

When fish shoals meet: outcomes for evolution and fisheries

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Abstract

The mechanisms underlying the social structure of free-ranging fish shoals have received little attention in comparison to functional studies on shoaling. Recently, however, a number of investigations, both in the marine and in the freshwater environment, have begun to address the underlying mechanisms by concentrating on interactions between free-ranging shoals. The rates of shoal encounters can influence the opportunities for individual assortment by phenotype and selection of shoal size; act as a constraint on the observed patterns of shoal structure by restricting individual choice behaviour and were found to be high in several small freshwater species (where inter-shoal distances were small), but lower in marine species where shoals were more dispersed. The duration of encounters may play a role in that it affects both the time available for assessment (of the encountered shoal) as well as that for exchange of individuals. Scarce published information on the outcome of shoal encounters suggests that the outcome of shoal encounters is influenced by shoal composition but not by shoal size. Individual behaviour may have evolved to maintain shoal size when shoals encounter, but when fish populations are depleted by fishing, this trait can exacerbate range and stock collapse. Furthermore, an understanding of the dynamics of shoal encounters has important consequences for the evolution of reciprocal altruism and the transmission of information through social learning within populations. Finally, information on encounter rates between shoals and the number of individuals that are exchanged on such occasions could be important for making predictions about the spread of disease through fish populations.

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Introduction

Encounters between fish shoals are a fundamental element of shoaling behaviour. For example, changes in ecological conditions, such as food and predators, and motivational conditions, such as hunger and sex may be expected to alter individual shoaling decisions, resulting in movements of individuals between shoals in order to maximise fitness in a changing environment (Mackinson *et al.* 1999).

An understanding of shoal dynamics can help to elucidate the evolutionary implications of group living. For example, the stability of group composition through time can have consequences for the evolution of reciprocal altruism: one theory about the operation of predator inspection (Pitcher 1992) relies on individual recognition and stable associations between individuals (Enquist and Leimar 1993).

Furthermore, the dynamics of shoaling is important in fisheries (Mackinson 2000), and shoaling fish are among the most heavily exploited species in the world's oceans (Parrish 1999). Commercial fisheries have exploited the susceptibilities of shoaling fish through various fishing techniques (Mackinson *et al.* 1997; Parrish 1999). In many cases, this exploitation has not been sustainable and has resulted in stock collapses (Winters and Wheeler 1985; Mackinson *et al.* 1997). An understanding of the structure and dynamics of fish shoals based on the mechanisms and constraints of fish shoal encounters is fundamental in fisheries management, and may be the key to avoiding over-exploitation and the conservation of fish stocks (Pitcher 1997).

The objective of this paper is to summarise the current understanding of the factors influencing shoal encounters, and by discussing their implications, place this information in both pure and applied contexts. An understanding of the mechanisms of shoal formation will shed light on how individual beha-

viour influences the patterns of both group and population structure.

Individual decisions of shoal-choice behaviour can influence the number and the size of groups within a given space, thus affecting the group-size distribution. This distribution will, in turn, affect individual decision-making processes by influencing the rates of encounters between groups, and thus the opportunity for individual exchange between groups. Through this process, behavioural decisions made by the individual will influence population-scale properties, which in turn will feed back to individual-level decision-making (see Fig. 1). In addition, the probability of a shoal encounter will, in part, be dependent on the shape and velocity of individual groups.

This paper is subdivided into four parts. Initially, we highlight the factors influencing the rates of shoal encounters and review the empirical data on the rates of shoal encounters (part one). Secondly, we investigate the factors influencing the outcomes of shoal encounters (part two). The ecological, evolutionary and fisheries implications of shoal encounters are discussed in part three. Finally, in part four, we highlight the direction that future research should take.

Factors influencing the rates of shoal encounters

In this section, we review the factors that may influence the rates of shoal encounters and examine the current empirical data on shoal encounter rates.

The spatial distribution and size distribution of shoals

Movements of shoals within a limited space will facilitate encounters between them, the rate of

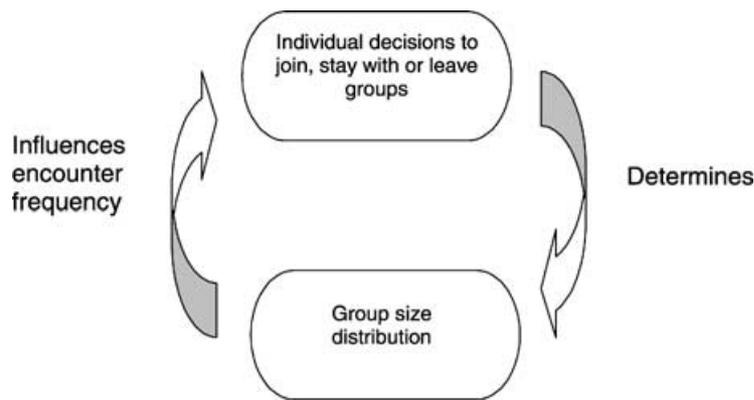


Figure 1 Diagram of the feedback process whereby individual decisions affect group-size distribution, which in turn will influence the opportunity for individual decisions.

which will depend on their spatial distribution and the shoal-size distribution, expressed as the number and size of shoals within a population, which in turn depends on the density of fish and their behavioural motivation (Flierl *et al.* 1999). As shoals become more clustered, and the number of shoals close by and available for interactions increase, so does the rate of shoal encounters. Physical and biological properties of the environment and the behavioural characteristics of the species may influence the spatial distribution of shoals such that the presence or absence of predators and the abundance of food may influence the spatial distribution of individuals (Huntingford 1993). For example, Pitcher and Wyche (1983) described a 'confusion zone' behind the leading edge of joining sandeel schools that attracted predators and might inhibit individuals from leaving. In contrast, differing hunger levels in herring schools led to splitting behaviour (Robinson and Pitcher 1989a). Moreover, shoaling individuals may have preferences for environmental conditions, such as particular currents, temperatures, light intensities and oxygen concentrations (Fréon and Misund 1999). The spatial distribution of shoals has also been shown to be dependent on their size. For example, Mackinson *et al.* 1999 found that the herring intershoal distance varied with shoal size, with smaller shoals having smaller nearest-neighbour shoal distances, although the individual behavioural mechanisms that underlie this phenomenon have yet to be elucidated.

The number of shoals close enough to interact will also be a function of the shoal-size distribution. This distribution reflects a balance between the rate of shoal encounters resulting in fusion and the rate of intrashoal fission (shoal splitting). The continued process of fission and fusion under a given set of ecological and behavioural conditions may eventually lead to an equilibrium distribution of group sizes

(Okubo 1986), although this may be unstable through time as ecological conditions change. Two types of shoal-size distribution have been described for free-ranging fish. First, when shoals are ephemeral with a high rate of fission relative to fusion events, as illustrated by the spot-tail shiner *Notropis hudsonius*, (Seghers 1981) a shoal-size distribution with an exponential decrease is observed. In contrast, Bonabeau and Dagorn (1995) found that a power-law distribution occurs in species where individuals are associated for longer periods, such as tuna: yellowfin *Thunnus albacares*, skipjack *Katsuwonus pelamis*, and bigeye tuna *Thunnus obesus* (see Niwa 1998 for other fish species).

Shoal shape and swimming speed

Within the constraints imposed by the spatial and size distribution of shoals, the rates of shoal encounter will be further influenced by shoal shape and swimming speed. The shape of a shoal will influence the rates of encounters between shoals. There is variability in the shape (Partridge 1980; Nøttestad *et al.* 1996) and density (Pitcher 1980; Nøttestad *et al.* 1996) of fish shoals. In general, however, shoaling fish tend to form an ellipsoid or an oblate spheroid elongated in the direction of travel (Pitcher 1980), with the horizontal dimensions being greater than the vertical (Fréon and Misund 1999). The shape of a shoal can, in some cases, partly be constrained by environmental factors. The effective depth of a shoal, for instance, may be limited in shallow water by the bottom substrate, or in a lake by a thermocline, or possibly in large pelagic shoals by differences in pressure (Pitcher 1980).

The behaviour and shape of shoals can differ depending on the motivational state of individuals, which changes rapidly in response to external and

internal factors (Keenleyside 1955), including predation risk (Partridge 1980; Magurran and Pitcher 1987), nutritional state (Robinson and Pitcher 1989a,b; Nøttestad *et al.* 1996) and swimming speed (Blaxter and Hunter 1982).

The swimming speed and the turning angle of a shoal will also determine the frequency at which it encounters other groups. The number of individuals in a group can influence group velocity (Romey 1996), as may the internal state of fish within a shoal. For example, during times of migration, shoals of herring swim faster (1.44 m s^{-1}) and on relatively straight trajectories; however, feeding shoals show higher turning rates and swim more slowly (1.23 m s^{-1}) (Nøttestad *et al.* 1996).

Empirical evidence of the rates of shoal encounters in the field

Empirical data on the rates of shoal encounter are largely missing from the literature. However, a small number of investigations have quantified the rates of shoal encounter for free-ranging fish shoals (Pitcher *et al.* 1996; Mackinson *et al.* 1999; Krause *et al.* 2000b). As predicted by theory, the rates of shoal encounter were dependent on the spatial distribution of the shoals whilst intershoal distances were relatively low for small freshwater fish, facilitating frequent encounters (Krause *et al.* 2000a; Croft *et al.* 2003). In banded killifish *Fundulus diaphanus* and golden shiners *Notemigonus crysoleucas*, each shoal had an encounter occurring on average every 1.1 min (Krause *et al.* 2000b), whilst guppy (*Poecilia reticulata*) shoals met every 14 s (Croft *et al.* 2003). In species of pelagic marine fish, shoals appeared to be more widely dispersed within the environment resulting in lower rates of shoal encounters. Investigations on interactions between herring shoals (Pitcher *et al.* 1996; Mackinson *et al.* 1999) revealed that shoal encounters were surprisingly frequent, given their spatial distribution, occurring on average every 13.7 min (Pitcher *et al.* 1996). These shoals were observed in coastal Norwegian waters where, in spring, fish predators of herring are plentiful and planktonic food grows in abundant small-scale patches. Further offshore, at the polar front for example, herring schools are more scattered, and thus probably meet less often (Fernö *et al.* 1998; Nøttestad *et al.* 2002). The rates of shoal encounter may show a diurnal pattern; for example, interactions between herring shoals occurred more frequently by night than by day (Mackinson *et al.* 1999). Intensification

of clustering of shoals in the night (Mackinson *et al.* 1999) could explain the increase in the rate of shoal encounter.

Factors influencing encounter outcomes

A number of factors may influence the outcome of a shoal encounter, including phenotype, sex and familiarity. In free-ranging shoals of the banded killifish, differences in body length and/or species between the shoals was important, but not the shoal size or the duration of shoal encounters (Krause *et al.* 2000b). In this section, we discuss the factors influencing the outcome of shoal encounters.

Phenotype

Predation risk for an individual is dependent on the homogeneity of group composition and the size of the group with which it associates (Theodorakis 1989). Laboratory investigations have demonstrated that individual shoal choice is often dependent on the phenotype of potential shoal mates (Pitcher and Parrish 1993). Descriptive field investigations support these findings, observing that shoals are assorted by phenotype measured by characters, such as body length and species (see Krause *et al.* 2000a for a review). This suggests that the outcome of shoal encounters is not random but that an element of active choice is involved (Krause *et al.* 2000b; Svensson *et al.* 2000). Passive sorting mechanisms, such as differential swimming speeds resulting from the positive relationship between body length and swimming speed (Blaxter and Holliday 1969), could also result in assortment by body size (Nøttestad *et al.* 1999) and have been suggested as a sorting mechanism in other taxa, such as ungulates (Gueron *et al.* 1996) and krill (Watkins *et al.* 1992), but have generally not been sufficient to explain observed dynamics in fish shoals (Pitcher and Parrish 1993).

Sex

The benefits of intershoal exchange in some species are dependent upon the sex of the individual. For example, male guppies benefit from intershoal exchange during encounters by increasing the number of females mated with (Kelley *et al.* 1999) and by encountering novel females that are more receptive to their displays (Hughes *et al.* 1999). Females, on the other hand, are expected to exchange shoals less freely due to the benefits of shoal fidelity (discussed

below). Croft *et al.* (2003) found that male guppies were involved in shoal encounters twice as frequently as females, and also moved between shoals more rapidly than did females.

Familiarity

The evolution of co-operative behaviour may depend on the rate at which social groups break up and new groups form, and on assortment by individuals during encounters (Michod and Sanderson 1985; Toro and Silio 1986; Mesterton-Gibbons 1992). Stability of groups tends to favour the evolution of reciprocal altruism, allowing partnerships to develop between individuals (Peck 1993). Mobility of individuals and high rates of intergroup exchange could constrain the evolution of reciprocal altruism, allowing free-riders, or individuals that do not reciprocate to move rapidly through a population and exploit co-operative individuals (Enquist and Leimar 1993). Therefore, during a shoal encounter there may be advantages of remaining with familiar individuals, including reduced risk of predation (Chivers *et al.* 1995) and increased feeding rates (Metcalf and Thomson 1995), and this may select against intershoal transfer of individuals during shoal encounters.

Despite the number of laboratory investigations that have reported individual recognition and preferences for familiar individuals (see Krause *et al.* 2000b for review), there is only limited evidence that familiarity influences the outcome of shoal encounters for free ranging fish. Most older literature shows no evidence for shoal fidelity (see Pitcher and Parrish 1993 for review), but using sonic tagging and remote detection of several individual yellowfin tuna at Hawaii, Klimley and Holloway (1999) have produced evidence of both shoal and site fidelity over a time scale of 9 months. Guppies were found to prefer shoaling with familiar conspecifics in the wild (Griffiths and Magurran 1997) whilst sticklebacks, *Gasterosteus aculeatus*, were observed to have consistent partner preferences for at least 5 days (Ward *et al.* 2002). In contrast, Helfman (1984) found no evidence for shoal fidelity in individually tagged yellow perch (*Perca flavescens*). Similarly, Hoare *et al.* (2000), using a mark and recapture procedure on the banded killifish, found that individuals mixed extensively after just 24 h.

High intergroup exchange places a constraint on the evolution of reciprocal altruism such that it is unlikely that this behaviour will evolve in systems where the rates of fission and fusion are high (Seghers

1981; Hoare *et al.* 2000; Krause *et al.* 2000a). However, there is some indication that reciprocal altruism occurs in small shoaling species that frequent shallow fresh water (e.g. sticklebacks: Milinski 1987; Utne-Palm and Hart 2000; guppies: Dugatkin 1988). Conditions for the evolution of reciprocal altruism may be more favourable in these species, and further work in this area is eagerly anticipated.

Implications of shoal encounters

The rates and outcomes of encounters between 'open' groups, where individuals are free to join and leave, will have both ecological and evolutionary implications. For example, the dynamics of shoal encounters will influence the rate at which transmissible factors, such as disease and information will spread through a population. In addition, information on the frequency of encounters between shoals may have implications for the management of commercial stocks. Finally, the outcome of shoal encounters will determine the stability of groups over time, a property known to be important in the evolution of reciprocal altruism. In the remainder of this section, we discuss the implications of shoal encounters in detail.

Disease transmission

The spatial structure of a population and the duration, frequency and outcome of interactions between groups are likely to play a crucial part in the spread of pathogens through a population (Loehle 1995; Mollison and Levin 1995). Low rates of intergroup contact and exchange may help to reduce pathogen transmission. However, this conflicts with the need for individuals to exchange between groups in order to adjust group size in response to the prevailing ecological and behavioural conditions (Loehle 1995). When the rates of intergroup contact and exchange are high (e.g. Seghers 1981), a pathogen may spread as it would in a continuous population (Loehle 1995). The patterns and dynamics of group encounters are therefore important in predicting, controlling or simply understanding the spread of an infective agent through a population and will consequently have important implications for wildlife management.

Information transmission

Just like disease, cultural traits can also be acquired horizontally within generations (Giraldeau 1998) and be transmitted both between and within groups

(Coussi-Korbel 1995). Social learning is facilitated within group-living species (Klopfer 1961), allowing the opportunity for accessing and utilising public information, such as information about places, objects and behaviour (Giraldeau 1998). The effect of group encounters on the transmission of information between groups has not received adequate consideration.

Social learning has been demonstrated in shoaling fish in a number of areas, including foraging locations (Pitcher and Magurran 1983), foraging routes (Laland and Williams 1997), predator recognition (Magurran and Higham 1988) and migration routes (Helfman and Schultz 1984). Under a given set of constraining factors, the rate and outcomes of group encounters could limit information flow within a population. For example, Pyanov (1993) found that after capture, fish are more wary of fishing gear and will often exchange shoals, creating the potential for the transfer of information. It is likely that naive fish in the new shoals will learn to avoid fishing gear, as experienced fish initiate the shoal level reaction to fishing equipment (Soria *et al.* 1993).

Commercial fish stocks

For shoals to encounter and interact, they need to be in close proximity. Encounters between shoals are required to allow the individual to make adjustments to the size of the shoal with which it associates, in response to environmental and behavioural changes. Intense fishing reduces population density, but mean shoal size may nevertheless be maintained (Ulltang 1980), reducing the rates of shoal encounters but increasing the catchability of fish to human fishers, ultimately leading to a stock collapse (Pitcher 1995). It is hypothesised that this will result in fish moving more rapidly in areas of low density until encountering other shoals, causing them to become concentrated in a local area (the size maintenance hypothesis of Pitcher 1997). The maintenance of a stable shoal size in association with a reduction in the range of movement of the fish means that a constant catch per unit effort can be maintained leading to an exacerbated stock collapse. The size maintenance hypothesis may provide a diagnostic tool for the identification of stock collapse, which would be achieved through the monitoring of the behavioural and spatial parameters of shoaling fish.

Although encounters between shoals may be fundamental to the adaptive significance of shoaling behaviour for the individual, very little is known

about the effects that commercial fishing has on shoal encounters and their outcomes. In depleted fish stocks, the size maintenance hypothesis suggests that movement of individuals between shoals may increase with an increase in fishing pressure and the constant resorting of individuals could disrupt behavioural processes with unknown consequences (Parrish 1999).

Future directions

Patterns of group structure are mediated at the level of the individual. Thus, to understand group and population structure, we must be able to link individual behaviour to population level biology. An understanding of how the phenotype and motivational state of individuals within groups affect the fission and fusion of shoals is a big step in achieving this. We need to assess the role of ecological conditions in mediating individual behaviour, and consequently the movement, structure and encounter rates of fish shoals. Manipulative investigations, both in the laboratory and in the field, are required to address these questions. Laboratory investigations need to allow fish to form relatively unrestricted shoals in large tank-arenas so that shoal encounters can occur under conditions approximating those of free-ranging shoals. Arena experiments such as these will allow shoal encounters to be observed, controlled and manipulated in terms of shoal composition, individual body lengths, sex ratios and shoal size. In the wild, the scale of the arenas can be increased, with pens being placed *in situ*, especially in shallow fresh water environments, that hold a number of shoals, allowing unrestricted multiple encounters to occur whilst manipulating population density, size and frequency of phenotypes.

In addition, field observations are required to provide background information on natural population density, shoal-size distribution, shoal dimensions and velocity. The rate and outcomes of shoal encounters need to be quantified for the majority of study systems reviewed here. The marking of individual fish of a known phenotype and motivational state, releasing, tracking and recording of the outcomes of shoal encounters will provide information on how ecological conditions influence individual behaviour. Although tracking individual fish is technically difficult in pelagic shoals, the method is suitable for species of small fresh water fish (e.g. guppy, Croft *et al.* 2003). Furthermore, the marking and releasing of a number of individual shoaling fish into a study

system followed by a period of recapture (Hoare *et al.* 2000) or detection with automated acoustic listening devices (Klimley and Holloway 1999), or archival tags can provide information on the stability of shoals through time.

In conclusion, we know from evolutionary theory that rapid and continuous individual shoaling decisions that we observe are likely to be tracking changes in the selective pressures on that individual as feeding, predation, mating and other environmental parameters change (Pitcher and Parrish 1993). As detection of change may be lagged, information may be incomplete or misleading and the fish may employ tactics to hedge uncertainty.

Artefacts may flaw laboratory experiments unless these are carefully designed and executed, whilst field observations are constrained by the limited ability to observe larger numbers of individual fish for long periods. Despite these potential obstacles, a further understanding of what happens when shoals meet will likely provide significant evolutionary insight into fish shoaling behaviour and is likely to have important implications for the management of wild stocks.

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