The social organization of fish shoals: a test of the predictive power of laboratory experiments for the field

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ABSTRACT

By contrast with a multitude of laboratory studies on the social organization of fish, relatively little is known about the size, composition and dynamics of free-ranging fish shoals. We give an overview of the available information on fish shoals and assess to what degree the predictions made from laboratory studies are consistent with field data. The section on shoal choice behaviour in the laboratory is structured so that the evidence for different shoaling preferences is discussed in the context of their mechanisms and functions. Predictions based on experiments in captivity regarding preferences for conspecifics, individuals of similar body length and unparasitized fish were highly consistent with field observations on free-ranging shoals whereas preferences for familiar conspecifics and kin remain to be conclusively demonstrated in the field. In general, there is a shortage of studies in which shoaling preferences have been investigated both in the laboratory and the field, and field studies have so far been largely descriptive revealing little about the underlying mechanisms of observed patterns. Given the great importance of fish shoals both in fundamental and applied research, an advancement of our knowledge of their social organization should significantly contribute to a better understanding of a whole range of topics including reciprocal altruism, group-living and self-organization.

Key words: group-living, fish, shoalmate choice, shoal structure.

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I. INTRODUCTION

Fish shoals have been the subject of much research in a number of different contexts, as examples of self-organization of complex systems based on autonomous agents (Huth & Wissel, 1992; Niwa, 1994; Reuter & Breckling, 1994), as study systems to unravel the functions of group living in animals (Godin, 1986; Magurran, 1990; Pitcher & Parrish, 1993) and to investigate the evolution of reciprocal altruism (Milinski, 1987), and as a resource base for exploitation by the fisheries industry (Pitcher & Hart, 1982), to give but a few examples. Many anecdotal observations of free-ranging fish shoals have been made and a large number of laboratory studies published on fish shoaling behaviour (reviewed in Pitcher & Parrish, 1993). Similarly, numerous reports on partial collections of fish shoals are available (Hilborn, 1991; Naish, Carvalho & Pitcher, 1993; DeBlois & Rose, 1996). However, only over the last few years have studies been carried out that give accurate reports on the structure of entire fish shoals (Krause, Godin & Brown 1996 *a*, *b*, 1998; Krause, Ruxton & Godin, 1999; Peuhkuri, Ranta & Seppä, 1997; Peuhkuri & Seppä, 1998). Precise data on free-ranging fish shoals make it possible for the first time to test quantitatively the predictions of laboratory studies concerning the social organization of shoaling fish.

The objectives of this article are: (i) to give an overview of the laboratory studies on shoal formation and of the available data on complete free-ranging shoals, (ii) to check the consistency of the field data with laboratory predictions, (iii) briefly to describe the analytic tools involved in testing the above consistency, and (iv) to point out areas of interest for future research. We have tried to structure each section such that the documentation of an association preference is mentioned first followed by a discussion of the mechanisms involved in such preferences and finally their potential function and evolutionary biology. The studies reviewed in this article are restricted to those dealing with teleost fishes and include both freshwater and marine species. In contrast to freshwater fishes (and some marine littoral fish which can be used for both laboratory and field studies), marine pelagic fish pose severe methodological problems as far as laboratory work is concerned because of their requirements for large spaces to carry out their natural behaviours. Therefore, the work presented for such fish will be restricted to field data. Coral reef fish present a problem of a different kind in the context of this review because their social organization is so different from other fishes. Many reef fish form groups which are highly site-specific (to the extent of spending their entire lives within a few square metres) and territorial (e.g. harem structures with one dominant male, Aldenhoven, 1986). Our approach to this problem is to include all studies related to group-living fish species irrespective of whether they are territorial or not.

II. LABORATORY STUDIES

(1) Methodology

Whether and on what basis fish may choose to associate with particular shoalmates has been the subject of numerous laboratory studies on fish behaviour. Three basic methods have been used to investigate fish shoaling preferences in these studies.

In experiments which we term 'two-way choice', test fish are given the choice between two stimulus fish or shoals, presented behind a barrier and generally at either end of a test tank. The association preference of the test fish is scored by, for example, recording the time it spends within a certain distance of each stimulus. This method gives clear, easily recorded results and enables investigation of cues mediating this choice, e.g. visual or olfactory, by changing the type of barrier used. However, the test situation is not one that the fish is likely to encounter in the wild. Some authors have modified the method in an attempt to make it more accurately reflect a natural situation, for example by presenting a test fish with moving shoals (Lachlan, Crooks & Laland, 1998). Results in two-way choice experiments may depend upon test duration or method of scoring association preference. In Krause (1994) and

Keenleyside (1955), fish showed different preferences at the beginning and at the end of the test. Warburton & Lees (1996) used several different approaches to scoring association preference of Trinidadian guppies, *Poecilia reticulata*, and found that the significance of the result depended upon the approach used.

The most commonly used alternative, which we term 'nearest neighbour', presents the test fish with a situation more accurately reflecting that found in nature. A group of fish is released into a tank and the location of a focal test fish relative to others is recorded at discrete time intervals. Only two studies have used both this method and the two-way choice method to investigate the same preference with the same fish (Ranta & Lindström, 1990; Krause, 1994); encouragingly, however, the results did not vary with the method used. The main drawback of this method over two-way choice is that accurate data are harder to collect. Again, the criteria used to assess association preference may affect the result.

A third method, which we term 'flow tank', is used to investigate association preferences mediated by olfaction. A test fish is given the choice between two different streams of water carrying olfactory cues from different classes of stimulus fish and the positioning behaviour of the test fish relative to these two streams is recorded. This technique has primarily been used with salmonids.

Several studies have used these methods to investigate shoaling behaviour of fish in what may be considered more natural environments, for example contained in moving cages in open water (Pitcher, Magurran & Edwards, 1985), in a modified section of river (Allan & Pitcher, 1986; Griffiths, 1997), and isolated in different pools (Griffiths & Magurran, 1997b). These can be considered both 'laboratory' and 'field' studies and have been dealt with in both sections.

Irrespective of the method used for assessing preferences, the origin of the fish used in such experiments should be considered when interpreting results. In particular, selection on fish in captivity may profoundly change their shoaling decisions compared to their wild conspecifics (see Ruzzante, 1994 for domestication effects).

(2) **Role of species**

A preference for conspecifics over heterospecifics has been reported in a number of species including rock bass, *Ambloplites rupestris* (Brown & Colgan, 1986), female Trinidadian guppies (Magurran *et al.*,

1994), banded killifish, *Fundulus diaphanus* (Krause & Godin, 1994b), Atlantic salmon, *Salmo salar*, and rainbow trout, *Oncorhynchus mykiss* (Brown, Brown & Crosbie, 1993) (Table 1). Keenleyside (1955) pointed out an important feature of species-association tests. Whether or not a significant test result in favour of a preference for conspecifics is obtained may largely depend on which species is offered as an alternative. This will in most cases be another shoaling and sympatric species to provide a biologically relevant test. Keenleyside (1955) observed a preference for conspecifics in threespine sticklebacks, *Gasterosteus aculeatus*, when the heterospecific stimulus fish were bitterlings (*Rhodeus sericeus*), but not when roach, *Rutilus rutilus*, were used. Fitzgerald & Morrissette (1992) found no preference for conspecifics in the same species given the choice between conspecifics and sympatric blackspotted stickleback, *Gasterosteus wheatlandi*, whilst Barber, Downey & Braithwaite (1998) did find a preference when the alternative species was the European minnow, *Phoxinus phoxinus*.

Fish have been shown to discriminate species using both visual (Keenleyside, 1955: threespine stickleback; Magurran *et al.*, 1994: guppies) and olfactory cues (Brown *et al.*, 1993: rainbow trout).

The functional significance of preferring to group with conspecifics is likely to be due to two main factors. Given that spatial proximity after hatching (when predation is highest and selection therefore strongest; Sogard, 1997) is more likely with conspecifics than with heterospecifics, the evolution of effective antipredator manoeuvres with conspecifics is probably favoured. In addition, by associating with conspecifics an individual reduces its chances of suffering the increased predation risk of the 'oddity effect' discussed later in this review. A similar case can be made for foraging behaviour. The probability of detecting suitable food is likely to be maximized in the company of conspecifics which have similar dietary preferences. However, the degree to which the latter is counterbalanced by post-detection competition is arguable and needs further testing.

(3) **Role of body length and colour**

In addition to preferences based on species-specific characteristics, individuals may use more general phenotypic traits as selection criteria for potential shoalmates. Association preferences for size-matched fish have been found in numerous studies (reviewed in Ranta, Peuhkuri & Laurila, 1994; see Table 2). This can occur both when shoalmates are conspecific

Table 1. *Studies investigating preference for conspecifics over heterospecifics and assortment by species. For each species the test method is indicated (see Section II for details) and whether the preference involved visual cues (V) and/or olfactory (O) ones. The heterospecific species is identified under the heading 'Alternative'*

| Species | Laboratory studies | | | | | | Field studies | | | | |
	Preference	Authors	Method	Sex/origin	Alternative	Notes	Preference/ assortment	Authors	Method	Sex	Notes
Threespine stickleback *Gasterosteus aculeatus*	Yes	Keenleyside (1955)	Two-way choice V	Mixed wild	Bitterling *Rhodeus sericeus*						
	Yes/no	Keenleyside (1955)	Two-way choice V	Mixed wild	Tenspine stickleback *Pygosteus pungitius*	Only at start of trial					
	No	Keenleyside (1955)	Two-way choice V	Mixed wild	Roach *Rutilus rutilus*						
	No	FitzGerald & Morrissette (1992)	Two-way choice VO	Mixed fry wild	Blackspotted stickleback *G. wheatlandi*						
	Yes	Barber *et al.* (1998)	Two-way choice V?	Mixed wild	European minnow *Phoxinus phoxinus*						
Trinidadian guppy *Poecilia reticulata*	Yes	Magurran *et al.* (1994)	Two-way choice V	Females descendants of wild fish	*Poecilia vivipara*						
	No	Warburton & Lees (1996)	Two-way choice V, VO	Mixed fry offspring of petshop fish	Swordtail *Xiphoporus helleri*	Heterospecific preferred					
Rainbow trout *Oncorhynchus mykiss*	Yes	Brown *et al.* (1993)	Flow tank	Mixed fry offspring of domestic fish	*Salmo salar*						

Species										
Atlantic salmon *Salmo salar*	Yes	Brown *et al.* (1993)	Flow tank	Mixed fry offspring of wild fish	*Oncorhynchus mykiss*					
Rock bass *Ambloplites rupestris*	Yes	Brown & Colgan (1986)	Two-way choice VO	Mixed offspring of wild fish	Pumpkinseed *Lepomis gibbosus*					
Banded killifish *Fundulus diaphanus*	Yes	Krause & Godin (1994*b*)	Two-way choice V	Mixed wild-caught	Common shiner *Notropis cornutus*	Yes	Krause *et al.* (1996*a*)	Capture of shoals	Mixed	Assortment between shoals
Dace *Leuciscus leuciscus*	Yes	Allan & Pitcher (1986)	Nearest neighbour	Mixed wild-caught	Single shoal	Yes	Allan & Pitcher (1986)	Nearest neighbour in semi-natural fluvarium	Mixed	With predation threat: single shoal
Gudgeon *Gobio gobio*	Yes	Allan & Pitcher (1986)	Nearest neighbour	Mixed wild-caught	Single shoal	Yes	Allan & Pitcher (1986)	As above	Mixed	As above
European minnow *Phoxinus phoxinus*	Yes	Allan & Pitcher (1986)	Nearest neighbour	Mixed wild-caught		Yes	Allan & Pitcher (1986)	As above	Mixed	As above
Golden shiner *Notemigonus crysoleucas*						Yes	Krause *et al.* (1996*a*)	Capture of shoals	Mixed	Assortment between shoals
White sucker *Catostomus commersoni*						Yes	Krause *et al.* (1996*a*)	Capture of shoals	Mixed	Assortment between shoals
Damselfish *Dascyllus aruanus* *D. reticulatus*						Yes	Sweatman (1983)	Capture of shoals	Mixed	Assortment between shoals

Table 2. *Studies investigating preference for size-matched individuals and assortment by size. For each species the test method is indicated (see Section II for details) and whether the preference involved visual cues (V) and/or olfactory (O) ones. The category 'Assort.' indicates whether size assortion occurred within or between shoals. Schreckstoff is an alarm substance derived from fish skin extract (see Smith, 1992)*

| Species | Laboratory studies | | | | | | Field studies | | | | |
	Preference	Authors	Method	Sex/origin	Assort.	Notes	Preference/ assortment	Authors	Method	Sex	Assort.
Zebrafish *Danio rerio*	Yes	McCann *et al.* (1971)	Two-way choice V	Mixed pet shop		Photographs as stimulus					
Saithe *Pollachius virens*	No	Partridge (1981)	Nearest neighbour	Wild-caught							
European minnow *Phoxinus phoxinus*	Yes	Pitcher *et al.* (1986)	Nearest neighbour	Mixed wild-caught	Within shoal	Increases with predator (large fish only)					
Fathead minnow *Pimephales promelas*	Yes	Theodorakis (1989)	Nearest neighbour	Mixed hatchery	Within shoal						
Bluntnose minnow *Pimephale notatus*	Yes	Theodakaris (1989)	Nearest neighbour	Mixed wild-caught	Within shoal	Increases with predator					
Stoneroller minnow *Campostoma anomalum*	Yes	Theodakaris (1989)	Nearest neighbour	Mixed wild-caught	Within shoal	Decreases with predator					
Brook stickleback *Culea inconstans*	Yes	Ranta *et al.* (1992 a)	Two-way choice V	Mixed wild-caught		Increases with predator					
Tenspine stickleback *Pygosteus pungitius*	Yes	Ranta *et al.* (1992 a)	Two-way choice V	Mixed wild-caught		Increases with predator					
Chub *Leuciscus leuciscus*	Yes/no	Krause (1994)	Two-way choice V+nearest neighbour	Mixed juveniles wild-caught	Within shoal	Only with Schreckstoff					

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Species	Reference	Method	Composition	Result	Shoal choice	Reference	Method	Composition	Location
Threespine stickleback *Gasterosteus aculeatus*	Ranta & Lindström (1990)	Two-way choice V + nearest neighbour	Mixed wild-caught	Split into two shoals	Yes	Peuhkuri et al. (1997)	Capture of shoals	Mixed fry	Between shoals
	Ranta et al. (1992b)	Two-way choice V	Mixed wild-caught		Yes	Ranta et al. (1992b)	Association with stimulus fish	Mixed	Wild fish in sea
Banded killifish *Fundulus diaphanus*	Krause & Godin (1994a)	Two-way choice V	Mixed wild-caught		Like-sized killifish + shiners Yes	Krause et al. (1996b)	Capture of shoals	Mixed	Between shoals
					Yes	Hoare et al. (1999)	Capture of shoals	Mixed	Between shoals
Golden shiner *Notemigonus crysoleucas*	Reebs & Saulnier (1997)	Two-way choice V	Mixed wild-caught	Depends on fish size	Yes/no	Krause et al., (1996a, b)	Capture of shoals	Mixed	Between shoals
					Yes	Hoare et al. (1999)	Capture of shoals	Mixed	Between shoals
Mackerel *Scomber scombrus*					Yes	Pitcher et al. (1985)	Nearest neighbour	Mixed in cage in loch	Within shoal
Herring *Clupea harengus*					Yes	Pitcher et al. (1985)	Nearest neighbour	Mixed in cage in loch	Within shoal
White sucker *Catostomus commersoni*					Yes	Krause et al. (1996a)	Capture of shoals	Mixed	Between shoals
					Yes	Hoare et al. (1999)	Capture of shoals	Mixed	Between shoals
Damselfish *Dascyllus aruanus*					No	Coates (1980)	Capture of shoals	Mixed	Between shoals
Damselfish *Dascyllus albisella*					No	Booth (1995)	Capture of shoals	Mixed	
Parrotfish *Chlorus sordidus*					Yes	Crook (1999)	Following individuals	Mixed juveniles	

Table 3. *Studies reporting preferences and assortments regarding body colour, competitive status etc. For each species the test method is indicated (see Section II.1 for details) and whether the preference involved visual cues (V) or olfactory ones (O). MHC, major histocompatibility complex.*

		Laboratory studies						Field studies			
Preference for	Species	Preference	Authors	Method	Sex	Origin	Notes	Preference/ assortment	Authors	Method	Sex
Like-coloured individuals	Domestic mollies *Poecilia latipinna*	Yes	McRobert & Bradner (1998)	Modified two-way choice V	Mixed	Pet shop					
	Zebrafish *Danio rerio*	Yes	McCann *et al.* (1971)	Two-way choice V	Mixed	Pet shop	Photographs as stimulus				
	Parrotfish *Chlorus sordidus*							Yes	Crook (1999)	Following individuals	Mixed juveniles
Poor competitors	European minnow *Phoxinus phoxinus*	Yes	Metcalfe & Thomson (1995)	Two-way choice VO	Mixed	Wild-caught					
Similar reproductive condition	Threespine stickleback *Gasterosteus aculeatus*	No	Van Havre & FitzGerald (1988)	Two-way choice VO	Females	Wild-caught					
Similar MHC genotype	Arctic charr *Salvelinus alpinus*	Yes	Olsén *et al.* (1998)	Flow tank	Juveniles	Wild-caught hatchery fish					
More cooperative individuals	Trinidadian guppy *Poecilia reticulata*	Yes	Dugatkin & Alfieri (1991)	'Inspection tank'		Descendants of wild fish					
Well-fed conspecifics	Zebrafish *Danio rerio*	Yes	Krause *et al.* (1999)	Two-way choice	Descendants of wild fish						
Similar shape	Tanganyika sardine *Limnonthrissa miodon*							Yes	Hauser *et al.* (1998)	Sampling of shoals	Mixed

Site preference	Damselfish *Dascyllus albisella*	Yes	Booth (1995)	Sampling of shoals	Mixed
	Damselfish *D. aruanus*	Yes	Forrester (1990)	Sampling of shoals	Mixed
	Damselfish *D. aruanus* *D. reticulatus*	Yes	Sweatman (1983)	Sampling of shoals	Mixed
	Damselfish *Pomacentrus* *amboinensis*	Yes	Jones (1990)	Sampling of shoals	Mixed
	Angelfish *Centropyge bicolor*	Yes	Aldenhoven (1986)	Sampling of shoals	Mixed
	Goatfish *Upeneus tragula*	Yes	Cormick (1994)	Sampling of shoals	Mixed

and when they are heterospecific (Ranta & Lindström, 1990, Krause & Godin, 1994*b*). Killifish, for instance, have a preference for con- over heterospecifics and for size-matched fish over smaller/larger ones. However, when given a choice between size-matched heterospecifics and larger conspecifics they strongly preferred the heterospecifics, illustrating how preferences can have different priorities if conflicts arise (Krause & Godin, 1994*b*). Size assortment often has been found to commence (Krause, 1994) or increase (Ranta, Juvonen & Peuhkuri, 1992*a*) in response to a perceived predation threat, simulated for example by adding Schreckstoff (alarm substance from fish skin extract, see Smith, 1992) to the water or displaying a predator model. Fish have been found to assort by size within a single shoal (e.g. Pitcher, Magurran & Allan, 1986: European minnows; Krause, 1994: chub *Leuciscus cephalus*), or split into several size-assorted shoals (Ranta & Lindström, 1990: threespine stickleback); however, these results are probably a function of the number of fish and size of the test arena used rather than indicating true species differences.

Some studies have also investigated preferences for stimulus fish based on body patterns and colouration (Table 3). McCann, Koehn and Kline (1971), using black and white photographs as the stimulus, showed that zebrafish, *Danio rerio*, preferentially associated with fish with the normal stripe pattern. McRobert & Bradner (1998) reported that domestic mollies of two colour morphs, which had been kept together in separate tanks, preferentially associated with fish of matching colour. These results are most easily explained by individuals preferring fish with familiar body colouration, perhaps because they are recognized as conspecifics.

The mechanisms involved in phenotype matching have not yet been identified. In the case of body length, which continually changes with age, a mechanism is required that allows an individual continuously to update its information about its own size relative to that of others. One possibility is that swimming performance could be used as an indicator of body length as the two are closely correlated (Beamish, 1978).

The functional basis of the above preferences is generally believed to be linked to differential predation and foraging efficiency (Ranta *et al.*, 1994). Fish whose phenotype differs markedly from that of the majority of the group are particularly prone to predation, a phenomenon known as the 'oddity effect' (Landeau & Terborgh, 1986 using

two types of differently coloured conspecific minnows; Theodorakis, 1989 using fish of two different size classes). As Ehrlich & Ehrlich (1973) pointed out, this kind of frequency-dependent selection could potentially lead to mimicry among different fish species, whereby a shoaling species that is numerically relatively rare would mimic a species that is numerically dominant to obtain shoal-size-related antipredator benefits from mixed-species shoaling.

If individual differences in competitive ability correlate with certain phenotypic characters, theory predicts that shoals should become assorted by that phenotype (Lindström & Ranta, 1993; Ranta, Rita & Lindström, 1993). Given that small fish are often poorer competitors than their larger conspecifics (Ranta & Lindström, 1990; Krause, 1994), the preference of small fish for size-assortative shoaling might be explained by avoidance of larger and better competitors, not just by the increased predation risk of appearing odd in a group. Most likely, however, these two selection pressures are not mutually exclusive but act simultaneously (Ranta *et al.*, 1994), although their relative importance may differ depending on the prevailing ecological conditions.

(4) Role of parasites

Avoidance of conspecifics carrying endo- or ecto-parasites has been observed in threespine sticklebacks and banded killifish (Dugatkin, FitzGerald & Lavoie, 1994; Barber *et al.*, 1998; Krause & Godin, 1996) (Table 4). There is evidence that parasite detection is based at least partly on visual cues in banded killifish (Krause & Godin, 1996). A prediction based on these preferences for the composition of free-ranging shoals is made difficult, however, by the fact that parasitized fish were also found to prefer unparasitized shoal mates over parasitized ones (Krause & Godin, 1996). Therefore, the composition of free-ranging shoals may depend on potential constraints regarding the above preferences such as swimming capacity, which is often reduced in parasitized fish (Videler, 1993).

Segregation behaviour in the case of ectoparasites (e.g., *Argulus canadiensis*, Dugatkin *et al.*, 1994) potentially reduces the probability of infection. However, fish with endoparasites (e.g. *Schistocephalus solidus*, Barber *et al.*, 1998; *Crassiphiala bulboglossa*, Krause & Godin, 1996) which are not directly transmittable between group members are probably avoided because parasitized shoalmates may attract predators or may generally be of low quality in terms

Table 4. *Studies investigating preference for unparasitised over parasitised fish and assortment by parasite status. For each species the test method is indicated (see Section II.1 for details) and whether the preference involved visual cues (V) and/or olfactory (O) ones.*

Species	Laboratory studies						Field studies				
	Preference	Authors	Method	Sex/origin	Parasite	Notes	Assortment	Authors	Method	Parasite	Notes
Threespine stickleback *Gasterosteus aculeatus*	Yes	Dugatkin *et al.* (1994)	Two-way choice VO	Juveniles wild-caught	*Argulus canadensis*						
	Yes/no	Barber *et al.* (1998)	Two-way choice V	Mixed adults wild-caught	*Schistocephalus solidus*	Preference for conspecifics overrides					
Banded killifish *Fundulus diaphanus*	Yes	Krause & Godin (1996)	Two-way choice V	Mixed juveniles wild-caught	*Crassiphiala bulboglossa*		Yes	Krause *et al.* (1999)	Capture of shoals (mixed species)	*C. bulboglossa*	Assortment by parasite prevalence
							Yes	Hoare *et al.* (1999)	As above	*C. bulboglossa*	Assortment by parasite load+ prevalence
Golden shiner *Notemigonus crysoleucas*							Yes	Hoare *et al.* (1999)	As above	*C. bulboglossa*	As above
White sucker *Catostomus commersoni*							Yes	Hoare *et al.* (1999)	As above	*C. bulboglossa*	Assortment by parasite load

Table 5. *Studies looking at association preferences for natural shoalmates. For each species the test method is indicated (see Section II.1 for details) and whether the preference involved visual cues (V) and/or olfactory (O) ones. The 'Together' category indicates how long the fish were kept together as shoalmates prior to the experiments.*

| Species | Laboratory studies | | | | | | Field studies | | | | |
	Preference	Authors	Method	Sex	Origin	Together after capture	Preference/ assortment	Authors	Method	Sex	Notes
Trinidadian guppy *Poecilia reticulata*	Yes	Griffiths & Magurran (1998)	Two-way choice VO	Females	Wild-caught shoals	< 1 day					
	No	Griffiths & Magurran (1998)	Two-way choice VO	Males	Wild-caught shoals	< 1 day					
Fathead minnow *Pimephale promelas*	Yes	Brown & Smith (1994)	Two-way choice VO, O	Mixed adults	Wild-caught shoals	> 28 days					
	No	Brown & Smith (1994)	Two-way choice V	Mixed adults	Wild-caught shoals	> 28 days					
Bluegill sunfish *Lepomis macrochirus*	Yes	Brown & Colgan (1986)	Two-way choice VO	Mixed juveniles	Wild-caught groups	3–7 days					
Pumpkinseed sunfish *Lepomis gibbosus*	No	Brown & Colgan (1986)	Two-way choice VO	Mixed juveniles	Wild-caught groups	3–7 days					
Rock bass *Ambloplites rupestris*	No	Brown & Colgan (1986)	Two-way choice VO	Mixed juveniles	Wild-caught groups	3–7 days					
European minnow *Phoxinus phoxinus*							Yes	Griffiths (1997)	Nearest neighbour	Mixed adults	In semi-natural fluvarium
Yellow perch *Perca flavescens*							Weak	Helfman (1984)	Observation of individuals	Mixed adults	
Spottail shiners *Notropis husonius*							No	Seghers (1981) (analysed by Helfman, 1984)	Observation of individuals	Mixed juveniles	
Grunts *Haemulon* spp.							Yes	McFarland & Hillis (1982) (as above)	Observation of individuals	Mixed juveniles	
Banded killifish *Fundulus diaphanus*							No	Hoare *et al.* (1999)	Mark-recapture	Mixed adults	

of shared antipredator benefits such as predator detection (Krause & Godin, 1994*a*).

(5) Role of familiarity

Recent studies have demonstrated that fish are capable of individual recognition (reviewed in Dugatkin & Wilson, 1993; Dugatkin & Sih, 1995). It is therefore to be expected that shoaling decisions may be based upon previous experience with other members of the shoal.

Several studies have reported shoaling preferences for familiar fish (Table 5). However, a number of these studies have used fish collected from the wild and designated as 'familiar' those individuals that are associating together when caught (Brown & Smith, 1994: fathead minnows; Brown & Colgan, 1986: bluegill sunfish *Lepomis macrochirus*; Griffiths, 1997: European minnows; Griffiths & Magurran, 1998: Trinidadian guppies). An observed preference for these 'familiars' does not rule out the possibility that some factor other than familiarity may be mediating shoal choice both in the wild and the test environment. In addition, the duration of association of these 'familiar' fish prior to their capture is not known. Brown & Smith's (1994) observation that minnows preferred original shoalmates after three months separation is interpreted as evidence for long-term memory for familiars but would also be expected if another discrimination factor were being used. The results of such studies, however, do support the idea that fish shoals are long-term, stable associations and as such familiarity may be an important element of intra-shoal interactions even if it is not a direct cause of shoaling preferences. Fish do not always prefer the shoals in which they were collected: Griffiths & Magurran (1998) found a preference for shoalmates in female, but not male Trinidadian guppies and Brown and Colgan (1986) found shoalmate preference in bluegill sunfish but not pumpkinseed sunfish (*Lepomis gibbosus*), two closely related species with differing shoaling habits.

A more robust test involves generating familiar groups at random in a laboratory environment. Preference for familiars using this method has been demonstrated in the bluegill sunfish (Dugatkin & Wilson, 1992), female Trinidadian guppies (Magurran *et al.*, 1994; Griffiths & Magurran, 1997*a*; Lachlan *et al.*, 1998) and mixed-sex guppy fry (Warburton & Lees, 1996; Griffiths & Magurran, 1999) (Table 6). In female guppies, this preference gradually increases over a period of 12 days (Griffiths & Magurran, 1997*a*), suggesting that

a certain degree of temporal shoal cohesion is required before preferences for familiars can become a factor mediating shoal choice.

The role of familiarity in mediating shoal choice is constrained by the ability of individuals to recognize familiars. Van Havre & Fitzgerald (1988) collected female sticklebacks from two large, temporarily separated, tidal pools and found that fish preferred to associate with fish from their own pool. They attributed this result to a preference for familiar fish, an interpretation which requires sticklebacks to be able to identify several hundred fish as familiar. However, a study of wild guppies, temporarily separated in small riverbed pools for a similar length of time (Griffiths & Magurran, 1997*b*), suggested that the number of familiars a female guppy can recognize is much more limited. It is possible that these two species are using different criteria to recognize familiars in these experiments, with sticklebacks perhaps using a general cue such as a group odour.

Cues involved in discriminating familiars have indeed been found to vary between species. Guppies are able to recognize familiars using either visual or olfactory cues (Griffiths & Magurran, 1999). Sticklebacks, however, cannot discriminate poolmates using visual cues alone (Van Havre & Fitzgerald, 1988) and in fathead minnows shoalmates seem to be recognized solely by smell (Brown & Smith, 1994).

Associating with familiars may have a number of advantages. Familiarity among the members of a shoal may reduce the fitness costs of competition by reducing aggression between the contestants. Höjesjö *et al.* (1998) found a decrease in antagonistic behaviour with an increase in familiarity among sea trout, *Salmo trutta*. Chivers, Brown & Smith (1995) reported that shoals of fathead minnows that originated from the same shoal exhibited more effective antipredatory tactics under predator threat than groups composed of individuals taken from different shoals. It remains to be shown, however, whether this effect is actually due to familiarity between individuals and whether the predation risk for the shoal is lowered as a result.

Fish performing specific behavioural tasks have been shown to choose associates based upon previous experience of the behaviour of these fish. Remaining in a temporally stable group would provide long-term experience of shoalmates and hence facilitate an individual's partner-choice decisions. In stable shoals of familiar individuals, fish may, for example, use the acquired knowledge about the competitive ability of others and choose the company of those

Table 6. *Studies investigating preferences for familiar fish. For each species the test method is indicated (see Section II.1 for details) and whether the preference involved visual cues (V) or olfactory ones (O). The 'Together' category indicates how long the fish were kept together as 'familiar' groups prior to the experiments.*

Species	Laboratory studies						Field studies					
	Preference	Authors	Method	Sex/origin	Together	Notes	Preference	Authors	Method	Origin	Together	Notes
Trinidadian guppy *Poecilia reticulata*	Yes	Magurran *et al.* (1994)	Two-way choice V	Females descendants of wild fish	2 months		Yes	Griffiths & Magurran (1997 *b*)	Nearest neighbour	Wild females from separate pools	> 3 months in pools	Depends on number in pool
	Yes/no	Warburton & Lees (1996)	Two-way choice V	Mixed fry pet shop offspring	1 week+ (from birth)	Depends on method used						
	No	Warburton & Lees (1996)	Two-way choice VO	Mixed fry pet shop offspring	1 week+ (from birth)							
	Yes	Griffiths & Magurran (1997 *a*)	Two-way choice V	Females descendants of wild fish	12–30 days							
	Yes	Lachlan *et al.* (1998)	Two-way choice moving shoals V	Females pet shop	14 days							
	Yes	Griffiths & Magurran (1999)	Two-way choice V, O	Mixed fry descendants of wild fish	3–6 weeks (from birth)							
Bluegill sunfish *Lepomis macrochirus*	Yes	Dugatkin & Wilson (1992)	Two-way choice V	Mixed wild	3 months							
Threespine stickleback *Gasterosteus aculeatus*	Yes	Van Havre & FitzGerald (1988)	Two-way choice VO	Females wild (two pools)	14 days+ > 14 days in pool							
	No	Van Havre & FitzGerald (1988)	Two-way choice V	Females wild (two pools)	14 days+ > 14 days in pool							

individuals with whom they have been most successfully foraging in the past (Dugatkin & Wilson, 1992; Metcalfe & Thomson, 1995). The formation of familiarity-based assemblages is also likely to be beneficial in co-operative interactions as individuals may then preferentially join those who have proven to be most co-operative in the past, e.g. in risky antipredator behaviours (Milinski, Külling & Kettler, 1990; Dugatkin & Alfieri, 1991).

(6) Role of kinship

Investigation of kin discrimination in fish has mainly focused on salmonids (see Brown & Brown, 1996, for a review). Preference for olfactory cues from siblings rather than non-siblings has been demonstrated in Arctic charr, *Salvelinus alpinus* (Olsén, 1989), coho salmon, *Oncorhynchus kisutch* (Quinn & Busack, 1985), Atlantic salmon and rainbow trout (Brown & Brown, 1992) (Table 7). As all test fish were reared in kin groups, these results may be due to preference for familiar odours rather than an innate kin recognition mechanism. Quinn and Hara (1986) showed that coho salmon reared with siblings and non-siblings showed no discrimination between them. Furthermore, Winberg & Olsén (1992) showed that young Arctic charr reared in isolation did not show a preference for siblings over non-siblings. A recent study by Olsén *et al.* (1998) however, demonstrated that association preferences of Arctic charr are at least partly based on major histocompatibility complex (MHC) genotype, suggesting that assessment of the genetic relatedness of individuals may indeed be playing a part in association decisions.

All salmonid studies to date have used young fish. Although usually regarded as territorial, juvenile salmonids may also form social groups (Power, 1980; Elliot, 1994) in which the kin-based association preference might play a similar role as in species more often regarded as typically group-living. Furthermore, salmonids form shoals when smolting and migrating to feeding grounds, and as adults in order to migrate to the natal streams. However, it remains to be seen whether the odour preferences of fry persist to adulthood.

Kin preferences have also been investigated in sticklebacks. Van Havre & Fitzgerald (1988) found that stickleback fry preferred to associate with siblings rather than non-siblings when given visual and olfactory cues. This preference was shown by individuals reared in isolation and those reared with non-siblings only, suggesting that sibling recog-

nition is innate. Fitzgerald & Morrissette (1992) also reported a preference for siblings, but in this study kinship may have been confounded with familiarity. More recently, Steck, Wedekind & Milinski (1999) found no preference for siblings in stickleback fry presented with olfactory cues alone.

Fish could gain advantages by choosing to shoal with kin in addition to the direct fitness benefits of shoaling (Pitcher & Parrish, 1993). For instance, associating with relatives may increase an individual's fitness because kin are likely to be more co-operative when engaging in risky behaviours such as predation inspection (Milinski, 1987). However, close kin may also compete more intensely than non-relatives due to potential similarities in their resource-utilisation patterns (Waldman, 1988).

III. FREE-RANGING SHOALS

One of the problems of studying free-ranging shoals is that they are often quite large (up to millions of individuals) and fast-moving, making accurate observations difficult. In most cases, it is necessary to capture an entire shoal to come to firm statistically testable conclusions regarding its size and composition. Capture of entire fish shoals is notoriously difficult and has led to a number of studies in which only fractions of shoals were caught and thus the same shoal may have been re-sampled (and may have been considered as an independent shoal) (Dowling & Moore, 1986; Avise & Shapiro, 1986; Hilborn, 1991; Naish *et al.*, 1993). Some studies also do not provide exact information on whether entire shoals or only fractions were caught (e.g. Ferguson & Noakes, 1986). Not surprisingly all of the information on entire fish shoals to date comes from species that are usually found in small to medium size groups such as threespine sticklebacks, banded killifish, golden shiners and different species of damselfish (Coates, 1980; Forrester, 1990, 1991; Booth, 1995; Krause *et al.*, 1996*a*, *b*; Peuhkuri *et al.*, 1997; Peuhkuri & Seppä, 1998; Hoare *et al.*, 1999).

(1) Methodological issues

When collecting fish shoals in the field it is important that the experimental design is appropriate for testing the specific hypotheses in question, as these determine the spatial and temporal scale of shoal collection and also the statistical test applied to the data set. Furthermore, the habitat characteristics of the capture locations need to be recorded to control for differences in habitat choice between different

Table 7. *Evidence for preferences for kin over non-kin. For each species the test method is indicted (see Section II.1 for details) and whether the preference involved visual cues (V) and/or olfactory (O) ones, 'Separated' indicates at what stage kin groups were divided.*

| Species | Laboratory studies | | | | | | Field studies | | | | |
	Preference	Authors	Method	Sex/origin	Separated	Notes	Preference/ assortment	Authors	Method	Sex	Notes
Threespine stickleback *Gasterosteus aculeatus*	Yes	Van Havre & FitzGerald (1988)	Two-way choice VO	Mixed fry offspring of wild fish	As eggs		No	Peuhkuri & Seppä (1998)	Allozyme markers	Mixed fry	Whole shoals
	?	FitzGerald & Morrissette (1992)	Two-way choice VO	Mixed fry offspring of wild fish		Kin also familiar?					
	No	Steck *et al.* (1999)	Flow tank	Mixed fry offspring of wild fish	As eggs						
Trinidadian guppy *Poecilia reticulata*	No?	Warburton & Lees (1996)	Two-way choice VO	Mixed fry petshop offspring	Within 4 h of birth	Possible kin effects in some trials					
	No	Griffiths & Magurran (1999)	Two-way choice V, O	Mixed fry descendants of wild fish	Within 24 h of birth						
Coho salmon *Oncorhynchus kisutch*	Yes	Quinn & Busack (1985)	Flow tank	Mixed juveniles hatchery	As eggs	Preference varies between families					
	No	Quinn & Hara (1986)	Flow tank	Mixed fry hatchery	As eggs	Familiar siblings *versus* familiar nonsiblings					
Arctic charr *Salvelinus alpinus*	Yes	Olsén (1989)	Flow tank	Mixed fry offspring of wild fish	7–13 months before test						
	Yes	Olsén *et al.* (1998)	Flow tank	Mixed hatchery	As eggs						

Atlantic salmon *Salmo salar*	Yes	Brown & Brown (1992)	Flow tank	Mixed fry offspring of wild fish	As eggs					
Rainbow trout *Oncorhynchus mykiss*	Yes	Brown & Brown (1992)	Flow tank	Mixed fry domestic	As eggs					
	Yes	Brown *et al.* (1993)	Flow tank	Mixed fry hatchery	As eggs					
Anthias squamipinnis						No	Avise & Shapiro (1986)	Allozyme markers	Juveniles	Shoal samples
European minnow *Phoxinus phoxinus*						No	Naish *et al.* (1993)	Allozyme + mDNA markers	Mixed	Shoal samples
Tanganyika sardine *Limnonthrissa miodon*						No	Hauser *et al.* (1998)	Allozyme mDNA markers	Mixed	Shoal samples
Common shiner *Notropis cornutus*						Yes	Ferguson & Noakes (1981)	One allozyme marker	Mixed adults	Shoal & juvenile samples
						No	Dowling & Moore (1986)	Allozyme markers	Mixed	Samples: several shoals?
Mouthbrooding tilapia *Sarotherodon melanotheron*						Yes	Pouyard *et al.* (1999)	mDNA markers	Mixed adults	Whole shoals

species or size classes (e.g. Foster, Garcia & Town, 1988). Such controls increase the probability that active shoal choice did indeed play a role in shaping shoal composition. Nevertheless, even if habitat characteristics are controlled for, it is still possible that factors other than active shoal choice, such as selective predation or differential swimming speeds of individuals, may have influenced the observed shoal structure. To date, few marine studies (e.g. Sweatman, 1983) and no freshwater studies have experimentally manipulated free-ranging shoals to obtain information about the underlying mechanisms of shoal size and shoal composition. All the information available on freshwater fish at present merely tells us whether or not the size and composition of observed free-ranging shoals is consistent with the predictions from laboratory studies.

In this context, it is important to mention how the data on free-ranging shoals are processed in order to obtain information regarding their composition. Usually a minimum of 10–20 entire shoals is collected to reflect the presence, phenotype frequency and distribution for a particular species at this time. The basic underlying assumption of the analysis is that, for the individuals collected, the total variation of a given phenotypic or genotypic character such as body-size can be partitioned into within-shoal variation and between-shoal variation. The null hypothesis usually assumes random mixing between shoals which is simulated by generating theoretical shoals of the same size as those observed in the field and whose body-size composition is a random sample from the population. This resampling process is usually repeated a large number of times (1000 or more). An appropriate test statistic, which depends on the experimental design, is calculated after each run for the generated set of shoals. The observed test statistic is then compared to the frequency distribution generated by the resampling procedure, which provides a test of whether the observed variation in the studied character is different from random (see Crowley, 1992, Efron & Tibshirani, 1993 for details on resampling tests). An important issue here is that all other factors potentially influencing shoal composition must be controlled for, otherwise inter-dependence of factors can produce erroneous results.

(2) Role of body length and species

A number of studies have found free-ranging shoals to be clearly species- and size-structured, with small and large fish being found in separate shoals which

are often multi-specific but usually numerically dominated by one species (Krause *et al.*, 1996*b*; Peuhkuri *et al.*, 1997). Most of the evidence for size-sorting comes from studies on freshwater fish (Hoare *et al.*, 1999) but there is some indication that this is also the case for some marine species (Sakakura & Tsukamoto, 1996). The above field observations are consistent with laboratory studies that report a strong preference for size-matched individuals and a weaker one for conspecifics (Tables 1, 2). The fact that species preferences can be overridden by body-size preferences in the laboratory may be responsible for the fact that multi-species shoals are common and may be even more frequent than single-species ones (Krause *et al.*, 1996*b*; Hoare *et al.*, 2000). There is indication that individuals of the less common species in mixed-species shoals may, however, leave the shoal under threat of predation, presumably in order to avoid phenotypic oddity (Wolf, 1985).

A correlation between the size of a shoal and the number of species found in it has been observed, but could easily be a statistical artefact (Krause, Godin & Brown, 1998). The larger a shoal the greater the probability that additional species are found in it by chance. A positive correlation has also been found between the number of species within a shoal and the body-size variation, a result which may be more promising in terms of providing insights into the mechanisms of shoal formation. There is evidence that both within-species and between-species variation in body-size increases with increasing number of species (Krause *et al.*, 1998). The between-species component can probably be explained by the fact that different fish species often have different average swimming speeds. Given that swimming speeds are body-size related (Videler, 1993) it is not surprising that slow-swimming species have to be slightly larger than fast-swimming ones to be present in the same shoal (Krause *et al.*, 1998). The within-species variation, however, remains unexplained and warrants further attention.

The group composition of coral reef species has to be seen in the context of their life cycle, which is fundamentally different from that of most freshwater species and marine pelagic fish. The larvae of most reef fish are planktonic and can potentially disperse widely from their natal reef. They settle in reefs as juveniles and adults show a relatively high degree of site-attachment, resulting in low mobility (Mapstone & Fowler, 1988). It has been shown that most reef fish larvae actively choose their settlement micro-habitat (Eckert, 1985). The length of this choice period partly depends on the ability of larvae to

delay metamorphosis if no suitable cues for settlement are encountered (Victor, 1986; Cowen, 1991; Cormick, 1994). It remains controversial, however, to what degree the co-occurrence of larvae with older conspecifics is simply a by-product of habitat choice or a result of an active choice for conspecifics. Sweatman (1983) demonstrated a preference for conspecifics in two species of damselfish (*Dascyllus aruanus* and *D. reticulata*). He removed all fish from a number of coral heads and reintroduced single-species groups of known size. Over a period of several months he monitored the settling process of fish larvae and reported that the larvae were predominantly found where older conspecifics were already established. Similar results were reported by Sale (1976) but do not correspond with findings by Williams (1980) and Sale, Doherty & Douglas (1980). To demonstrate an active preference of larvae for conspecifics it is necessary to show that other effects such as differential survival in mixed-species (compared to single-species) groups are not responsible for the above pattern (Sweatman, 1983). Furthermore, passive dispersal processes (such as currents) that act differently on different species could also play a role. Given that larvae often settle in sites which already contain adult fish it should not come as a surprise that body-length variation in groups is generally high (Coates, 1980; Sale, 1991; Booth, 1995). High variation in body length results in smaller individuals being outcompeted by larger ones (Coates, 1980; Forrester, 1990). However, the high costs of competition (which are measurable in terms of slower growth) are probably outweighed by the increased safety from predators provided by larger fish which detect predators earlier than smaller conspecifics and readily attack and expel predatory species from their corals (Sweatman, 1983; Martinez & Marschall, 1999). Furthermore there is a high cost associated with switching groups because movement between corals is risky in the absence of cover (Shulman, 1985).

(3) Role of parasites

Shoals assorted by parasite load and parasite prevalence (defined as the percentage of individuals infected within a shoal) have been found in three different species so far (see Table 4). Parasite load tends to be closely linked to other factors such as body length and species identity. For instance, in banded killifish, body length and parasite load are strongly correlated (Hoare *et al.*, 2000). Therefore, if shoals are assorted by body length then they will automatically appear to be assorted by parasite load as well, which makes statistical control of the correlated factors necessary. The interaction patterns of parasitized and unparasitized fish are of great interest because the existence of parasite-assorted shoals may have important consequences for the spread of infectious diseases in fish populations.

(4) Role of familiarity

Vital not only for an understanding of how fast infectious diseases can spread, but for studies on the social organization of shoals in general, is detailed information on the exchange rates of individuals between shoals – a topic about which relatively little is yet known. Helfman (1984) found no evidence for strong shoal fidelity when following shoaling behaviour of individually tagged yellow perch, *Perca flavescens*. Similarly, a larger-scale project involving skipjack tuna, *Katsuwonus pelamis*, found exchange rates to be quite high (16–63% of individuals changed shoals during a single day; Hilborn, 1991) which is supported by a recent study on banded killifish (Hoare *et al.*, 2000). In the latter, 788 marked killifish belonging to 10 different shoals were released in the shallow area of a Canadian lake. Just 24 h after their release the distribution of the marked fish between shoals was not different from random suggesting low shoal fidelity which may be a result of breakdown of shoals overnight and/or random reformation in the mornings (Hoare *et al.*, 2000). A recent study by Klimley & Holloway (1999), however, suggests that school fidelity is high among yellowfin tuna, *Thunnus albacares* (see also Bayliff, 1988 on skipjack tuna). Thirty-eight individuals were tagged with coded ultrasonic beacons and the results showed that they arrived at the same time of day in specific sites indicating social cohesion in this species.

Given that a number of laboratory studies have reported individual recognition and preference for familiar individuals in fish (Tables 5 & 6), it seems surprising that there is no support so far from field studies for familiarity to be of great importance for the social organization of free-ranging fishes. As shoal size is likely to constrain the ability of individuals to recognize and preferentially shoal with particular conspecifics (Griffiths & Magurran, 1997*b*), shoal fidelity, based on individual recognition and preferential association with known conspecifics, should be more likely in relatively small shoals rather than in larger ones. The threshold for the critical shoal size below which such a preference should be observed may also depend on the species in

question. In Helfman's (1984) study shoal size varied from 3 to 75 individuals, thus providing potential, at least in smaller shoals, for individual discrimination on the grounds of familiarity. Hilborn (1991) instead followed groups of thousands of individuals. Only a few field studies have been conducted so far and further investigations are needed to test for the importance of familiarity for shoal choice in freshwater and pelagic marine shoals.

By contrast, coral reef fishes generally occur in groups that are highly stable over long periods up to and exceeding one year (Mapstone & Fowler, 1988; Forrester, 1991; Booth, 1995). A number of mark-recapture studies have been carried out showing that reef fish usually do not move more than a few metres away from their coral (or other shelter) with only a few per cent of marked fish being found away from their original site (Jones, 1990; Forrester, 1991; Booth, 1995). High stability of groups in connection with a high degree of body-length variation are associated with strong hierarchies in many reef fish (Ehrlich, 1975; Mapstone & Fowler, 1988; Sale, 1991). In some species, males are territorial and keep harems thus controlling group structure (Aldenhoven, 1986). The great stability of groups in coral reef fish makes them highly suitable for studies on reciprocal altruism and 'tit-for-tat' because the long-term association between individuals guarantees repeated interactions – a topic that was controversially discussed for the stickleback system, which Milinski (1987) used for his investigation of the 'prisoner's dilemma' and the evolution of co-operative behaviour (Pitcher, 1992; Dugatkin, 1995). However, a preference for familiar individuals should not necessarily be inferred for reef fish because group stability is primarily a consequence of site fidelity.

(5) Role of site fidelity

A factor that could potentially be important for shoal composition, and which is closely related to shoal fidelity, is site fidelity. Fish may develop an attachment to familiar sites based on the fact that familiarity with their surroundings may increase their chances of survival and successful reproduction. Remaining in the same area will allow an individual to build up an increasing store of information on predator habits and distribution and food locations. There is some evidence from tagged juvenile French grunts, *Haemulon flavolineatum*, and white grunts, *H. plumieri*, species which form daytime resting aggregations in specific schooling sites, that individuals

may repeatedly occupy the same sites and even particular localities within these sites (McFarland & Hillis, 1982). In addition the twilight migration routes to feeding areas appear relatively constant in these fish, depending, however, on the size of the juvenile fish (Helfman, Meyer & McFarland, 1982). By contrast, a recent study that looked at the distribution of marked killifish found no trend for individuals to remain within particular subsections of a 100 m long stretch of shore line (Hoare *et al.*, 2000). As mentioned above, high site fidelity has been observed in most coral reef species (Forrester, 1991; Booth, 1992, 1995). Coral heads are defendable resources, whereas most shoaling freshwater species and marine pelagic fish are not strongly substratum-dependent and thus have few incentives for high site specificity and territorial behaviour. The low degree of movement between groups is probably also related to the fact that predation risk is high away from shelter, limiting the ability of reef fish to explore their surroundings (Shulman, 1985).

In conclusion, site fidelity is well supported in reef fish but more studies need to be carried out in freshwater species.

(6) Role of kinship

Detection of a tendency to associate with kin in the field is possible, in principle, by using genetic markers to determine relatedness among shoal members. There have been rather few studies of this type and, until recently, the results have been equivocal: four studies concluded that there is no kin grouping (Avise & Shapiro, 1986; Dowling & Moore, 1986; Naish *et al.*, 1993; Peuhkuri & Seppä, 1998), while only one indicated that there might be (Ferguson & Noakes, 1981). However, none of these studies has really been sufficiently powerful to rule out biologically significant contributions of kin association to shoal composition. There have been shortcomings in three areas: the sampling of fish, the genetic markers used, and the statistical testing. A new study (Pouyard *et al.*, 1999) has overcome these limitations and revealed significant kin grouping in the mouth-brooding tilapia *Sarotherodon melanotheron*.

Only Peuhkuri & Seppä (1998) and Pouyard *et al.* (1999) sampled whole shoals. However, the most significant sampling problem is the need to separate shoal effects on genetic structure within a population from spatial subdivision or genetic differentiation between cohorts. For example, Hansen *et al.* (1997) found a non-random distribution of genotypes among samples of juvenile brown trout, which they

attribute to the small number of families that contribute to the fry present in any given stretch of river. Similarly, Hauser, Carvalho & Pitcher (1998) detected significant genetic structure in Lake Tanganyika sardines, *Limnothrissa miodon*. However, this structure is unlikely to be due to coherence of kin groups because the genetic data suggest that many female parents had contributed to the group. The samples may have contained more than one shoal and the observed genetic differentiation could represent population subdivision due to limited dispersal. The genetic structure could also have been due to fish from different cohorts tending to shoal together, perhaps because of size assortment. This would result in some genetic differentiation among shoals without any kin preferences being exercised. To demonstrate association of kin in shoals, the sampling pattern must be sufficient to distinguish the potential effects of spatial structure and cohort structure. Pouyard *et al.* (1999) sampled shoals that were only approximately 10 m apart so that population structure was unlikely to be confounded with shoal structure.

The relatively low polymorphism in allozyme markers used in early studies had limited power to resolve kin relationships. For example, Avise and Shapiro (1986) found three relatively highly polymorphic loci in *Anthias squamipinnis* which was sufficient to reject the hypothesis that social groups contained offspring of only a small number of parents but would have limited power to resolve more subtle patterns of relatedness. Mitochondrial DNA is maternally inherited and so provides a different type of information. If sufficiently polymorphic mitochondrial markers are available, they can be used to estimate the number of female parents contributing to a shoal (Naish *et al.*, 1993; Hauser *et al.*, 1998). Multilocus DNA fingerprinting can reveal much more variation than allozymes but did not reveal much variation among minnow shoals, giving estimates for the partitioning of genetic variation very similar to those for allozymes (Naish *et al.*, 1993). Multilocus fingerprints can be difficult to score and allelism of bands is generally unknown. Therefore, this would no longer be the method of choice, having been supplanted by microsatellite analysis. Microsatellite loci typically have very high heterozygosities permitting discriminating estimates of relatedness (Marshall *et al.*, 1998). They have recently been applied to the analysis of relatedness in Atlantic cod, *Gadus morhua*, (Herbinger *et al.*, 1997) and specifically to the study of fish shoals (Pouyard *et al.*, 1999). In the mouthbrooding tilapia, just three microsatellite loci provided a total of 43 alleles, with expected multilocus heterozygosities ranging from 0.43 to 0.56 across sample sites.

Two types of statistic have been used to investigate kin structure of natural shoals: genetic differentiation among shoals and relatedness. The among-shoal component of genetic variation can be expressed as F_{ST} or one of its analogues and tested for departure from zero. This has the advantage that it can be integrated into an hierarchical analysis that also takes account of spatial population subdivision. Data on common shiners, *Notropis cornutus* (Ferguson & Noakes, 1981), and minnows (Naish *et al.*, 1993) suggest that approximately 95 % of genetic variation is within shoals and only 5 % is between shoals, much less than would be expected if shoals were composed of kin groups. When measuring kin structure of shoals with the relatedness estimate r, the average relatedness within shoals can simply be used as an indication of the level of kinship-based structuring within the population (Naish *et al.*, 1993), or the estimate can also be compared to some theoretical expectation (Peuhkuri & Seppä, 1998). Neither Naish *et al.* (1993), by using multilocus fingerprint data, nor Peuhkuri & Seppä (1998), by using allozymes as genetic markers, found evidence for close relatedness within shoals of minnows and sticklebacks, respectively. These mean relatedness values might be somewhat misleading. Ideally, one would like to compare the distribution of pairwise r values within shoals with the distribution in the population as a whole, perhaps taking account of spatial population structure. This would show whether groups of siblings ($r = 0.5$) or half-siblings ($r = 0.25$) occurred together more often in shoals than would be expected from their frequency in the population. However, this requires robust estimates of r for individual pairs of fish which in turn requires the power of highly informative microsatellite loci.

Pouyard *et al.* (1999) observed significant heterozygote deficits in lagoon samples of mouthbrooding tilapia but not in riverine samples. However, to maximise the use of information in their data, they tested for relatedness in shoals by comparing the observed pattern of allele sharing between individuals, within and between shoals, with patterns generated by randomization. They found very strong evidence for kin grouping of fish in eight shoals from one lagoon, suggestive of full- or half-sibling broods.

Given the breeding behaviour of group-living freshwater and marine fishes it seems more likely that preferences for shoaling with kin might have

evolved in freshwater species. In the latter many shoaling species build nests and lay eggs and hatching fry are siblings or half-siblings that could at least initially form kin shoals (Scott & Crossman, 1973) as seems to be the case for the mouthbrooding tilapia (Pouyard *et al.*, 1999). By contrast many marine pelagic species and coral reef fishes have planktonic larvae which may get widely dispersed thus reducing the chances of kin associations (Sale, 1991; Herbinger *et al.*, 1997). Although recent studies have shown for reef fish that a substantial proportion of fish larvae returns to their native reef it seems highly unlikely that related individuals stay together during the planktonic period because of low larval mobility (Jones *et al.*, 1999; Swearer *et al.*, 1999).

IV. CONCLUSIONS

(1) It appears that the predictions of laboratory studies which tested size, species and parasite assortativeness have been largely met by field studies on free-ranging fish shoals. However, laboratory studies that showed strong evidence for preferences for familiar fish and for kin either still await testing under field conditions or have been found to have had little predictive power. It may well be that in the confinement of captivity preferences for familiar individuals or kin find their expression but have only limited implications for the larger scale social organization of free-ranging shoals.

(2) For many species we have only laboratory data or field data (see gaps in Tables); more studies are needed which investigate shoaling preferences under both conditions for given species. The Tables show in which areas future studies can make contributions in this context.

(3) Shoals of freshwater fish species and marine pelagic ones have a number of similarities in their social organization being generally composed of unrelated individuals that are assorted by species and body length (and in some cases also parasite presence). The exchange of individuals between shoals is frequent (and associated with rapid group size changes) and potentially counteracts association with familiar individuals. By contrast, coral reef fishes form highly stable groups (after larval settlement) which hardly exchange any individuals (even over periods of years) and consist of fish that are familiar but not related. Species-sorting is common but body-length sorting is usually not the case.

(4) Most of the current field data are purely descriptive, comparing whether the composition of free-ranging shoals is consistent with the predictions from laboratory experiments on active shoal choice. There are obviously a number of other factors that can strongly influence shoal composition such as differential habitat preferences, swimming speeds of fish or selective predation. Thus, there is a need to test for alternative explanations of the observed patterns and for experimental manipulations to be carried out in the field to get an understanding of the mechanisms underlying the social dynamics of fish shoals.

(5) Most tests of shoal composition consist of comparing the observed composition with a null model assuming a random distribution of individuals. This may be a reasonable starting point, but needs to be gradually refined by developing models which incorporate potential mechanisms underlying shoal choice in the wild and that can generate predictions of non-random fish shoal composition to be compared to field data.

(6) Fish making a choice of which shoal to join will have multiple issues on their agenda, as we can see from the list of factors discussed in this review. Which factors are given priority and in which context remains an interesting area to be explored by future studies, both in the laboratory and in the field. In the case of field studies, it should be possible to test how much of the within-shoal variation can be accounted for by each particular factor thus providing information on their relative importance.

(7) Many studies are restricted to the documentation of an association preference and the investigation of the mechanism involved, whereas others are entirely focused on functional aspects. More studies are needed that take an integrated view of both the mechanisms and functions of association preferences concerning grouping behaviour.

V. ACKNOWLEDGEMENTS

VI. REFERENCES

ALDENHOVEN, J. M. (1986). Local variation in mortality rates

and life-expectancy estimates of the coral-reef fish *Centropyge bicolor* (Pisces: Pomacanthidae). *Marine Biology* **93**, 237–244.

ALLAN, J. R. & PITCHER, T. J. (1986). Species segregation during predator evasion in cyprinid fish shoals. *Freshwater Biology*, **16**, 653–659.

AVISE, J. C. & SHAPIRO, D. Y. (1986). Evaluating kinship of newly settled juveniles within social groups of the coral reef fish *Anthias squamipinnis*. *Evolution* **40**, 1051–1059.

BARBER, I., DOWNEY, L. C. & BRAITHWAITE, V. A. (1998). Parasitism, oddity and the mechanism of shoal choice. *Journal of Fish Biology* **53**, 1365–1368.

BAYLIFF, W. H. (1988). Integrity of schools of skipjack tuna, *Katsuwonus pelamis*, in the eastern pacific-ocean, as determined from tagging data. Fishery Bulletin **86**, 631–643.

BEAMISH, F. W. H. (1978). Swimming capacity. In: *Fish physiology* (ed. W. S. Hoar and D. J. Randall), vol. VII, pp. 101–187. Academic Press, New York.

BOOTH, D. J. (1992). Larval settlement and preferences by domino damselfish *Dascyllus albisella* Gill. *Marine Biology and Ecology* **155**, 85–104.

BOOTH, D. J. (1995). Juvenile groups in a coral-reef damselfish: density-dependent effects of individual fitness and population demography. *Ecology* **76**, 91–106.

BROWN, G. E. & BROWN, J. A. (1992). Do rainbow trout and Atlantic salmon discriminate kin? *Canadian Journal of Zoology* **70,** 1636–1640.

BROWN, G. E. & BROWN, J. A. (1996). Kin discrimination in salmonids. *Reviews in Fish Biology and Fisheries* **6**, 201–219.

BROWN, G. E., BROWN, J. A. & CROSBIE, A. M. (1993). Phenotype matching in juvenile rainbow trout. *Animal Behaviour* **46**, 1223–1225.

BROWN, G. E. & SMITH, R. J. F. (1994). Fathead minnows use chemical cues to discriminate natural shoalmates from unfamiliar conspecifics. *Journal of Chemical Ecology* **20**, 3051–3061.

BROWN, J. A. & COLGAN, P. W. (1986). Individual and species recognition in centrachid fishes: evidence and hypotheses. *Behavioral Ecology and Sociobiology* **19**, 373–379.

CHIVERS, D. P., BROWN, G. E. & SMITH, R. J. F. (1995). Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): implications for antipredator behaviour. *Canadian Journal of Zoology* **73**, 955–960.

COATES, D. (1980). Prey-size intake in humbug damselfish, *Dascyllus aruanus* (Pisces, Pomacentridae) living within social groups. *Journal of Animal Ecology* **49**, 335–340.

CORMICK, M. I. (1994). Variability in age and size at settlement of the tropical goatfish *Upeneus tragula* (Mullidae) in the northern Great Barrier Reef lagoon. *Marine Ecology Progress Series* **103**, 1–15.

COWEN, R. W. (1991). Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher*. Maine. *Ecology Progress Series* **69**, 9–15.

CROOK, A. C. (1999). Quantitative evidence for assortative schooling in a coral reef fish. Marine Ecology Progress Series **176: 17–23.**

CROWLEY, P. H. (1992). Resampling methods for computation-intensive data analysis in ecology and evolution. *Annual Review of Ecology and Systematics* **23**, 405–447.

DEBLOIS, E. M. & ROSE, G. A. (1996). Cross-shoal variability in the feeding habits of migrating Atlantic cod (*Gadus morhua*). *Oecologia* **108**, 192–196.

DOWLING, T. E. & MOORE, W. S. (1986). Absence of population

subdivision in the common shiner, *N. cornutus* (Cyprinidae). *Environmental Biology of Fishes* **15**, 151–155.

DUGATKIN, L. A. (1995). *Cooperation.* Oxford Series of Ecology and Evolution, Oxford.

DUGATKIN, L. A. & ALFIERI, M. (1991). Guppies and tit-for-tat strategy: preference based on past interaction. *Behavioral Ecology and Sociobiology* **28**, 243–246.

DUGATKIN, L. A., FITZGERALD, G. J. & LAVOIE, J. (1994). Juvenile three-spined sticklebacks avid parasitized conspecifics. *Environmental Biology of Fishes* **39**, 215–218.

DUGATKIN, L. A. & SIH, A. (1995). Behavioral ecology and the study of partner choice. *Ethology* **99**, 265–277.

DUGATKIN, L. A. & WILSON, D. S. (1992). The prerequisites for strategic behaviour in bluegill sunfish, Lepomis macrochirus. *Animal Behaviour* **44**, 223–230.

DUGATKIN, L. A. & WILSON, D. S. (1993). Fish behaviour, partner choice experiments and cognitive ethology. *Reviews in Fish Biology and Fisheries* **3**, 368–372.

ECKERT, G. J. (1985). Settlement of coral reef fishes to different natural substrata and at different depths. *Proc. 5ᵗʰ Coral Reefs Congr.* **5**, 385–390.

EFRON, B. & TIBSHIRANI, R. J. (1993). *An Introduction to the Bootstrap. Monographs on Statistics and Applied Probability,* **57**. Chapman & Hall, New York.

EHRLICH, P. R. (1975). The population biology of coral reef fishes. *Annual Review of Ecology and Systematics* **6**, 211–247.

EHRLICH, P. R. & EHRLICH, A. H. (1973). Coevolution: heterospecific schooling in Caribbean reef fishes. *The American Naturalist* **107**, 157–160.

ELLIOT, J. M. (1994). *Quantitative Ecology and the Brown Trout.* Oxford University Press, Oxford.

FERGUSON, M. M. & NOAKES, L. G. (1981). Social grouping and genetic variation in common shiners, *N. cornutus* (Pisces, Cyprinidae). *Environmental Biology of Fishes* **6**, 357–360.

FITZGERALD, G. J. & MORRISSETTE, J. (1992). Kin recognition and choice of shoal mates by threespine stickleback. *Ethology Ecology and Evolution* **4**, 273–283.

FORRESTER, G. E. (1990). Factors influencing the juvenile demography of a coral reef fish. *Ecology* **71**, 1666–1681.

FORRESTER, G. E. (1991). Social rank, individual size and group composition as determinants of food consumption by humbug damselfish, *Dascyllus aruanus. Animal Behaviour* **42**, 701–711.

FOSTER, S. A., GARCIA, V. B. & TOWN, M. Y. (1988). Cannibalism as the cause of an ontogenetic shift in habitat use by fry of the threespine stickleback. *Oecologia* **74**, 577–585.

GODIN, J.-G. J. (1986). Antipredator functions of shoaling in teleost fishes: a selective review. *Naturaliste canadien* **113**, 241–250.

GRIFFITHS, S. W. (1997). Preferences for familiar fish do not vary with predation risk in the European minnow. *Journal of Fish Biology* **51**, 489–495.

GRIFFITHS, S. W. & MAGURRAN, A. E. (1997*a*). Familiarity in schooling fish: how long does it take to acquire? *Animal Behaviour* **53**, 945–949.

GRIFFITHS, S. W. & MAGURRAN, A. E. (1997*b*). Schooling preferences for familiar fish vary with group size in a wild guppy population. *Proceedings of the Royal Society of London B* **264**, 547–551.

GRIFFITHS, S. W. & MAGURRAN, A. E. (1998). Sex and schooling behaviour in the Trinidadian guppy. *Animal Behaviour* **56**, 689–693.

GRIFFITHS, S. W. & MAGURRAN, A. E. (1999). Schooling decisions in guppies (*Poecilia reticulata*) are based on familiarity

rather than kin recognition by phenotype matching. *Behavioural Ecology and Sociobiology* **45**: 437–443.

HANSEN, M. M., MENSBERG, K. L. D., RASMUSSEN, G., SIMONSEN, V. (1997) Genetic variation within and among Danish brown trout (*Salmo trutta* L.) hatchery strains, assessed by PCR-RFLP analysis of mitochondrial DNA segments. *Aquaculture* **153**, 15–29.

HAUSER, L., CARVALHO, G. R. & PITCHER, T. J (1998). Genetic population structure in the Lake Tanganyika sardine *Limnothrissa miodon*. *Journal of Fish Biology*, Supplement A, **53**, 413–429.

HELFMAN, G. S. (1984). School fidelity in fishes: the yellow perch pattern. *Animal Behaviour* **32**, 663–672.

HELFMAN, G. S., MEYER, J. L. & MCFARLAND, W. N. (1982). The ontogeny of twilight migration patterns in grunts (Pisces: Haemulidae). *Animal Behaviour* **30**, 317–326.

HERBINGER, C. M., DOYLE, R. W., TAGGART, C. T., LOCHMANN, S. E., BROOKER, A. L., WRIGHT, J. M. & COOK, D. (1997). Family relationships and effective population size in a natural cohort of Atlantic cod (*Gadus morhua*) larvae. *Canadian Journal of Fisheries and Aquatic Science* **54** (Suppl. 1), 11–18.

HILBORN, R. (1991). Modelling the stability of fish schools: exchange of individual fish between schools of skipjack tuna (*Katsuwonus pelamis*). *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 1081–1091.

HOARE, D., KRAUSE, J., GODIN, J.-G. J. & RUXTON, G. D. (2000). Social organization of free-ranging fish shoals. *Oikos* **89**, 546–554.

HÖJESJÖ, J., JOHNSSON, J. I., PETERSSON, E., & JÄRVI, T. (1998). The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*). *Behavioral Ecology* **9**, 445–451.

HUTH, A. & WISSEL, C. (1992). The simulation of the movement of fish shoals. *Journal of theoretical Biology* **156**, 365–385.

JONES, G. P. (1990). The importance of recruitment to the dynamics of a coral reef fish population. *Ecology* **71**, 1691–1698.

JONES, G. P., MILLICICH, M. J., EMSLIE, M. J. & LUNOW, C. (1999). Self-recruitment in a coral reef fish population. *Nature* **402**, 802–804.

KEENLEYSIDE, M. H. A. (1955). Some aspects of the schooling behaviour of fish. *Behaviour* **8**, 183–248.

KLIMLEY, A. P. & HOLLOWAY, C. F. (1999). School fidelity and homing synchronicity of yellowfin tuna, *Thunnus albacares*. *Marine Biology* **133**, 307–317.

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

KRAUSE, J. & GODIN, J.-G. J. (1994b). Shoal choice in banded killifish (*Fundulus diaphanus*, Teleostei, Cyprinodontidae): The effects of predation risk, fish size, species composition and size of shoals. *Ethology* **98**, 128–136.

KRAUSE, J. & GODIN, J.-G. J. (1994a). Influence of parasitism on the shoaling behaviour of banded killifish, *Fundulus diaphanus*. *Canadian Journal of Zoology* **72**, 1775–1779.

KRAUSE, J. & GODIN, J.-G. J. (1996). Influence of parasitism on shoal choice in the banded killifish (*Fundulus diaphanus*, Teleostei, Cyprinodontidae). *Ethology* **102**, 40–49.

KRAUSE, J., GODIN, J.-G. J. & BROWN, D. (1996a). Phenotypic variability within and between fish shoals. *Ecology* **77**, 1586–1591.

KRAUSE, J., GODIN, J.-G. J. & BROWN, D. (1996b). Size-assortativeness in multi-species fish shoals. *Journal of Fish Biology* **49**, 221–225.

KRAUSE, J., GODIN, J.-G. J. & BROWN, D. (1998). Body-size variation among multi-species fish shoals: the effects of shoal size and number of species. *Oecologia* **114**, 67–72.

KRAUSE, J., RUXTON, G. D. & GODIN, J.-G. J. (1999). Distribution of *Crassiphiala bulboglossa*, a parasitic worm, in shoaling fish. *Journal of Animal Ecology* **68**, 27–33.

LACHLAN, R. F., CROOKS, L. & LALAND, K. N. (1998). Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour* **56**, 181–190.

LANDEAU, L. & TERBORGH, J. (1986). Oddity and the 'confusion effect' in predation. *Animal Behaviour* **34**, 1372–1380.

LINDSTRÖM, K. & RANTA, E. (1993). Foraging group structure among individuals differing in competitive ability. *Annales Zoologici Fennici* **30**, 225–232.

MAGURRAN, A. E. (1990). The adaptive significance of schooling as an anti-predator defence in fish. *Annales Zoologici Fennici* **27**, 51–66.

MAGURRAN, A. E., SEGHERS, B. H., SHAW, P. W. & CARVALHO, G. R. (1994). Schooling preferences for familiar fish in the guppy, *Poecilia reticulata*. *Journal of Fish Biology* **45**, 401–406.

MAPSTONE, B. D. & FOWLER, A. J. (1988). Recruitment and the structure of assemblages of fish on coral reefs. *Trends in Ecology and Evolution* **3**, 72–77.

MARSHALL, T. C., SLATE, J., KRUUK, L. E. B., PEMBERTON, J. M. (1998). Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* **7**, 639–655.

MARTINEZ, F. A. & MARSCHALL, E. A. (1999). A dynamic model of group-size choice in the coral reef fish *Dascyllus albisella*. *Behavioral Ecology* **10**: 572–577.

McCANN, L. I., KOEHN, D. J. & KLINE, N. J. (1971). The effects of body-size and body markings on nonpolarized schooling behavior of zebra fish (*Brachydanio rerio*). *Journal of Psychology* **79**, 71–75.

McFARLAND, W. N. & HILLIS, Z.-M. (1982). Observations on agonistic behavior between members of juvenile French and white grunts–family Haemulidae. *Bulletin of Marine Science* **32**, 255–268.

McROBERT, S. P. & BRADNER, J. (1998). The influence of body coloration on shoaling preferences in fish. *Animal Behaviour* **56**, 611–615.

METCALFE, N. B. & THOMSON, B. C. (1995). Fish recognize and prefer to shoal with poor competitors. *Proceedings of the Royal Society of London B* **259**, 207–210.

MILINSKI, M. (1987). Tit-for-tat in sticklebacks and the evolution of cooperation. *Nature (London)* **325**, 433–437.

MILINSKI, M., KÜLLING, D. & KETTLER, R. (1990). Tit-for-tat: sticklebacks 'trusting' a cooperating partner. *Behavioral Ecology* **1**, 7–12.

NAISH, K. A., CARVALHO, G. R. & PITCHER, T. J. (1993). The genetic structure and microdistribution of shoals of *Phoxinus phoxinus*, the European minnow. *Journal of Fish Biology*, Supplement A, **43**, 75–89.

NIWA, H. S. (1994). Self-organizing dynamic model of fish schooling. *Journal of theoretical Biology* **171**, 123–136.

OLSÉN, K. H. (1989). Sibling recognition in juvenile Arctic charr (*Salvelinus alpinus* (L.)). *Journal of Fish Biology* **34**, 571–581.

OLSÉN, K. H., GRAHN, M., LOHM, J. & LANGEFORS, A. (1998).

MHC and kin discrimination in juvenile arctic charr, *Salvelinus alpinus* (L.). *Animal Behaviour* **56**, 319–327.

PARTRIDGE, B. L. (1981). Internal dynamics and the interrelations of fish in schools. *Journal of Comparative Physiology* **144**, 313–325.

PEUHKURI, N., RANTA, E. & SEPPÄ, P. (1997). Size-assortative schooling in free-ranging sticklebacks. *Ethology* **103**, 318–324.

PEUHKURI, N. & SEPPÄ, P. (1998). Do three-spined sticklebacks group with kin? *Annales Zoologici Fennici* **35**, 21–27.

PITCHER, T. J. (1992). Who dares, wins – the function and evolution of predator inspection behavior in shoaling fish. *Netherlands Journal of Zoology* **42**: 371–391.

PITCHER, T. J. & HART, P. J. B. (1982). *Fisheries Ecology*. Croom. Helm, London.

PITCHER, T. J., MAGURRAN, A. E. & ALLAN, J. R. (1986). Size segregative behaviour in minnow shoals. *Journal of Fish Biology*, Supplement A, **29**, 83–95.

PITCHER, T. J., MAGURRAN, A. E., & EDWARDS, J. I. (1985). Schooling mackerel and herring choose neighbours of similar size. *Marine Biology* **86**, 319–322.

PITCHER, T. J. & PARRISH, J. K. (1993). Functions of shoaling behaviour in teleosts. In: *Behaviour of Teleost Fishes*, T. J. Pitcher (ed.). pp. 363–439. Chapman & Hall, London.

POUYARD, L., DESMARAIS, E., CHENUIL, A., AGNESE, J. F. & BONHOMME, F. (1999). Kin cohesiveness and possible inbreeding in the mouthbrooding tilapia *Sarotherodon melanotheron*. *Molecular Ecology* **8**, 803–812.

POWER, G. (1980). The brook charr, *Salvelinus fontinalis*. In: *Charrs. Salmonid Fishes of the Genus Salvelinus* (ed. E. K. Balon), pp. 141–203. Dr W. Junk bv Publishers, The Hague, Netherlands.

QUINN, T. P. & BUSACK, C. A. (1985). Chemosensory recognition of siblings in juvenile salmon (*Oncorhynchus kisutch*). *Animal Behaviour* **33**, 51–56.

QUINN, T. P. & HARA, T. J. (1986). Sibling recognition and olfactory sensitivity in juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Zoology* **64**, 921–925.

RANTA, E., JUVONEN, S.-K. & PEUHKURI, N. (1992a). Further evidence for size-assortative schooling in sticklebacks. *Journal of Fish Biology* **41**, 627–630.

RANTA, E. & LINDSTRÖM, K. (1990). Assortative schooling in three-spined sticklebacks? *Annales Zoologici Fennici* **27**, 67–75.

RANTA, E., LINDSTRÖM, K. & PEUHKURI, N. (1992b). Size matters when three-spined sticklebacks go to school. *Animal Behaviour* **43**, 160–162.

RANTA, E., PEUHKURI, N. & LAURILA, A. (1994). A theoretical exploration of antipredatory and foraging factors promoting phenotype-assorted fish schools. *Ecoscience* **1**, 99–106.

RANTA, E., RITA, H. & LINDSTRÖM, K. (1993). Competition versus cooperation – success of individuals foraging alone and in groups. *The American Naturalist* **142**, 42–58.

REEBS, S. G. & SAULNIER, N. (1997). The effect of hunger on shoal choice in golden shiners (Pisces: Cyprinidae, *Notemigonus crysoleucas*). *Ethology* **103**, 642–652.

REUTER, H. & BRECKLING, B. (1994). Self organization of fish schools – an object-oriented model. *Ecological Modelling* **75**, 147–159.

RUZZANTE, D. E. (1994). Domestication effects on aggressive and schooling behavior in fish. *Aquaculture* **120**, 1–24.

SAKAKURA, Y. & TSUKAMOTO, K. 1996. Onset and development of cannibalistic behaviour in early life stages of yellowtail. *Journal of Fish Biology* **48**, 16–29.

SALE, P. F. (1976). The effect of territorial adult pomacentrid fishes on the recruitment and survival of juveniles on patches of coral rubble. *Journal of Experimental Marine Biology and Ecology* **24**, 297–306.

SALE, P. F. (1991). *The Ecology of Fishes on Coral Reefs*. Academic Press, New York.

SALE, P. F., DOHERTY, P. J. & DOUGLAS, W. A. (1980). Juvenile recruitment strategies and the coexistence of territorial pomacentrid fishes. *Bulletin of Marine Science* **30**, 147–158.

SCOTT, W. B. & CROSSMAN, E. J. (1973). *Freshwater fishes of Canada*. Fisheries Research Board of Can. Bull 184.

SEGHERS, B. H. (1981). Facultative schooling behavior in the spottail shiner (*Notropis hudsonius*): possible costs and benefits. *Environmental Biology of Fishes* **6**, 21–24.

SHULMAN, M. J. (1985). Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* **66**, 1056–1066.

SMITH, R. J. F. (1992). Alarm signals in fishes. *Reviews in Fish Biology and Fisheries* **2**, 33–63.

SOGARD, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60**, 1129–1157.

STECK, N., WEDEKIND, C. & MILINSKI, M. (1999). No sibling odor preference in juvenile three-spined sticklebacks. *Behavioral Ecology* **10**, 493–497.

SWEARER, S. E., CASELLE, J. E., LEA, D. W. & WARNER, R. R. (1999). Larval retention and recruitment in an island population of a coral-reef fish. *Nature* **402**, 799–802.

SWEATMAN, H. P. A. (1983). Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *D. reticulatus*) on coral reefs. *Marine Biology* **75**, 225–229.

THEODORAKIS, C. W. (1989). Size segregation and the effects of oddity on predation risk in minnow schools. *Animal Behaviour* **38**, 496–502.

VAN HAVRE, N. & FITZGERALD, G. J. (1988). Shoaling and kin recognition in the three-spine stickleback (*Gasterosteus aculeatus* L.). *Biology of Behaviour* **13**, 190–201.

VICTOR, B. C. (1986). Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 1208–1213.

VIDELER, J. J. (1993). *Fish Swimming*. Chapman & Hall, London.

WALDMAN, B. (1988). The ecology of kin recognition. *Annual Review of Ecology and Systematics* **19**, 543–571.

WARBURTON, K. and LEES, N. (1996). Species discrimination in guppies: learned responses to visual cues. *Animal Behaviour* **52**, 371–378.

WILLIAMS, D. McB. (1980). Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). *Bulletin of Marine Science* **30**, 159–170.

WINBERG, S. & OLSÉN, K. H. (1992). The influence of rearing conditions on the sibling odor preference of juvenile Arctic charr, *Salvelinus alpinus* L. *Animal Behaviour* **44**, 157–164.

WOLF, N. G. (1985). Odd fish abandon mixed-species groups when threatened. *Behavioral Ecology and Sociobiology* **17**, 47–52.