12 FUNCTIONS OF SHOALING BEHAVIOUR IN TELEOSTS

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Predators and food are the keys to understanding fish shoals; synchronised co-operation defeats predators, and optimal food gathering in shoals reflects a shifting balance between joining, competing in, or leaving the group. In the wild, predators may arrive while shoaling fish are feeding, and so vigilance is a crucial behaviour. Once detected, predator defence takes precedence over feeding, since an animal's life is worth more than today's dinner.

Travelling fish schools display impressive co-ordination and were once viewed as egalitarian leaderless societies (Breder 1954; Shaw 1962; Radakov 1973) in which co-operation preserved the species. In contrast to such classical group-selectionist views, contemporary ethology reveals social behaviour to be nothing more than animals co-operating only when it pays. Distinct coexisting behavioural strategies of sneaking or scrounging are often evolutionarily stable (Barnard 1984; Parker 1984). In fish shoals, homogeneity and synchrony have been overemphasised; recent work reveals that individuals constantly reappraise the costs and benefits of being social. Reappraisal is reflected in decisions to join, stay with or leave groups, and observed behaviour allows us a glimpse of these underlying tensions. In teleosts, a major constraint is swimming; fish physiologically and morphologically adapted to cruise fast, such as mackerel, break ranks less often to avoid the alternative of rapid dispersal. Under some circumstances, however, the underlying tensions between individuals may be uncovered in even the most phalanx-like of cruising fish shoals.

Shoaling behaviour has attracted much speculation about function (e.g. Shaw 1978; Partridge 1982a), but until recently few critical experiments have been performed. The aim of this chapter is to review in the light of current theory the areas where such evidence of function has been gathered. The arguments presented in this chapter do not support the views of Hamilton (1971) or Williams (1964) that shoaling is primarily a matter of cover-seeking, or Breder's (1976) view that hydrodynamics is the major factor. Furthermore, I will present arguments that, for fish shoals, simple attack avoidance and attack dilution have been incorrectly associated with selection for grouping behaviour.

Definitions of Shoaling

A clarification of terms will facilitate discussion of function, since shoaling behaviour continues to suffer from the semantic confusion of the 1960s

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(Keenleyside 1955; Hemmings, 1966; Radakov 1973). Groups of fish which remain together for social reasons are best termed 'shoals' (Kennedy and Pitcher 1975; Pitcher 1983), in an analogous way to the term 'flock' for birds. Defined as a social group of fish, 'shoal' has no implications for structure or function.

Synchronised and polarised swimming groups are termed 'schools'. Schooling is therefore one of the behaviours exhibited by fish in shoals (Figure 12.1), and schools have a structure measured in polarity and synchrony. Shoals which travel are almost bound to school on the way. Other action patterns of fish in social groups, such as foraging or anti-predator manoeuvres, can be accommodated within the taxonomy outlined in Figure 12.1 (Pitcher 1983).

In North America the term 'school' is still used to cover both phenomena distinguished in this chapter. The dichotomy between 'facultative' and 'obligate' schooling fish introduced by Breder (1959) has, however, been largely rejected in favour of direct estimates of the proportion of time which shoaling fish spend travelling in polarised groups

Figure 12.1: Relationship of Definitions of Shoaling and Schooling Behaviour Illustrated by a Venn Set-theory Diagram. Criteria for the two behaviours are indicated. Three other behaviours are superimposed as examples of how other functional categories relate to these terms. Some further specific examples of anti-predator tactics are shown: spawning and foraging behaviours might be similarly elaborated. Unlike previous definitions, this scheme can augment descriptions of observed behaviours (from Pitcher 1983)