

# A review of multi-species foraging associations in fishes and their ecological significance.

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**Abstract** Multi-species fish foraging associations occur whenever individuals of one or more species forage in association with one another. Although common, the theoretical background regarding foraging benefits and predator avoidance for multi-species fish foraging associations is sparse and poorly developed. However there is a vast literature on multi-species foraging associations in birds, and on the formation of single-species fish shoals, which proposes that these associations increase food availability and reduce the risk of predation compared with foraging alone. In this review paper we assess the role these factors play in determining multi-species foraging associations in fishes. A case study of foraging in the tropical benthic carnivorous goatfish, *Parupeneus barberinus*, is used to illustrate the importance and complexity of multi-species foraging associations to reef trophodynamics. From a review of the entire available literature of multi-species fish foraging associations, that comprises less than 45 papers, these associations could be categorised into two main types, *attendant* associations and *shoaling* associations. *Attendant* associations are small, comprising one or two *nuclear* individuals of one species that lead foraging activities, and several *associate* or *attendant* fishes. By contrast, *shoaling* associations are large, and the distinction between the fishes that lead foraging activities and those that attend is less clear. *Attendant* associations can be further divided into 4 subtypes: following and scavenging; interspecific joint hunting; hunting by riding; and aggressive mimicry. This classification is a first attempt to provide a comprehensive framework to enable the systematic evaluation of the ecological significance of these associations, and evolutionary forces that drive them.

## Introduction

Multi-species fish foraging associations occur whenever individuals of two or more species of fishes forage together. These associations have received little attention despite their potential importance to coral reef trophodynamics. Less than 45 studies dealing with multi-species fish foraging associations, mostly from the Caribbean and the Red Sea, have been published in the last 30 years. The theoretical background regarding the ecological significance of foraging associations is therefore sparse and poorly developed for fish. By contrast there is an extensive literature on the adaptive significance to individuals of multi-species feeding associations in birds (Crook, 1965; Morse, 1970; Krebs, 1973; Bertram, 1978) and single species fish shoals (reviewed by Pitcher & Parrish, 1993). In the present review, these two sources of literature are used to broaden the theoretical background within which research on multi-species fish foraging associations is interpreted.

Multi-species fish foraging associations can range from simple to complex, and from highly transient to obligate associations. They are formed by a wide range of fish species, from many families, and include most trophic groups. For example the carnivores that form foraging associations include the Mullidae, Nemipteridae, Labridae, Lethrinidae, Balistidae and Muraenidae while herbivores include species from the Scaridae and Acanthuridae. Many multi-species foraging associations involve interactions between members of different trophic groups. While the effects of each trophic group on the coral reef community have been explored in isolation (Bakus, 1972; Choat, 1982; Choat, 1991; Jones *et al.*, 1991), little attention has been given to the effects of foraging

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interactions between trophic groups on the trophodynamics of coral reef communities. The basis of multi-species foraging associations appears to be that they increase the range of usable resources, such as food and space, to individuals or groups of fishes not participating in these associations. In addition they are likely to influence benthic invertebrate and algal community structure, and the small-scale distribution and abundance patterns of fishes. Ontogenetic changes in fish size, diet and foraging behaviour may also influence the type of association that individuals participate in (Ormond, 1980; Strand, 1988).

There is currently no system of classification for the diverse range of multi-species fish foraging associations described in the literature. Thus a systematic and comprehensive framework within which to evaluate the ecological significance and the evolutionary forces that drive these associations is needed. One goal of this review is to describe and discuss a classification scheme that encompasses the full range of multi-species fish foraging associations described in the literature. In addition we address the following questions. What families and species most frequently participate in these associations, and what trophic groups do they represent?. What is the adaptive significance of multi-species fish foraging associations to participating individuals? How have studies quantified the costs and benefits of these associations, and what conclusions did they reach? How important are these associations to the community dynamics of coral reefs?

Finally we identify the important features of these associations by drawing on examples of the foraging associations formed with the dash-dot goatfish, *Parupeneus barberinus*, in the Great Barrier Reef. *Parupeneus barberinus* is an important tropical benthic microcarnivore that forages vigorously over soft sediments adjacent to coral reefs. It has a considerable impact on the soft sediment invertebrate community as it is both common and abundant, and devotes more than 50% of its time budget to foraging. The disturbance it creates in the sediment while foraging exposes prey items and attracts many fish species to engage in foraging associations.

### **Adaptive significance**

Most hypotheses regarding the benefits and costs of foraging in groups have been developed for multi-species bird flocks and single species fish

shoals. These hypotheses fall into two main categories: foraging benefits (Ward & Zahavi, 1973; Morse, 1977; Bertram, 1978; Pulliam & Millikan, 1982; Caraco & Pulliam, 1984; Pulliam & Caraco, 1984; Barnard, 1985; Clark, 1986; Spotte, 1996) and predator avoidance (Ward & Zahavi, 1973; Morse, 1977; Bertram, 1978; Pulliam & Millikan, 1982; Caraco & Pulliam, 1984; Pulliam & Caraco, 1984; Barnard, 1985; Clark, 1986). The hypotheses are often not mutually exclusive, so more than one explanation may be necessary to account for the benefits of different types of multi-species foraging associations (Krebs, 1973).

Group feeding can increase an individual's ability to catch otherwise unobtainable prey. This may apply to all members of a group in mutualistic associations or a subsection of the group in commensal associations. It is also possible that some members of the group are disadvantaged due to competition from the foraging of other group members. In terms of advantages, single species fish shoals benefit by gaining access to defended algal resources of territorial herbivores that are not available to individuals (Robertson *et al.*, 1979). In multi-species insectivorous bird flocks individuals gain access to insects that are flushed out by the movement or 'beating' of the flock as a whole (Rand, 1954; Morse, 1970; Morse, 1977). In some feeding associations one species or individual obtains food by interacting with other species or individuals that forage for food (Barnard, 1985). This may take the form of kleptoparasitism as found in hawks, eagles or hyenas (Barnard, 1984), or more commonly through scavenging as shown in single and multi-species bird flocks (Barnard & Sibly, 1981; Barnard *et al.*, 1982).

Social foraging may enhance the ability of some individuals in a group locate and consume prey through the transfer of information regarding the location and/or the nature of potential food sources. Enhanced prey detection occurs when individuals are attracted to a food source or patch when behavioural cues of successful foraging are displayed by other individuals in the group (Pulliam & Millikan, 1982; Ryer & Olla, 1992). Enhanced prey detection is most important for animals foraging on scarce, patchily distributed and unreliably located food sources (Giraldeau, 1984; Clark, 1986; Ryer & Olla, 1995). Enhanced prey detection can operate on large spatial scales, whereby animals find large prey

aggregations and small spatial scales, when individuals are attracted to food patches through social attraction within a foraging group (Waite, 1981). The advantages of social foraging are greater to multi-species groups compared with single species groups as individuals benefit from the combined searching skills of each individual species (Krebs, 1973). Movement patterns of multi-species finch flocks in the Mohave Desert indicated that feeding was maximised in areas where flocks travelled while depleted areas were avoided (Cody, 1971). By contrast when birds fed alone they would often search for food in areas previously visited by other birds. Social facilitation results when foraging by some individuals stimulates foraging in other group member, thus increasing their food intake (Krebs *et al.*, 1972).

Foraging in groups may also facilitate earlier detection of predators (Magurran & Pitcher, 1983; Morgan, 1988). Alarmed conspecifics trigger a change in behaviour of other group members to increased vigilance or hiding. Fish interpret conspecifics feeding as a sign that it is safe to feed, thus spend more time feeding and less maintaining antipredator vigilance (Godin, 1986; Magurran & Higham, 1988; Ryer & Olla, 1991; Magurran, 1993). Other predator avoidance benefits include injury to predators by prey, eg mobbing in birds (Pulliam & Millikan, 1982), decreasing the chance of an individual becoming the target of the predator (Bertram, 1978), individuals in a group using each other for cover (Morse, 1977), and confusing the predator by preventing it from focusing on a particular target (Pulliam & Caraco, 1984).

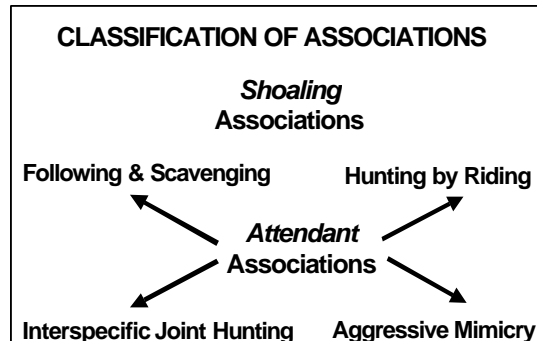
### Classification scheme

Multi-species fish foraging associations can usefully be divided up into two broad classification types, *shoaling* associations and *attendant* associations (Figure 1). Both types of association are characterised by two key elements, the nuclear species and associate species. One or more individuals from the nuclear species forms the core of the association and leads in the foraging activities, and is responsible for forming and maintaining the foraging association (Strand, 1988). One or more associate species follow the nuclear species for varying periods of time. This is mostly while the nuclear species is foraging, but also while travelling between foraging events (Strand, 1988). In general it is hypothesised that associate species benefit from the association while the

nuclear species does not benefit, and may even be disadvantaged due to competition for food. However this hypothesis does not hold for all types of multi-species foraging association engaged in by fishes.

Mixed species *shoaling* associations are generally larger than *attendant* associations and may comprise several hundred individuals. The nuclear species generally comprises more individuals than the associate species in the group combined: there may be one or more species of associates. Tropical fishes involved in *shoaling* associations are predominantly herbivorous scaridae and acanthuridae (Ogden & Buckmann, 1973; Barlow, 1974; Robertson *et al.*, 1979; Wolf, 1983), however these associations have also been described for opportunistic feeders such as the labridae, blennidae and pomacanthidae (Montgomery, 1981; Foster, 1987).

**Figure 1.** Classification scheme of multi-species fish foraging associations. There are two major types of association, *shoaling* associations and *attendant* associations. There is only one type of *shoaling* association while *attendant* associations are further divided up into four sub-types (After Ormond 1980).



*Attendant* associations are usually small and have a maximum of around 10 individuals. They consist of one or two nuclear individuals of one species followed by associates of one or more species. While there is only one type of *shoaling* association, *attendant* associations comprise four different types. These are 1). 'following and scavenging', 2). 'interspecific joint hunting', 3). 'hunting by riding' and 4). 'aggressive mimicry'. These comprise the four types of multi-species foraging association recognised by Ormond (1980) in the only previous review of these associations. Interestingly *shoaling* associations were not described in Ormond's (1980) review

although 17 of the 40 papers that we reviewed focused on this type of association.

'Following and scavenging' associations are by far the most common type of *attendant* associations. They are usually formed between large predatory carnivores, such as mullidae, muraenidae and octypodidae as the nuclear individuals, and one or more associates, usually carnivores or opportunistic feeding species (Karplus, 1982; Strand, 1988; Forsythe & Hanlon, 1997). Herbivores, such as scaridae, and acanthuridae, occasionally act as the nuclear species in these associations (Ogden & Buckmann, 1973; Montgomery, 1975; Ormond, 1980).

'Interspecific joint hunting' occurs when two species of active predators hunt together. There is little distinction between the nuclear and associate individuals and the species involved can readily switch from one role to another. 'interspecific joint hunting' has been described between the elephant wrasse, *Gomphosus caeruleus* and the yellow goatfish, *Parupeneus chryseredros*, and between serranids such as *Cephalopholis argus* and *Plectropomus maculatus* (Ormond, 1980).

'Hunting by riding' occurs when a predatory associate swims alongside or above a nuclear species that is either non-predatory or feeds on different prey. The classical example of this is the trumpet fish, *Aulostomus maculatus*, (Fricke, 1972; Kaufman, 1976; Ormond, 1980; Aronson, 1983) which rides with fishes such as the foxface, *Siganus vulpinus*, that feeds on benthic algae. It has also been documented for the cornetfish, *Fistularia petimba*, (Hobson, 1968), the serranid, *Diploprion drachi*, and labrids such as *Cheilinus diagrammus*, *Cheilio inermis* and *Thalassoma purpuraceum* (Ormond, 1980). Finally 'aggressive mimicry' occurs when associate species is a predator and it mimics the nuclear species which is harmless. It has mostly been reported in the Blennidae that mimic the cleaning labrids they forage with and prey on the species that are being cleaned (Hobson, 1969), however it has also been documented for a range of other species (Ormond, 1980).

These four types of associations are not independent of one another, and it may be difficult to unequivocally assign some feeding associations onto one category or another. The lutjanid associate *Ocyurus chrysurus* is a mimic

of the nuclear mullid *Mulloides martinicus* however it also scavenges food flushed out by this nuclear species (Sikkel, 1992). In addition the congeneric Indian goatfish *Parupeneus indicus* forages with *P. barberinus*. These two species have similar markings, white bodies with yellow and black along the sides, and can be the nuclear or associate individual. Similar sized individuals tend to forage together, at times scavenging from the other's feeding scars, then moving along the sandy bottom feeding side by side. Thus they demonstrate a combination of 'aggressive mimicry', 'joint hunting', and 'following and scavenging'.

### **Benefits and costs of multi-species fish foraging associations**

Both the nuclear and the associate species are thought to benefit in multi-species *shoaling* associations, i.e. they are mutualistic associations, by swamping territorial herbivores and gaining access to defended resources. However, of the 17 papers that comprise the bulk of the available literature, only 9 studies attempted to quantify the costs and benefits of multi-species *shoaling* associations for individuals. Four studies quantified this using bite rates as a measure of energetic benefit. These studies showed that large multi-species shoals of scarids and acanthurids had higher bite rates in defended territories than smaller shoals (Robertson *et al.*, 1976; Wolf, 1983; Foster, 1985a; Reinthal & Lewis, 1986). In addition Foster (1985b) found that larger groups of scarids and acanthurids spent more time feeding in *Stegastes dorsopunicans*' territories with higher algal biomass compared with smaller groups. Wolf (1987) used time budgets to show that *Acanthurus bahianus* spent more time feeding when part of a group than when alone. In addition, large multi-species shoals of wrasses only formed when eggs defended by territorial pomacentrids were available. This enabled them to gain access to the eggs (Foster, 1987).

The benefits to the nuclear and associate species in *attendant* associations vary depending on which of the four types of *attendant* association is being considered. In general it is thought that the associates benefit through the exposure of food items by the feeding activities of the nuclear species. This food would not be available to the associates while foraging alone. There may also be an advantage due to enhanced prey detection. On the other hand the nuclear species is thought not to benefit from *attendant*

associations, in which case these associations would be examples of commensalism. Alternatively the nuclear species may be disadvantaged due to competition.

There is little quantitative evidence presently available to show costs and benefits to the individuals participating in multi-species foraging associations. For example, only three of nineteen studies of 'following and scavenging' associations quantified bite rates as a measure of the potential energetic benefits to associate species. Aronson & Sanderson (1987) found that the wrasse, *Halichoeres garnotti*, had higher strike rates at the substratum when foraging in association with the goatfish, *Mulloidichthys martinicus* and *Pseudupeneus maculatus*, than when alone. Increased feeding and success rates were also shown for the lutjanid, *Ocyurus chrysurus*, feeding with the mullid, *M. martinicus*, compared with solitary foraging (Sikkel, 1992), and for 3 species of *Cephalophois* (Serranidae) following *Octypus cyaneus* (Diamant & Shpigal, 1985). In addition Mather (1992) used time budgets to show benefits for the labrid, *Halichoeres bivittatus*, and the blenny, *Labrisomus nuchipinnis*, that followed the octopus, *Octopus vulgaris*. However the presence of associate fishes may reduce the effectiveness of the well developed camouflage used by octopus to avoid predation and therefore represent a cost for octopus (Mather, 1992).

By contrast, Baird (1993) found that the nuclear wrasse, *Halichoeres maculatus*, had both increased bite rates and search rates when followed by the associate bar jack, *Caranx ruber*. This was possibly due to social facilitation (Baird, 1993). *Caranx ruber* however had higher bite rates but lower search rates when following the wrasse than when alone, indicating increased prey detection efficiency. *Halichoeres maculatus* also actively followed *C. ruber* when the latter was foraging indicating that the roles of nuclear and associate were reversible (Baird, 1993). Individuals in this association may benefit from 'following and scavenging', through increased access to food, and 'joint hunting', due to enhanced prey detection. Increased feeding rates or faster patch discovery by group foragers may however be interpreted incorrectly as benefits of group foraging. It may be that individuals foraging in a group need to exert more effort in order to obtain their share of the available resource (Clark, 1986). Thus the association between the congeners *P. barberinus* and *P.*

*indicus*, may benefit both species through increased access to food, enhanced prey detection and social facilitation, however it may also result in competition between the two species. At present there are no data to quantify the advantages or disadvantages for either species.

In 'hunting by riding' the predatory associate uses the cover provided by the nuclear individual to gain access to prey that is elusive and visually wary. It is however not clear whether participating in this type of association results in costs or benefits to the nuclear species (Aronson, 1983). Similarly 'aggressive mimicry' is thought to allow the associate easier access to its prey, however Hobson (1969) found that this was not true for the blennies from the genera *Runula* and *Aspidontus* that imitate the cleaning labrid *Labroides dimidiatus*. These blennies were not approached by large fishes for cleaning in the way that the cleaning labrids are. They were however able to attack these large fishes as they passed by and this may represent a benefit of 'aggressive mimicry' to the blennies (Hobson, 1969).

#### **The importance of foraging associations: a case study**

*Parupeneus barberinus* is a tropical benthic carnivore that was found to be both common and abundant around Lizard Island in the northern GBR. Its distribution and abundance was investigated using 5 replicate 200m by 10m strip transects at each of 14 locations around Lizard Island. These locations represented the full range of depths and exposure types for Lizard Island. *Parupeneus barberinus* was found on the reef slope and base at each of the 14 locations sampled. It was the most abundant of the nine mullid species found around Lizard Island, with a mean of  $6.1 \pm 0.5$  per  $2000\text{m}^2$  for all locations combined. The lowest location mean was  $2.4 \pm 0.7$  per  $2000\text{m}^2$  for an exposed deep location, while the highest was  $12 \pm 3.1$  per  $2000\text{m}^2$  for a sheltered deep location.

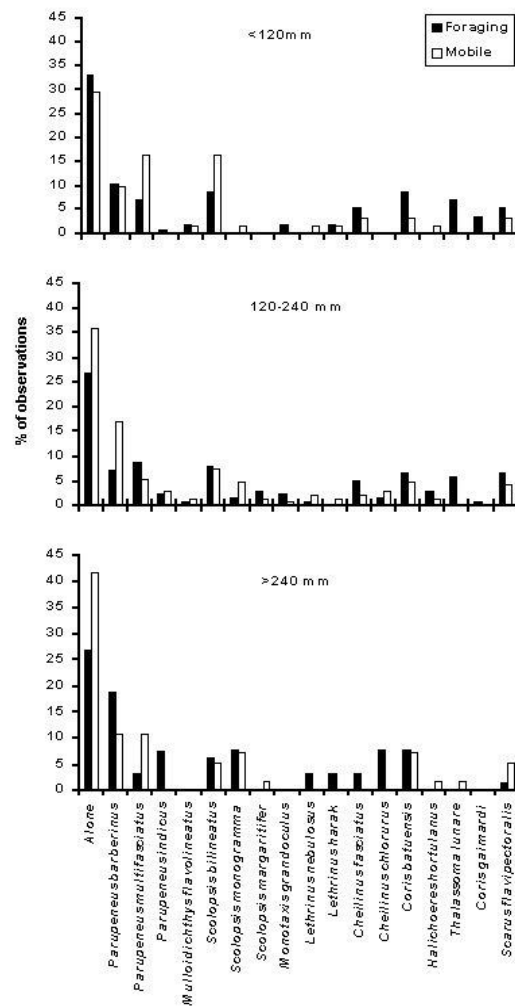
The foraging associations formed with *Parupeneus barberinus* at Lizard Island were investigated using instantaneous sampling. For each of 435 observations the behaviour of *P. barberinus* (either foraging or travelling) was recorded as well as whether *P. barberinus* was alone or with other fishes. Fishes in association with *P. barberinus* were identified to species. Total length of *P. barberinus* was also recorded.

This was grouped into 3 size classes: 1) Small <120mm, 2) Medium 120-240mm and 3) Large >240mm, in order to investigate ontogenetic changes in the foraging associations formed with *P. barberinus*. Nine and a half hours of focal animal observations of *P. barberinus* were recorded to determine the duration of foraging associations and time spent alone.

Multi-species foraging associations were very important for *P. barberinus* in terms of time. *Parupeneus barberinus* spent approximately half of its time foraging and only 30% of this time was spent foraging alone. Seventy percent of the foraging time was spent as the nuclear species in multi-species foraging association. However the associations formed with *P. barberinus* were also important in terms of group size and composition. Most of the foraging associations formed with *P. barberinus* had between 1 to 5 individual associates but some were much larger, to a maximum of 17 associates. Fifty percent of the associations had more than one associate individual and 40% of the associations had more than one associate species.

The mean length of foraging bouts for *P. barberinus* were significantly larger when it was part of a foraging association, ( $21 \pm 0.6$ se seconds,  $n = 364$ ), compared with when foraging alone, ( $16 \pm 0.4$ se seconds,  $n = 556$ ). The reasons for this are not clear but are unlikely to represent lower foraging efficiency due to direct interference by the associate species, as behavioural observations showed that associates do not feed directly from the substratum until *P. barberinus* has stopped foraging. The increased length of foraging bouts when in association may be related to the observation that associates were attracted to *P. barberinus* which foraged for longer periods of time, as longer foraging time may be a sign of successful foraging on a good source of food. Unfortunately, there are no data available to quantify this observation. Interestingly, Spotte (1996) found that foraging associations formed with the yellow goatfish, *Mulloidichthys martinicus*, were considerably longer (mean  $120 \pm 21$ se seconds) than those of *P. barberinus* in this study.

Altogether 17 species from 11 genera and 5 families (Labridae, Nemipteridae, Mullidae, Lethrinidae and Scaridae) formed 93% of the foraging associations with *P. barberinus* (Figure



**Figure 2** Percent of observations that *P. barberinus* was alone or with associate fishes for 93% of observations of each of two behaviours: foraging and travelling.

2). In spite of this diversity in associate-species the majority of foraging associations that were formed with *Parupeneus barberinus* were 'following and scavenging' associations. In this type of association *P. barberinus* acted as the nuclear species, vigorously digging in the substratum, and the associates hovered close by and would often follow *P. barberinus* while travelling between foraging bouts (Figure 2). The associates foraged on prey items liberated while *P. barberinus* was feeding, and from the feeding scar when *P. barberinus* had finished.

The most important family, in terms of both the number of species involved and the proportion of associations they participated in, was the labrids (Figure 2). The wrasse species most commonly found in these associations were the yellow tailed coris, *Coris batuensis*, the red breasted maori wrasse, *Cheilinus fasciatus*, the moon wrasse, *Thalassoma lunare*, and the floral maori wrasse, *Cheilinus chlorurus*. Each of these species made up between 5 to 8 percent of the foraging associations with *P. barberinus*. However there were differences in the size-classes with which they associated. For example, *C. batuensis* and *C. fasciatus* associated with all three size classes of *P. barberinus*. By contrast *T. lunare* only foraged with small and medium sized *P. barberinus*, while *C. chlorurus* foraged primarily with the large and to a lesser extent medium *P. barberinus*, but not with the small individuals.

The next most important family was the nemipterids. The two important species from this family were the bridled monocle bream, *Scolopsis bilineatus*, and the monocle bream, *S. monogramma*. They were both found 8% of all foraging associations. Again there was an ontogenetic effect in that *S. bilineatus* foraged with all size classes of *P. barberinus* while *S. monogramma* was found primarily with large *P. barberinus* (Figure 2).

In general, the sizes of the nuclear and associate individuals were very similar in these associations. This pattern was also found for two important congeneric associate species *P. multifasciatus* and *P. indicus*. Juvenile *P. multifasciatus* were mostly found in foraging associations with small and medium size *P. barberinus*, however adults rarely formed foraging associations with *P. barberinus*, though they did travel together in mixed schools at times (Figure 2). By contrast, adult *P. indicus* was found predominantly in associations with large *P. barberinus*, yet juvenile *P. indicus* rarely formed foraging associations with small and medium *P. barberinus*. Strand (1988) found similar ontogenetic effects. Smaller juvenile *Mycteroperca rosacea* and *Bodianus diplotaenia* both spent more time as associates in foraging associations than larger adults. This is probably because juveniles feed on benthic invertebrates, that are flushed out by the nuclear species with which they associate, whereas the adults tend to be piscivores (Strand, 1988).

## Conclusion

Multispecies fish foraging associations are very important and *P. barberinus* provides a good example of why this might be the case. *Parupeneus barberinus* spends over half of its time foraging and 70% of that time is spent in foraging associations. This means that the foraging choices that it makes will have a major influence on the foraging behaviour of many other fishes. Thus the foraging activities of one species has a major impact on the distribution of the overall foraging effort of benthic carnivores and herbivores on coral reefs.

In spite of the demonstrated importance of foraging associations, these associations have seldom been studied and many of the existing studies have lacked a clear theoretical framework. This review has provided a classification scheme that places the existing studies into a context that will assist the development of a systematic approach to further research, especially with regards to the adaptive significance of the different types of foraging associations.

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