppies, Laland and Reader (1999) discovered that male fish that were relatively poor competitors in a scramble situation were more likely to be innovative and exploratory when presented with a novel foraging task.

In any foraging group the optimal feeding strategy of each competitor depends on its rank. For example, Milinski (1982) showed using three-spined stickleback that poor competitors may opt for less profitable food items in a selective manner according to the competitive environment. Shifts in diet under the influence of competition are considered at greater length in the section dealing with ecological consequences of competition. Where direct aggression occurs, subordinate individuals may be forced to take what prey they can (Croy and Hughes 1991), however, in larger groups subordinate Atlantic salmon may adopt alternative feeding strategies which attract less attention and aggression from dominants, trading off lower rates of food intake and growth against a reduction in injury (MacLean *et al.* 2000). One subordinate strategy is to feed whilst dominant individuals are handling prey and hence disarmed, allowing the subordinate to gain access to a clumped food

resource (Bryant and Grant 1995). Dominant individuals are also known to behave strategically so as to maintain their status. Cutts *et al.* (2002) reported that dominant Atlantic salmon were less likely to feed than subordinates in a novel environment, arguing that high initial levels of aggression in these circumstances are more likely to enable the fish to acquire a feeding territory.

The competition costs of being in a social group may be minimized if individual fishes are choosy about whom they associate with. This may be achieved either by selectively associating with poorer competitors or by associating with individuals which are good at locating food patches. In the former case, Metcalfe and Thomson (1995) showed that European minnows (*Phoxinus phoxinus*) were able to determine the competitive abilities of individuals in small groups in a non-foraging context and when given a choice between two shoals, associated preferentially with a group of poorer rather than a group of stronger competitors. Alternatively, an individual may associate with successful foragers. Krause *et al.* (1999) reported that zebrafish which had been deprived of food showed an association preference for well-fed conspecifics and subsequently foraged more successfully than individuals in a shoal of hungry fish. The likely mechanism underlying the choice and the associated benefit is that well-fed fish have less motivation to feed and so are temporarily weaker competitors. An alternative explanation is that fish are able to recall individuals with whom they have previously shared positive foraging experiences and preferentially associate with them (Dugatkin and Wilson 1992).

Shoaling behaviour itself also provides some feeding benefits – fish within a shoal are able to locate food more swiftly than when solitary (see Ranta and Juvonen 1993) and are also able to gain access to defended resources (Foster 1985). However, the competition costs of shoaling are well documented (see Krause and Ruxton 2002), the average proportion of food available at each patch to each shoal member decreases linearly with increasing shoal size. In a study on free-ranging banded killifish (*Fundulus diaphanus*) Hensor *et al.* (2003) showed that hungry fish formed smaller shoals than well-fed fish. In extreme cases, killifish even elect to forage on their own (Ward *et al.* 2002). As an alternative to leaving the shoal, hungry fish may adopt positions in the vanguard of the shoal where feeding rates and per capita predation risk tend to be highest (Bumann *et al.* 1997), retreating into the relative safety of the centre of the shoal when satiated (Krause *et al.* 1992; Krause 1993).

## Reciprocity and relatedness

Clear theoretical frameworks exist to suggest that competitive intensity should be reduced where familiar or related animals interact. Familiar individuals may compete less aggressively simply because aggression is associated with costs such as injury and the possibility of the loss of the contested resource either because it escapes (if it is a live prey animal) or is taken by a third party during competition. In fact, Mathis *et al.* (1995) and Chivers *et al.* (1996) suggest this as a possible adaptive function of alarm substance, which is released by certain fish families when the epidermis is damaged, for example, when a predator attacks (see also Cashner 2004). The alarm substance acts to recruit other predators to the scene to compete for prey with the original predator. This may then allow the prey fish to escape. Empirical support for the idea of reduced competition between familiars is equivocal. Utne-Palm and Hart (2000) reported lower levels of aggression between familiar pairs of three-spined sticklebacks competing for prey than between unfamiliar pairs; however, a more recent study of competition within larger groups of sticklebacks found no change in competitive intensity with increasing familiarity (M.M. Webster & P.J.B. Hart, unpublished data). Despite this there may be other feeding benefits to associating with familiars, for example, a recent study by Ward *et al.* (2004a,b) showed that groups of familiar sticklebacks were significantly better at locating food patches than non-familiar groups. Reduced aggression between familiar individuals may also convey feeding benefits. Evidence from salmonids shows that groups comprising familiar sea trout (*Salmo trutta*) had higher rates of food intake and group members ultimately gained greater fitness benefits than groups composed of non-familiar fish (Hojesjo *et al.* 1998). This is assumed to be because familiar groups have stable established dominance hierarchies, reducing the frequency of aggressive encounters and consequently allowing more time for feeding. Seppä *et al.* (2001) examined the fitness consequences of familiarity by allocating individual Arctic charr (*Salvelinus alpinus*) to familiar or non-familiar groups and measuring survival and

condition. Individuals in familiar groups fared significantly better than those in non-familiar groups over a 21-day period.

Theoretically, the possibility of gaining indirect fitness benefits suggests that animals should behave less competitively towards kin (Hamilton 1964); however, there is little evidence to support this contention. Fish possess the ability to recognize related individuals (see Ward and Hart 2003) probably by MHC-based recognition (Olsen *et al.* 1998, 2002) yet information on relatedness seems to be used mainly in mate choice by many fishes (Landry *et al.* 2001; Aeschlimann *et al.* 2003; Milinski 2003). Salmonids are known to show a range of kin-biased behaviour, including a preference for holding feeding territories near siblings (Brown and Brown 1993a), sharing feeding territory space with siblings and reduced aggression amongst siblings (Brown and Brown 1993b; Griffiths and Armstrong 2002). Whilst these benefits usually translate into higher rates of growth for individuals in sibling groups (Brown *et al.* 1996; Olsen and Jarvi 1997), this is not always the case (Greenberg *et al.* 2002; see also Griffiths and Armstrong 2001). Anderson and Sabado (1999) conducted an enclosure experiment on larval kelp perch (*Brachyistius frenatus*), reporting no difference in growth rates between fish in sibling groups and groups of unrelated individuals.

## Ecological and evolutionary consequences of intraspecific competition

The constraints that competition imposes upon a population directly influences the extent of adaptive individual variation within that population (Darwin 1859). High levels of intraspecific competition, for example, are thought to produce an expansion in the niche width of a population as individuals seek to exploit under-utilized resources (Smith and Skulason 1996; Doebeli and Dieckmann 2000) (see Table 5). Thus, the development of inter-individual habitat and feeding differences and the expansion in the niche of the population as a whole is thought to act as a pressure-valve to reduce the intensity of intraspecific competition (see van Valen 1965; Roughgarden 1972; Bolnick *et al.* 2003). There are a number of means by which inter-individual niche differences may arise, ranging from ontogenetic and sexual niches (Polis 1984; Shine 1989; Wisheu 1998), to individual prey-type specializations (Kohda 1994) and discrete trophic poly-

morphisms (Smith and Skulason 1996; Schluter 2000). Whilst these categories are not mutually exclusive, for the purposes of this review we shall consider each separately.

### Ontogenetic and sexual niches

Ontogenetic habitat and diet shifts result in niche expansion and a reduction in inter-cohort competition (Polis 1984; Wisheu 1998). Differences in the physiological abilities between cohorts, particularly, in terms of swimming ability (Weihs 1977) and mouth and jaw size, allow a wider range of habitats and prey to be exploited as fish grow. Lightfoot and Jones (1996) reported that the distribution patterns of juvenile roach (*Rutilus rutilus*) in the River Hull in the UK were related to water velocity: juveniles were initially restricted to a narrow habitat along the margins of the river where the water speed is lowest, but the habitat available to them expanded as they grew. Developments in jaw musculature allow cichlids of the species *Haplochromis piceatus* to expand their diet with increasing age (Galis and Dejong 1988; Galis 1993). Similarly, piscivorous fish, such as zander (*Stizostedion lucioperca*) switch from feeding on Daphnids to outright piscivory as they grow; however, the timing of this switch is at least partly dependent on cohort density (Persson and Bronmark 2002). Different size classes of red moki (*Goniistius spectabilis*) feed simultaneously in the same shallow waters and using the same feeding methods yet juveniles eat mostly gammarids whilst adults feed mostly on the larger ophiuroid brittle stars. The mechanism underlying this diet shift seems to be the greater suctorial forces that the adults are capable of (McCormick 1998). In addition to their greater physiological abilities, large fish are also have a lower risk of predation (Persson *et al.* 1996; Sogard 1997), again allowing them to move more freely throughout the habitat than smaller fish (Mittelbach and Osenberg 1993). However, set against this is the fact that small fish have a higher mass-specific metabolism than larger conspecifics (Wootton 1994; Krause *et al.* 1998), meaning that they need to feed more often and possibly less selectively; their behaviour hence tends to be less risk averse. Studies on a number of species including the poecilid fish, *Brachyraphis episcopi* (Brown and Braithwaite 2004), the banded killifish (*F. diaphanus*) (Dowling and Godin 2002) and the three-spined stickleback (Krause *et al.* 1998) have shown that the latency of fish to exit a refuge is positively

**Table 5** Niche expansion, habitat and diet shifts

| Reference | Scientific name | Common name | Location | Method | Outcome |
|---|---|---|---|---|---|
| Dettmers and Wahl (1999) | *Dorosoma cepedianum* | Gizzard shad | F | Study of young of the year growth, density and prey density | Growth was negatively affected by intraspecific competition for prey |
| Enz *et al.* (2001) | *Coregonus suidteri* | Lake Hallwil whitefish | F | Stomach content analysis | Benthic and limnetic prey specialization was seen to occur during spring months |
| Holbrook and Schmidt (1992) | *Embiotoca lateralis* | Striped surfperch | F | Stomach content and habitat use analyses | Three different diet specialist types were identified. However, specialization was revealed to be passive consequence of subhabitat selection related to competition, rather than active choice |
| La Mesa *et al.* (2004) | *Trematomus bernacchii* | Emerald notothen | L | Stomach content analyses | Intraspecific competition may be mediated through differences in habitat preferences and foraging strategies |
| McLaughlin (2001) | *Salvelinus fontinalis* | Brook trout | F | Study of foraging tactics used by trout competing for spatially segregated prey in small channel pools | Two behavioural morphotypes, a sedentary benthivore and a mobile drift feeder were identified |
| Taylor *et al.* (2001) | *Gambusia holbrooki*; *Poecilia latipinna*; *Lucania goodei* | Eastern mosquitofish; Sailfin molly; Bluefin killifish | LE | Mesocosm study of inter- and intraspecific and intercohort competition | Intra- and interspecific competition slowed growth rates in mosquitofish and sailfin molly juvenile, and juvenile mosquitofish were seen to alter dietary components at higher densities |
| Venne and Magnan (1995) | *Salvelinus fontinalis* | Brook trout | L | Analysis of abundance, growth, spatial distribution, and feeding habits of allopatric and sympatric (with white sucker, *Catostomus commersoni*) brook trout populations | In one lake, young of the year were seen to be highly abundant; here littoral and profundal groups, differing in growth, condition, and feeding habits were observed |

correlated with fish size, in other words, small fish leave refuges soonest.

Ontogenetic habitat shifts are seen in many coral reef species, for example, three-spot damselfish (*Stegastes planifrons*) exhibit different coral habitat preferences at different ages, reducing competition between adults and juveniles (Lirman 1994). Intracohort competition for food and cover is also implicated in the habitat use of tidepool sculpins (*Oligocottus maculosus*), wherein smaller fish are compelled to accept less profitable and theoretically riskier habitats (Szabo 2002). Spina (2000) reported habitat partitioning by different size groups of rainbow trout in a stream pool environment and resultant increase in segregation between age classes. In contrast, Amundsen *et al.* (2001) found a high degree of overlap in habitat use and diet between different cohorts of Atlantic salmon, although this may reflect spatial and temporal limitations in prey availability in the study system.

Niche expansion may also occur where the sexes exploit the environment differently. Sexual dimorphism is a widespread phenomenon in fishes and, in addition, a number of species are reported to display different inter-sexual habitat and activity patterns (Sims *et al.* 2001). Several different mechanisms have been suggested to account for sexual segregation amongst which are differences in predation risk, food requirements and activity budgets between the sexes (Main *et al.* 1996; Ruckstuhl and Neuhaus 2000, 2002). In most cases, niche expansion is likely to be an effect of sexual segregation, rather than a direct cause.

Sexual segregation in fishes has perhaps been studied most extensively in guppies: female guppies grow larger than males and are able to exploit different habitats as a result of size-related reduction in predation risk and sexual differences in social behaviour (Magurran and Garcia 2000; Croft *et al.* 2003, 2004). Female American eels (*Anguilla rostrada*) also attain a greater overall size than males and in addition show significantly faster growth rates in early life allowing them to exploit a wider niche and, again, to benefit from a body size refuge (Oliveira and McCleave 2002).

Differences in diet between the sexes were documented in the clingfish (*Diademichthys lineatus*) by Sakashita (1992). These differences occurred as a result of inter-sexual differences in the mouthparts of adults which may be a sexually selected characteristic, although the author considers that niche partitioning may also partly explain this dimorphism. Reimchen and Nosil (2004) report that the manner in which the sexes exploit the habitat has implications for sexual dimorphism in three-spined sticklebacks. Females, which typically inhabited the pelagic zone, exhibited longer spines as a defence against avian predators whereas shorter-spined males were more associated with the littoral zone where long spines may be more of a liability. Different habitat preferences between the sexes are also linked to sexual dietary niches and, consequently, different patterns of parasite infection in this species (Reimchen and Nosil 2001).

## Individual feeding specializations

Niche variation within a population may occur as a result of particular size- or sex-based characteristics or by individual-level variations, which may range along a continuum from strategic dietary specialization to discrete bi- or multimodal trophic polymorphism (Bolnick *et al.* 2003). In most cases, niche variations tend to be an effect, rather than a cause of sexual and ontogenetic factors whereas in contrast, individual-level feeding differences tend to be a source of niche variation.

The extent of individual feeding specialization in a population is dependent on an array of different ecological, behavioural and physiological factors. Important amongst these are the rate at which the foragers encounters a given prey type, the value of that prey type and the anti-predator defences of the prey. However, short-term differences in individuals' diet may also simply reflect clumped prey distributions (Byron *et al.* 1983). By specializing on a particular resource or prey type, an individual is likely to become more effective at foraging in that particular niche. A corollary of this is that by specializing on one type of prey, an individual may become less able to feed effectively on a different prey, especially if the required foraging skills vary between different prey types. Ultimately, if the specialization yields greater benefits than a generalist approach, then it is likely to be maintained. Werner *et al.* (1981) provided a demonstration of rapid improvements in foraging efficiency with experience in bluegill sunfish, whilst Persson (1985) reported reductions in foraging efficiency for perch confronted with a range of different prey types. Kohda (1994) described hunting specializations in a population of the piscivorous cichlid, *Lepidiolamprologus profundicola*, which were ascribed

to the need to learn specific techniques to hunt different prey fish species.

A number of studies have suggested that the strategy of an individual fish may be density dependent, or conditional on levels of intraspecific competition. In a 9-year study on free-ranging populations of perch (*Perca fluviatilis*), Svänback and Persson (2004) found that individual diet special-ization and the niche breadth of the population were highest when the adult population density was high (but see also Schindler *et al.* 1997). Venne and Magnan (1995) observed that at high densities, brook charr (*Salvelinus fontinalis*) segregated into two feeding guilds based on habitat use. Similarly, McLaughlin (2001) reported that brook charr made adaptive adjustments in their foraging tactics in response to competition. Some individuals opted for a sedentary strategy and ate crustaceans, others were more active and fed on insects near the water's surface.

However, higher population densities may cause fish to expand their individual niche. Taylor *et al.* (2001) found that juvenile mosquitofish (*Gambusia holbrooki*) shifted their prey preferences at high conspecific densities to include a higher proportion of cladocerans and fewer chironomid larvae, poss-ibly because cladocerans can be consumed quickly and are hence potentially associated with lower levels of kleptoparasitism and contest competition than the larger chironomids which require some handling time. At higher population densities, dietary specialization may result from dominance effects, especially where niches are associated with different profitability. In a study on striped surf-perches (*Embiotoca lateralis*), Holbrook and Schmitt (1992) identified three different dietary regimes of differing quality. As differing prey species were associated particularly with certain habitats, the most profitable prey species could be monopolized by dominant fish on the basis of algal patch selection. Subordinate fish were restricted to feeding on other, less profitable prey and suffered significant fitness costs as a result.

## Trophic polymorphism

The appearance of morphologically diverse charac-ters in a species may occur due to adaptations to local foraging conditions, the most famous example of which was first commented on in the adaptive radiation of Galapagos finches by Darwin (1859) (see also Grant *et al.* 1976) or by phenotypic plasticity, whereby individual animals are able to modulate their morphology in response to foraging conditions (see Table 6). This phenomenon of trophic or resource polymorphism, is increasingly being recognized as widespread in fishes and the number of examples in the literature has increased considerably in the last couple of decades (see Bolnick *et al.* 2003 for a review). Trophic poly-morphism occurs where distinct sympatric feeding guilds within a population are phenotypically adapted to their habitat and feeding specialization. The classic example of trophic polymorphism in fish describes a divergence between pelagic and littoral morphotypes. Pelagic fish spend the majority of their time swimming and feeding on plankton in a relatively uncluttered environment. The optimal body form for this mode of life is that of a cruiser (Webb 1984), involving a hydrodynamically effi-cient fusiform body and short pelvic and pectoral fins (Dynes *et al.* 1999). By contrast, littoral fish require manoeuvrability in their structurally com-plex environment and this is best achieved by having a laterally compressed disciform body plan with large-paired fins (Webb 1984; Dynes *et al.* 1999). In addition to the overall body shape, littoral forms tend to be specialized for benthivory and have a wider mouth gape, allowing them to handle larger prey items (Adams and Huntingford 2002), whereas pelagic forms tend to be specialized for planktivory which is often associated with longer and more densely packed gill-rakers, allowing greater efficiency in feeding on small invertebrates (Malmquist 1992; Schluter 1993).

Trophic polymorphism is thought to be a response to competitive pressures within a popula-tion favouring conditions for an expansion of the niche via character release (Robinson *et al.* 1993; Skulason and Smith 1995). The ability to respond adaptively to ecological conditions confers signifi-cant fitness benefits (Swanson *et al.* 2003). The extent of the polymorphism can range from a fairly continuous distribution of traits to clear, discrete morphotypes (Mann and McCart 1981; Robinson *et al.* 1993, 1996; Pigeon *et al.* 1997). Many of these morphological traits are purely due to a plastic response to the environment without any genetic component (West-Eberhard 1989). In extreme cases, individual fish may be capable of switching from one morphotype to another over a period if environmental pressures alter (Proulx and Magnan 2004). However, some components of trophic polymorphism may be under both environmental

**Table 6** Trophic polymorphism.

| Reference | Scientific name | Common name | Location | Method | Outcome |
|---|---|---|---|---|---|
| Amundsen et al. (2004) | Coregonus albula | Whitefish | F | Habitat and foraging preferences of two morphs of whitefish, densely and sparsely gill rakered, were investigated in lakes where both occur sympatrically and in lakes where the sparsely rakered morphotype occurs in allopatry | In allopatry, the sparsely rakered morphotype occupied both the littoral and limnetic zones, exploiting both macroinvertebrates and zooplankton. In sympatry, it occurred only in the littoral zone; the densely gill rakered morphotype exploited both the limnetic zone and zooplankton prey, indicating niche segregation between morphotypes |
| Bentzen and McPhail (1984) | Gasterosteus aculeatus | Three-spined stickleback | F | Study of the foraging performances of limnetic, benthic and hybrid morphotypes | Morphotypes were better adapted to foraging in their respective habitat type, whilst hybrids were seen to be poorer competitors than specialists when in either habitat type |
| Bourke et al. (1997) | Salvelinus fontinalis | Brook trout | F | Assessment of habitat use over 3 years of transmitted tagged individuals | Differences in habitat preference and morphology suggest the existence of limnetic, littoral and generalist trophic morphotypes |
| Kahilainen et al. (2004) | Coregonus lavaretus | Whitefish | F | Study of seasonal habitat and food segregation in three sympatric trophic morphotypes | The three trophic morphotypes were seen to utilize different habitats and prey types within the lake |
| Robinson (2000) | Gasterosteus aculeatus | Three-spined stickleback | L | Laboratory study of foraging efficiency of open- and shallow-water morphotypes of three-spined stickleback from within a single lake | The open- and shallow-water morphological variants were seen to forage more efficiently on prey types typical of those found in their preferred habitats |
| Ruzzante et al. (2003) | Percichthys trucha | Creole perch | F | Morphological and dietary analyses of populations of Creole perch in three southern Andean lakes | Two sympatric morphotypes, distinguishable by differences in gill raker length were identified, though the degree of morphotypic divergence varied between populations. Differences in gill raker structure are often associated with benthic/limnetic specialization in other species |
| Schluter (2003) | Gasterosteus aculeatus | Three-spined stickleback | F | Either limnetic or benthic morphotypes of the three-spined stickleback were added to experimental ponds containing target populations of intermediate morphotypes of the same species | It was observed that growth rates were lower in target individuals whose phenotypes most closely matched those of the introduced morphotypes in each treatment |
| Schluter and McPhail (1992) | Gasterosteus aculeatus | Three-spined stickleback | F | Study of trophic morphotypes of three-spined sticklebacks in several lakes | Limnetic and benthic morphotypes, indicative of competition-induced character displacement and divergence were identified |
| Swanson et al. (2003) | Herichthys minckleyi | Minkley's cichlid | FE | Enclosure study with mixed and single trophic morphotype treatments | Competition was lower in treatments with mixed-trophic morphotypes |
| Werner et al. (1981) | Lepomis macrochirus | Bluegill sunfish | F | Fish were introduced into a previously unpopulated lake containing both benthic and littoral prey | Individuals rapidly became trophic specialists, and were seen to outperform intermediate forms when competing for prey |
| Yonekura et al. (2002) | Lepomis macrochirus | Bluegill sunfish | F | Dietary and morphological analyses of bluegills introduced to a water body in Japan | Three adult morphs specializing in plankton, benthic and epibenthic prey and two juvenile morphs were detected |

and genetic control and as such may be heritable (Adams and Huntingford 2002). In a study on juvenile Arctic charr, Alexander and Adams (2004) found that although fish from different populations displayed inherited differences in trophic polymorphism, exposure to a common environment and feeding regime eroded these differences and fish converged on a similar body plan during early growth. Juvenile Arctic charr typically feed on small benthic invertebrates following emergence, before gradually differentiating during early ontogeny into pelagic, littoral or piscivorous forms (Jonsson and Jonsson 2001). The direction of this differentiation appears to be under both genetic and environmental control, with diet, population dynamics and predation pressure implicated in the latter (Andersson 2003). The existence of an element of genetic control suggests the possibility that resource-use patterns and accompanying polymorphisms may ultimately lead to sympatric specialization (Jonsson and Jonsson 2001; Gertseva et al. 2003).

Morphological specialization naturally tends to increase the foraging efficiency of fish in the habitat to which they are adapted and similarly constrains their efficiency in alternative environments (Ehlinger and Wilson 1988; Smith 1990; Malmquist 1992; Robinson et al. 1993; Schluter 1995). Svänback and Eklöv (2003) examined the tradeoffs between foraging efficiency and growth among different trophic morphotypes in a perch population. They found that deeper-bodied fish grew more quickly in the littoral environment and that the more streamlined fish performed better in the open, pelagic habitat. In laboratory trials, littoral specialists outperformed pelagic specialists when directly competing for typical littoral prey types in a structured environment, whereas when the experiment was correspondingly biased towards the pelagic habitat, the pelagic specialists outperformed littoral specialists. This functional tradeoff of increased efficiency in a one environment against a reduction in another promotes divergence and enables the distinct morphotypes to coexist. The inability of intermediate, generalist forms, to compete effectively with either morphotype is another factor which suggests ecological character displacement and which should theoretically maintain diversity (Schluter 1993; Jonsson and Jonsson 2001). Where a species contains more than one trophic morphotype, the niche width of each morphotype may be dependent of the level of competition between them. Amundsen et al.

(2004) reported that pelagic-specialist whitefish morphotypes exploited the littoral as well as the pelagic habitats when living in allopatry but the niches were clearly segregated along expected lines according to trophic specialism when living in sympatry.

## Future directions

A detailed understanding of competitive interactions, particularly, in terms of predicting the intensity and the outcome of competition in a given situation, is fundamental to both behavioural ecology and to fisheries management. Studies conducted on competition over the past few decades have made a significant contribution to this goal, providing strong theoretical frameworks and a wealth of empirical data from the laboratory. The major challenge for the future in this and other disciplines of animal behaviour is to extend and test our existing perspectives in natural habitats and to use this knowledge more effectively in fisheries applications.

Although studies of competition arising from the laboratory provide a valuable insight into ecological processes, the aquarium is clearly an artificial environment. The greater complexity of the natural environment may have consequences for the outcome of competitive interactions that cannot be predicted on an *a priori* basis (Sloman and Armstrong 2002). Dominance relationships, for example, may alter with local conditions (Sloman et al. 2002). Simple extrapolations from the laboratory to the field may hence be misleading as factors intrinsic to an individual's competitive ability may be more complex than first thought. Instead, an integrated approach, incorporating dynamical modelling and directly linking laboratory and field studies is likely to represent the best way forward.

By employing an integrated approach, we will be able to use competition studies to gain a greater insight into how fish communities work. One application of this is in the implementation of strategies to better manage and sustainably harvest commercially important species. Studies of the intraspecific competitive interactions can provide valuable data on such factors as seasonal variation in mortality, temporal changes in recruitment patterns and in year-class strength. This information is key to the development of accurate ecosystem predictive models and sustainable management policies. At present ecosystem modelling methods,

such as Ecopath with Ecosim, ignore subtle interactions between predators and prey and within-species effects. Only by gaining more information on these interactions will it be possible to understand whether they have a significant part to play in the dynamics of exploited ecosystems. It remains a concern, furthermore, that predictions about the competitive behaviour of commercially important species are based all too often on extrapolations from experimental work on other, unrelated species, a situation which clearly requires remedying in the near future if we are to produce more accurate models.

Research on intraspecific competition in fishes is also of vital importance to aquaculture. Although a substantial body of information now exists, its practical application has been limited. Empirical information on the causes of competitive asymmetry would potentially allow fisheries managers to minimize the impact of competition in groups of farmed fish and to thereby maximize yields. Captive breeding and release programmes provide another application for competition studies. Future work could examine the role of competition between stocked individuals and between introduced and established individuals of the same species in determining post-release survival, with the aim of improving the efficiency and effectiveness of future stocking programmes.

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