

Butterflyfish social behaviour, with special reference to the incidence of territoriality: a review

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Synopsis

Butterflyfishes (Chaetodontidae) are among the best studied of coral reef fishes. Feeding ecology and some aspects of behaviour have been firmly established. However, spacing behaviour remains controversial. Two major studies made in the 1970s concluded that the majority of species were not territorial. We suggest that these and other studies which have concluded that territories are not held have generally suffered from short observation periods, and have not mapped the ranges occupied by individuals. Further, low frequencies of agonistic behaviour have been interpreted as evidence of non-territoriality. By contrast, studies which have proven territoriality have had long observation periods and have mapped ranges. These have shown that territories are usually maintained with very little overt aggression. Spacing behaviour and feeding behaviour are clearly linked, with territoriality common among benthic-feeding species, especially obligate corallivores. Species with broad dietary flexibility tend to have flexible social systems, while plankton feeders are usually gregarious. The widespread occurrence of monogamy in butterflyfishes appears linked to territoriality, the majority of territorial species identified to date occurring predominantly as pairs. Data currently available suggest that this is because pair defence of the territory is more efficient than by individuals. However, several alternative hypotheses for the evolution of monogamy based on spawning constraints and predation risk cannot yet be ruled out.

Introduction

Butterflyfishes (Chaetodontidae) are a diverse family of very colourful fishes, primarily found in tropical waters. In the most recent taxonomic revision, Blum (1989) recognised 120 species in 11 genera. Adults of different species attain maximum sizes ranging from 10 cm to around 30 cm total length. Butterflyfishes are almost exclusively associated with coral reefs, although a few species are found in estuarine areas and over soft bottom habitats (Burgess 1978, Steene 1978, Allen 1979). Re-

gardless of genus, all butterflyfishes are deep-bodied and strongly compressed (Fig. 1).

The majority of species are corallivorous to varying extents, from obligate hard coral feeders (scleractinian corals) to facultative corallivores for which hard corals only constitute a small part of the diet (Hiatt & Strasburg 1960, Talbot 1965, Randall 1967, Reese 1973, 1975, Hobson 1974, Harmelin-Vivien & Bouchon-Navaro 1981, 1983, Sano 1989). A wide variety of other foods are taken, from benthic algae to plankton, and benthic invertebrates comprise the bulk of the diet of many species (Har-

melin-Vivien & Bouchon-Navaro 1983). No completely herbivorous species are known, although herbivory has been claimed for a few, based primarily on stomach contents data from small samples (Hiatt & Strasburg 1960, Talbot 1965).

The social behaviour of butterflyfishes has attracted considerable research during the past 25 years and their biology has been the subject of a recent symposium (Motta 1989). They now rank among the best known of tropical reef fishes but many questions remain, and some controversies are unresolved. Two aspects of their biology have been of particular interest: their conspicuous 'poster' colouration (Lorenz 1962) and its importance in social interactions within and among species, and the widespread occurrence of monogamy (Reese 1973, 1975, Ehrlich et al. 1977, Neudecker 1989). Lorenz (1962) hypothesised that poster colouration was a species-specific signal serving to space-out conspecific individuals in territories over the reef, and preventing unnecessary aggression between non-competing members of different species. He believed that all poster-coloured fishes were territorial, that all territorial fishes were poster-coloured and that intraspecific aggression between individuals of such species was both frequent and intense (Lorenz 1966). Since Lorenz proposed this theory a large body of data has been collected which indicates that it is an oversimplification. Many territorial fishes are not poster-coloured (e.g. adults of most territorial damselfishes) and many species are interspecifically territorial, recognising and aggressing against a broad range of species regardless of similarities or differences in colouration (Low 1971, Myrberg & Thresher 1974, Sale 1978, Thresher 1978). Additionally, studies of butterflyfishes, perhaps the most obviously poster-coloured fishes on coral reefs, revealed very low levels of intraspecific aggression in all but a few species, leading many to the conclusion that most butterflyfishes do not hold territories (Reese 1975, Ehrlich et al. 1977, Ehrlich & Ehrlich 1982, Neudecker & Lobel 1982, Neudecker 1989). However, despite generally low levels of aggression, attacks do occur on conspecifics and, less frequently heterospecifics, which along with other evidence led some to the conclusion that many butterflyfishes

are territorial (Ormond 1972, Fricke 1973a, 1986, Sutton 1985, Tricas 1985, Hourigan 1989).

Categorisation of species as being territorial or home-ranging clearly depends on how these terms are defined. Territorial animals are characterised as having exclusive access to a resource or resources (Kaufman 1983). Early workers emphasised active defence and incorporated it into their definitions. Hence Noble (1939), for example, defined territories as 'any defended area'. However, more recently it has been appreciated that displays and other forms of advertisement may be just as important, if not more so, in the maintenance of territories (Kaufman 1983). For example, many mammals mark territory boundaries with scent, perhaps rarely encountering neighbouring individuals (Owen-Smith 1977). Definitions of home ranges also differ among authors. Most consider them to be areas used for feeding and possibly, but not necessarily, also reproduction (Sale 1978). These are undefended and commonly overlap those of conspecifics. In general, home-ranges are understood by reef fish ecologists (and by us) to be relatively fixed areas, although ontogenetic habitat shifts may result in a fish inhabiting several different areas during its lifetime.

If indeed some butterflyfishes are territorial, then most hold territories as pairs since most species are seen as pairs (Reese 1975, Ehrlich et al. 1977, Steene 1978, Allen 1979). Studies to date have shown pair-fidelity of periods of up to seven or more years where pair members have been individually identifiable (e.g. Reese 1973, 1981, Fricke 1986, Driscoll & Driscoll 1988, Hourigan 1989). It is widely assumed that other paired species form long-term bonds.

Monogamy and territoriality in fishes appear to be closely linked. In a review of monogamy in teleosts, Barlow (1984) concluded that for tropical marine fishes, wherever data were sufficient, the monogamous pairs were found to be territorial. The data available for butterflyfishes provided an exception to this.

In recent years it has become widely accepted that there is a strong interaction between ecology and behaviour of species (Brown & Orians 1970, Fricke 1975, Reese 1975, Wilson 1975, Sale 1978,

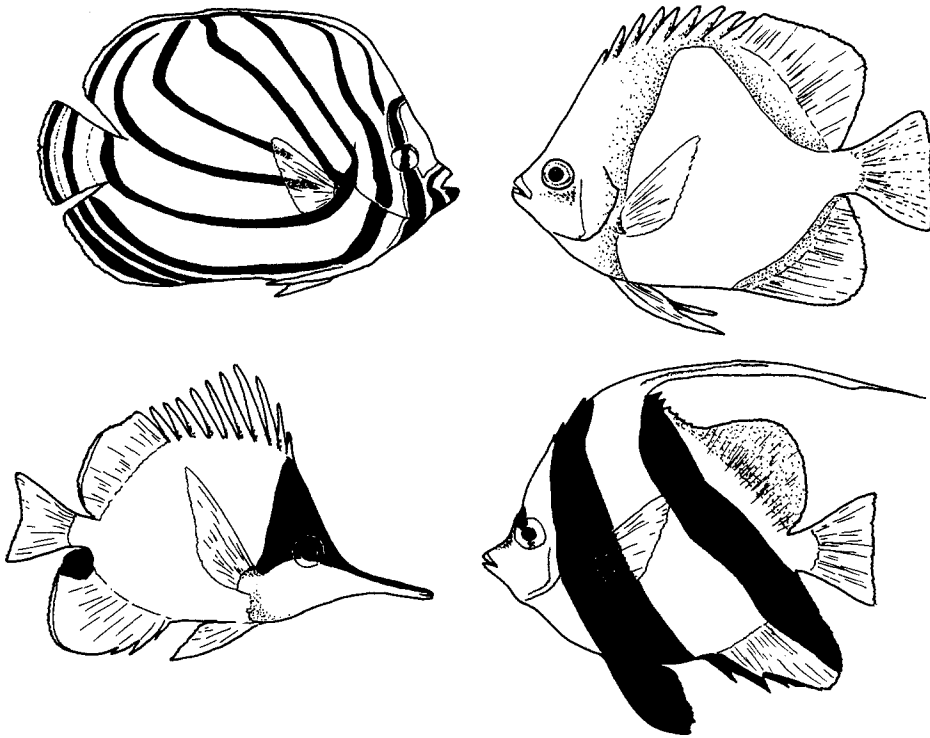


Fig. 1. Representatives of the four most abundant genera of butterflyfishes: *Chaetodon meyeri* (top left), *Hemitaenichthys polylepis* (top right), *Forcipiger flavissimus* (bottom left), and *Heniochus acuminatus* (bottom right).

Krebs & Davies 1981). In particular, the distribution and nature of food resources has been shown to be a strong influence on social behaviour (Horn 1968, Brown & Orians 1970), although other factors such as availability of refuge from predators and predator pressure are clearly very important (Wilson 1975). However, Barlow (1984) noted that the evidence which existed for butterflyfishes 'challenges the assumption that animals' social systems are adaptations to their ecology', and specifically 'that the nature of the food and its pattern of distribution strongly affect the social system'.

Hourigan (1989), building on the earlier work of Reese (1975), has now gone some way towards showing that diet and social behaviour are related in butterflyfishes. In this paper we extend this analysis, using both published and unpublished data. In an attempt at a synthesis of current knowledge of butterflyfish social systems, we reconsider previously published data and their interpretation, particularly concerning the incidence of territorial behaviour.

Materials and methods

Interaction between diet, resource distribution and social structure

To investigate the relationship between feeding ecology and social structure we compiled data on 43 species, from 42 literature sources and using unpublished data we have collected in the Red Sea. This represents about 37% of known butterflyfish species so our findings should be representative of general behaviour patterns within the family.

Much information is available on diet, and some widely distributed species have been studied in several regions of their ranges. For this analysis, species have been placed into five dietary categories: (1) obligate hard coral feeders (fishes which browse or graze only scleractinian coral polyps or mucus), (2) feeders on sessile and sedentary invertebrates (scleractinian corals may be included in the diet), (3) feeders predominantly on motile invertebrates (such as crustaceans and errant polychaetes), (4)

generalist omnivores (opportunistic feeders on a broad range of foods including algae), and (5) planktivores (feeding primarily on zooplankton). Obviously diet will vary among individuals within sites, among sites, and temporally, depending on food availability. For example, Ralston (1981) found significant spatial and temporal variability in diet of *Chaetodon miliaris* in Hawaii, and Irons (1989) found dietary composition of *C. trifascialis* varied among habitats at Johnston Atoll. Differently sized individuals also took different prey. Similarly, regional differences exist in reported diets (e.g. Birkeland & Neudecker 1981, Gore 1984, Lasker 1985, Neudecker 1985). Hence any dietary categorisation of species necessarily represents an approximation. We have attempted to define categories on a functional basis, fishes from different categories gathering food in broadly different ways (Motta 1985, 1988). Categories are sufficiently broad that, for the majority of species, local or regional differences in diet are insufficient to alter the classification given (Harmelin-Vivien & Bouchon-Navaro 1983).

Four categories of social grouping have been defined: (1) solitary, (2) paired, (3) gregarious, and (4) mixed. Classification of species is dependent on the predominant social grouping observed, and species are said to have a mixed grouping where neither solitary, paired nor aggregated individuals obviously predominate. Social grouping may be subject to a variety of influences such as resource distribution, density of individuals, or time of day. Variation in grouping within species will be discussed throughout this paper.

Published data on ranging behaviour of species are less reliable than those on diet, due primarily to differences in methodology used and in interpretation of results by different authors. Two categories of ranging behaviour predominate in tropical reef fishes (Sale 1978) and we use these as a basis for our analysis: (1) territorial species, and (2) home-ranging species. Some have used a third category of 'wandering' (Reese 1975). However, given that most coral reef fishes are strongly site-attached (Fricke 1975, Sale 1978) it is likely that these are simply species with large ranges of movements. As for diet and social grouping there will inevitably be

among-site differences in behaviour dependent on factors such as physical features of the environment, food availability and density of individuals. In this study individuals were classified by the most frequent ranging behaviour observed in the field.

Results and discussion

Territoriality and aggression

Contradictory statements about territoriality in butterflyfishes have frequently been made. For example, Fricke (1973b) stated 'Butterflyfishes are territorial. . .' and Ehrlich et al. (1977) in a study of twenty species claimed that '...for most species there is no evidence of territoriality'. In a prior study Reese (1975) could also only be certain that two of twenty species studied were territorial. However, it is clear from Table 1 that territoriality is a common strategy in benthic-feeding butterflyfishes. Differences of definition have led to some of the controversy. Reese (1975) and Ehrlich et al. (1977) favoured a restricted definition involving aggressive defence of territories, whilst others have often used broader criteria. Aside from such differences, what other factors have led to this division of opinion? There appear to be four main differences between studies in which territoriality has been reported and those in which it has been regarded as the exception.

First is the difference in the amount of time spent observing behaviour. Both Reese (1975) and Ehrlich et al. (1977) spent a total of 150 and 100 hours respectively observing 20 species each, an average of only 7.5 and 5 hours per species. In contrast, studies showing territoriality have involved fewer species and a much greater total observation period per species (e.g. Sutton 1985, Tricas 1985, 1989, Fricke 1986, Driscoll & Driscoll 1988, Irons 1989).

Second, studies showing territoriality have, almost without exception, involved plotting the movements of individuals and pairs (Appendix 1), while those which have concluded it as uncommon have not (e.g. Reese 1975, Ehrlich et al. 1977, Neudecker & Lobel 1982). In most cases where plots have been made, intraspecifically, individuals

or pairs have been found to inhabit contiguous, non-overlapping ranges, usually a clear indication of territoriality (Kaufman 1983).

Third, interpretational differences among authors have caused confusion. Following the studies of Lorenz (1962) and Zumpe (1965) on captive butterflyfishes and studies on territorial damselfishes (e.g. Low 1971, Myrberg & Thresher 1974) high levels of aggression might have been expected among territorial butterflyfishes in the field. However, it has been almost universally found that acts of aggression, such as chasing, are infrequent in wild populations, although a few species are more aggressive (e.g. Ormond 1972, Sutton 1985, Tricas 1985, 1989, Reese 1975, 1989). Studies suggest that territories are maintained predominantly by display and 'advertisement' (Ormond 1972, Reese 1977, Tricas 1985, Fricke 1986, this paper), rather than physical aggression such as chasing or butting. Ehrlich et al. (1977) accepted Noble's (1939) definition of a territory but apparently did not consider display a form of defence. Display and 'advertising' clearly should be considered actions associated with territory maintenance (Brown & Orians 1970).

Fourth, intermittent formation of aggregations of fishes, comprising one or more species, has led some to the conclusion that individuals were not holding territories (e.g. Ehrlich et al. 1977, Gore 1983). Extraterritorial movements have been described many times (Vine 1974, Thresher 1980a, Sale 1978, Bartels 1984, Roberts 1985, Reese 1989), and often result in temporary group forma-

tion. Similarly, aggregations of fishes may form at shelter sites at dusk (Ehrlich et al. 1977, Gore 1983). In most cases the latter is probably a response to a shortage of suitable night-time shelter within territories. It does not preclude maintenance of diurnal feeding territories.

Reassessment of previous data

Two major papers on butterflyfish social behaviour have been published previously by Reese (1975) and Ehrlich et al. (1977). In both the authors concluded that only a few species were territorial, the majority being home-ranging. In reaching these conclusions, much weight was given to the low levels of agonistic behaviour observed (Reese 1989.) Reese (1975) argued that infrequency of aggression was attributable to fishes resident in an area recognising each other as individuals, displays and occasionally more intense forms of aggression acting to structure intra- and interspecific social relationships. Reese described only two of twenty species as territorial. Ehrlich et al. (1977) considered individual recognition unlikely because fish occupied large areas of reef. However, later work showed that individual recognition was probable (Ehrlich & Ehrlich 1982). Like Reese (1975), Ehrlich et al. (1977) considered only *Chaetodon baronessa* and *C. trifascialis* territorial, the other 23 species (studies combined) being classified as home-ranging based on low levels of interspecific aggression.

Table 1. Summary results of the literature survey of social behaviour and feeding ecology of butterflyfishes. Bracketed numbers between categories indicate species for which individuals were commonly observed in both categories. * Harem species. Data and sources used to compile the table are shown in Appendix 1.

Diet	Predominant social grouping				Predominant ranging behav.		Total no. species
	Solitary	Paired	Gregarious	Mixed	Territorial	Home-ranging	
Obligate hard coral feeders	2 (2)	10	0	0	7	7	14
Sessile & sedentary invertebrates	0 (1)	6	1*	1	5	4	9
Motile invertebrates	2	0	0	0	1	1	2
Generalist omnivores	0	7	0	4	2 (2)	7	11
Planktivores	0	1	6	0	0	7	7

Since these papers were published, detailed studies of four of the species considered by Reese (1975) and Ehrlich et al. (1977) as home-ranging have shown them to be territorial (Sutton 1985, Tricas 1985, Hourigan 1986, Driscoll & Driscoll 1988). Reese and Ehrlich et al. probably failed to establish territoriality in these species for reasons discussed earlier. We consider it very likely that future studies will reveal territorial behaviour in many of the other species.

Dietary correlates of social behaviour

Territoriality is a widespread strategy among butterflyfishes which are obligate corallivores (Table 1). [Note that data for obligate corallivores herein classified as home-ranging were taken from Reese (1975) and Ehrlich et al. (1977); some or all may prove to be territorial when more detailed studies are made]. Territoriality seems favoured as a strategy when resources are evenly distributed and temporally stable (Brown & Orians 1970). Tricas (1985) noted that 'Relative to other prey types, corals represent an evenly dispersed, predictable, and long-term renewable food resource. . .'. However, not only obligate corallivores have adopted territorial behaviour. There are territorial representatives in all benthic-feeding categories shown in Table 1. Most feeders on sessile and sedentary invertebrates feed by tearing pieces off larger prey, such as soft corals, zoanthids and sedentary polychaetes (Randall 1967, Harmelin-Vivien & Bouchon-Navaro 1981, 1983, Motta 1985, 1988). Such prey often continue growth after damage and may regenerate the damaged parts. Like corals, at the scale of butterflyfish movements these resources are also relatively evenly dispersed, stable and renewable, and thus can be most efficiently harvested by spaced-out individuals (Horn 1968).

Only two species are known to feed primarily on motile benthic invertebrates: *Chaetodon aculeatus* (Birkeland & Neudecker 1981) and *Forcipiger longirostris* (Hobson 1974, Harmelin-Vivien & Bouchon-Navaro 1983). *C. aculeatus* has been reported to inhabit non-overlapping home-ranges in the Caribbean (Neudecker & Lobel 1982) and is here

considered territorial. Data are unavailable on social behaviour of *F. longirostris*. Individuals of both species are observed more often alone than in pairs (Okuno 1963, Hobson 1974, Steene 1978), although pairs of *F. longirostris* are common in Hawaii (Motta personal communication). In contrast, only two of the twenty three species in Table 1 which eat hard corals or other sedentary or sessile invertebrates usually occur as solitary individuals. Neudecker & Lobel (1982) attribute solitary behaviour of *C. aculeatus* to the nature of the diet, arguing that species feeding on cryptic, motile prey with predator avoidance mechanisms hunt more efficiently alone.

Six of seven species classified as plankton feeders are gregarious. All forage high in the water column, in the case of *Chaetodon miliaris* up to 15–40 m above the bottom (Brock & Chamberlain 1968). Unlike benthic prey, planktonic organisms represent an effectively indefensible resource. Planktivorous species usually occur in large aggregations on upcurrent sides of reefs, sometimes near to drop-offs, where their prey are most abundant (Hobson 1974). Fishes which feed in open water are believed more vulnerable to predatory fishes, such as jacks and sharks, than those foraging close to the substratum. Gregarious behaviour is common among species living or feeding in open habitats. Benefits of group formation accrue mainly from predator confusion and increased overall vigilance allowing more time to be spent feeding (Hamilton 1971, Kenward 1978, Major 1978, Bertram 1980). The only planktivorous species which is not gregarious, *Chaetodon kleinii*, occurs in loosely associated pairs foraging close to the substratum, and only venturing 1–2 m above the reef (Hobson 1974). However, they do join aggregations of *C. miliaris* and *Hemitaenichthys* spp. in Kona, Hawaii (E.S. Reese personal communication).

Hourigan (1989) emphasises the importance of mobility to plankton feeders, noting that plankton is a patchy and unpredictable resource. Mobile aggregations will be able to track such variability whereas site-attached species will not. However, plankton feeding schools can also be strongly site-attached, with narrow ranges of movement (CR unpublished data).

Territorial behaviour is also common among generalist omnivores and seven of eleven species are most commonly observed as pairs (Table 1). Four commonly occur alone, in pairs or in groups (*Chaetodon auriga*, *C. fasciatus*, *C. flavirostris* and *C. lunula*). It is interesting that these species which have broad dietary flexibility also have flexible social behaviour. Concomitant with dietary flexibility many generalist omnivores are also broadly distributed over the reef (Bouchon-Navaro 1979, 1981). Environmental influence on social behaviour is most apparent amongst these species. For example, *C. auriga* and *C. fasciatus* are often found foraging in groups of up to 30 or so in lagoonal habitats in the Red Sea, but on the fore-reef are generally paired and hold territories (Ormond 1972). Compared with the fore-reef, food resources are more patchily distributed in lagoonal habitats, and considerably less rich. Perhaps territories would need to be too large to be defensible in the lagoon.

Hemitaurichthys zoster and *Heniochus intermedius* appear to have a dual strategy. Individuals feeding predominantly on benthic foods generally occur as pairs while some, feeding mainly on plankton, are found in aggregations (Fricke 1986, CR unpublished data). *Hemitaurichthys polylepis* adopts a similar strategy in Hawaii (Reese personal communication). Species such as these and the generalist omnivores discussed above, which show a range of social behaviours, can provide fertile testing grounds for hypotheses concerning relationships between ecology and behaviour.

Juvenile behaviour

So far we have primarily discussed behaviour of adult butterflyfishes. Little study has been directed at juvenile fishes and, with few exceptions, reports found in the literature are anecdotal. However, one or two tentative generalizations can be made. First, for the majority of species, juveniles are solitary, remaining very close to shelter (Okuno 1963, Allen & Kuitert 1978, Bouchon-Navaro 1981, Fricke 1973b, Gore 1983, Harmelin-Vivien 1989). Groups of juveniles have only been noted for a few

species, for example *Chaetodon mertensii*, *C. trifascialis* and *C. reticulatus* (Steene 1978, Bouchon-Navaro 1981). Second, juveniles are found on different parts of the reef from adults in many species (Longley & Hildebrand 1941, Fricke 1973b, Aiken 1975, Bouchon-Navaro 1979, 1981, Thresher 1980b, Lindquist & Gilligan 1986, Harmelin-Vivien 1989). Usually they occur in shallower water, closer inshore than adults.

Both the above observations probably relate to minimization of predation risk. Adult butterflyfishes appear to be preyed upon infrequently, the evidence usually given being that they are rarely found in gut contents of larger fishes (Ehrlich et al. 1977, Neudecker 1989). Neudecker (1989) has argued that adult butterflyfishes are risky prey, since their compressed, spiny bodies may lodge in a predator's mouth. In contrast, juveniles are probably subject to heavy predation, being poor swimmers and easily handled by even small predators (Neudecker 1989, CR personal observation). Hence they must remain very close to cover, foraging near to their refuges. Similarly, predatory fishes such as groupers and snappers are much less common in shallow, inshore reef areas than in deeper parts of the reef (Goldman & Talbot 1976, Harmelin-Vivien 1977, CR unpublished data). Settlement of juveniles into shallow habitats may thus be an adaptation to differences in predator density. (Alternatively, it is possible that butterflyfishes settle over all parts of the reef but persist longer in shallow areas, thus being more regularly seen there.)

After some period of growth, young fishes must make their way to more suitable habitats (those inhabited by adults), often requiring a migration of considerable distances (Thresher 1980b, Lindquist & Gilligan 1986). Fishes moving across unknown areas of reef are probably more at risk of predation than those remaining within a known area and so juveniles will be vulnerable unless they have grown considerably before beginning this migration (although they may seek better habitats in a series of short moves spread over a long time).

Ralston (1976) noted that early growth in *Chaetodon miliaris* was very rapid, and that individuals grew to over 8 cm total length within their first

year. He later suggested that this was an adaptation to predator pressure, rapid growth allowing individuals to quickly attain a size-refuge from predation (Ralston 1981). *Chaetodon rainfordi* and *C. plebius* reached a standard length of around 5 cm (approx. 6 cm total length) in 300 days on the southern Great Barrier Reef but compared to several other reef fishes these rates were unexceptional (Fowler 1989). Further data will be necessary to determine whether early growth is faster than average in butterflyfishes.

Little is known about interactions among juveniles. However, their restricted movements coupled with possible low rates of settlement may make it unlikely that small juveniles interact very often. Where densities are high, juveniles possibly defend resources from others. Burgess (1978) observed groups of very small *C. trifascialis* inhabiting *Acropora* colonies and noted that as they grew, fewer individuals were left until only one remained as an adult. Juveniles are often found in territories of adult fishes (Tricas 1985, Fricke 1986) and appear to escape exclusion by retreating into small holes. As they grow, they may be forced to move elsewhere by the territory holders.

Adaptive significance of pairing

Butterflyfishes are gonochoristic (Burgess 1978, Thresher 1984, Tricas 1989) and the majority of species are found frequently as pairs (Table 1, Appendix 1). Where they have been sexed, pairs are almost always found to be heterosexual (Reese 1975, 1981, Fricke 1986, Hourigan et al. 1988, CR unpublished data). In addition, paired fishes are usually similar in size (e.g. Reese 1981). Monogamous pairs have been found to be stable for periods of more than six years, although individuals which have lost a partner readily pair with others (Fricke 1986). Monogamy has widely been suggested to have evolved in response to the need for biparental care of offspring (Wittenberger & Tilson 1980, Wickler & Seibt 1983, Barlow 1984). However, butterflyfishes lay pelagic eggs and so do not care for eggs or young (Lobel 1978, Neudecker & Lobel

1982, Thresher 1984). Hence monogamy must have evolved in response to other selective pressures.

Territory maintenance

Monogamy may be favoured where defence of a resource or resources by a pair is more effective than by a solitary individual. If two territories are combined then the circumference will increase less than the area. Thus if intrusions are a linear function of perimeter length, two co-operating fishes will be able to defend the same area as when alone but with less energetic cost (Fig. 2). However, increases in the number of fishes sharing a territory above two would further decrease the perimeter defended per fish and so a harem rather than monogamous system might be favoured, although the maximum advantage gained lies with an increase from one to two fishes in the territory (Fig. 2). This advantage will only be available if fishes patrol the territory independently. If they move around together then each will have the same equivalent feeding area but must defend a greater area and a larger perimeter (Hamilton & Watt 1970). Since most paired butterflyfishes remain close together and patrol the territory as a unit (Reese 1975, Ehrlich et al. 1977, Fricke 1986) they cannot be reducing territory defence costs in this simple way.

Lorenz (1962) suggested that the brilliant colours of butterflyfishes served as territorial advertisements, eliciting furious aggressive behaviour in conspecifics and acting to space out individuals over the reef. Lorenz's theory is clearly too simplistic to apply to field populations of butterflyfishes. Aggression is not exclusively against conspecifics (Table 2), and is infrequent in the field. However, Ormond (1972), Reese (1975), Tricas (1985) and Fricke (1986) all consider non-aggressive 'advertisement' very important. Tricas (1985) argues that territories are primarily maintained by such advertisement making butterflyfish territoriality very efficient. This still does not explain pairing behaviour. Fricke (1986) conducted experiments involving removal of one pair member of *Chaetodon*

within the pair bond, females requiring to invest more energy in gamete production than males, and males sharing in the increased fecundity of the female. However, somewhat contradictorily, Hourigan argued further that monogamy results from a system whereby females defend food resources from other females, and males defend territories containing a female from other males. Males attempt to obtain more than one female but are unable to defend large enough territories. Hourigan (1989) presented limited evidence in support of this hypothesis showing that where a female was removed, males were able to defend the full territory, but where a male was removed, the female was not. Hourigan stated that this outcome was expected under his hypothesis. However, the result actually implies a male role in defence of food resources, since females alone should be able to maintain the entire territory against other females, if they are simply defending food. Further, continued defence of a territory by a male in the absence of a female suggests that males are defending resources, possibly to attract females.

An alternative hypothesis is that females consider male assistance with territory defence as a resource, and act to prevent other females from gaining access to this (Arcese 1989). Where successful, male and female territories will be matched in size and location, and pair territories result. The generally close co-ordination of movements of males and females within territories could thus be explained as mutual partner guarding (Fricke 1986).

The available data are in accord with the hypothesis that pair defence of the territory is important to its maintenance. However, there are insufficient data to allow a full understanding of why paired fishes may be able to hold territories more efficiently than unpaired ones.

Mate availability and spawning constraints

A number of other hypotheses applicable to butterflyfishes attempt to explain evolution of monogamy. They relate to reproductive constraints (Neudecker & Lobel 1982, Barlow 1984). Pair formation may be favoured by (1) low densities of available

mates (relative or absolute), (2) synchronous spawning throughout a population, (3) predation risk while searching for mates, or (4) risk of territory usurpation whilst the holder is absent searching for a mate. These hypotheses are not mutually exclusive.

Since butterflyfishes spawn frequently throughout long breeding seasons (Lobel 1978, 1988, Ralston 1981, Neudecker & Lobel 1982), in non-gregarious species monogamy may have evolved to assure constant availability of a fecund mate. In low density populations, much time could be spent searching for a mate. Low densities of available mates need not be restricted to populations at absolutely low densities. If females space themselves out, then even if population density is relatively high, males may find it difficult to spawn with more than one female, especially if females spawn in phase (Barlow 1984). An individual must search for a ripe female, and after locating one may have to fight another male for access to her. Barlow (1984) also notes that where food resources are dispersed, monogamy may be favoured by this spacing-out effect alone.

If sexual activity is limited to a restricted period synchronized throughout a population, then location of a suitable mate, courtship and spawning must take place quite quickly (Knowlton 1979, Neudecker & Lobel 1982, Colin 1989, Lobel 1989). Individuals suffer reduced fitness if they cannot locate a mate when otherwise able to spawn. The limited information available indicates that butterflyfishes spawn only at dusk (Lobel 1978, 1989, Neudecker & Lobel 1982, Thresher 1984, Colin 1989). Spawning is thus synchronized throughout stocks and the period during which mates can be sought and spawned with is short. Ready access to a mate would thus appear advantageous.

The possibility of partner guarding has already been raised. Mate guarding is a means of ensuring access to a female for spawning. However, recent observations show that 'sneak' spawnings by other males can occur (Lobel 1989) and so paternity is still not guaranteed.

Predation risk is also highest for reef fishes during crepuscular periods (Hobson 1972) and fishes leaving territories and moving over unfamiliar ter-

rain at dusk are probably at increased risk. This selective pressure could favour monogamy, although adults are not regularly eaten (Neudecker 1989).

Lobel (1978) and Neudecker & Lobel (1982) have suggested that crepuscular spawning evolved to reduce predation on zygotes. Diurnal planktivores become inactive at dusk while nocturnal planktivores have yet to become active (Hobson 1965, 1972, Starck & Davis 1966). A further benefit would appear to apply to territorial species which are monogamous. They will not have to leave the territory to reproduce, thus not leaving it open to invasion by other individuals in their absence.

Fricke (1973b) offered another hypothesis to explain monogamy, suggesting it had evolved to reduce the frequency of wasteful heterospecific matings in species-rich communities. This hypothesis can be discounted for three reasons. First, as Thresher (1984) pointed out, there should be a correlation between frequency of monogamy and regional species richness, and this cannot be demonstrated. Second, there are many other species-rich families of reef fishes in which monogamy is rare (e.g. damselfishes and wrasses). Third, most coral reef fishes have good colour and pattern recognition capabilities (Ormond 1972) and, in some cases, appear able to recognize each other as individuals (Reese 1975, Thresher 1979, Ehrlich & Ehrlich 1982). Mistaken spawnings with other species would thus seem very unlikely, although hybrid fishes have been observed in the field (Steen 1978, Randall & Fridman 1981).

Conclusions

A majority of butterflyfish species are found in monogamous pairs which are site-attached and restrict their movements to relatively small areas of reef (from a few to several hundred square meters). Aggressive interactions between conspecifics and heterospecifics are infrequent. In those species currently recognized as territorial, defence is intra-specific. The available data suggest that aggressive behaviour towards heterospecifics is not space-related. Where previous authors have not classed

species as territorial, this has generally been due to insufficient data on agonistic behaviour. We argue that, when more data have been collected, territoriality will prove to be the predominant form of spacing behaviour in butterflyfish populations.

There appears to be a broad correlation between diet and social behaviour. Territoriality is common among species which feed on benthic prey. The relatively even distribution of such prey in relation to the scale of butterflyfish movements, and the temporal stability of these resources make them economically defensible. Territories are maintained by advertisement and display with only occasional reinforcement by more intense forms of aggression. Nearly all planktivorous species are gregarious, zooplankton being essentially indefensible. The formation of aggregations by species feeding in open water may be favoured by anti-predator advantages.

Mixed behavioural strategies are common among species with a generalist omnivorous diet. Individuals may forage alone, in pairs or in aggregations. Territories may or may not be defended. Which strategy is adopted appears to depend mainly on the nature and distribution of food, but is likely also to be influenced by factors such as population density and distribution of refuges.

The evolution of monogamy in butterflyfishes remains to be explained satisfactorily. Data available are consistent with a number of hypotheses: (1) cooperation in defence of food resources, (2) low densities of available mates (relative or absolute), (3) synchronous spawning within populations, (4) increased predation risk while searching for mates, and (5) risk of territory usurpation whilst absent searching for mates. Limited experimental evidence suggests that paired fishes can more economically defend territories than solitary individuals but it remains to be seen whether this is a proximate or ultimate cause of monogamy.

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Appendix 1

Results of literature survey of social and ranging behaviour of butterflyfishes. Sol. = solitary, Pair. = paired, Greg. = gregarious, Territ. = territorial, and Home-rng = home-ranging. For social grouping: o = a behaviour rarely observed, + = relatively frequent, ++ = predominant behaviour. For spacing behaviour, an asterisk indicates where ranges of individuals have actually been plotted. ? = uncertain, h = Harem species. Sources are: (1) Aliño et al. (1988), (2) Allen (1979), (3) Allen & Kuitert (1978), (4) Birkeland & Neudecker (1981), (5) Bouchon-Navaro (1979), (6) Bouchon-Navaro (1981), (7) Burgess (1978), (8) Cox (1986), (9) Driscoll & Driscoll (1988), (10) Ehrlich et al. (1977), (11) Fricke (1973a), (12) Fricke (1986), (13) Gore (1983), (14) Gore (1984), (15) Harmelin-Vivien (1979), (16) Harmelin-Vivien (1989), (17) Harmelin-Vivien & Bouchon-Navaro (1981), (18) Harmelin-Vivien & Bouchon-Navaro (1983), (19) Hiatt & Strasburg (1960), (20) Hobson (1974), (21) Hourigan (1986), (22) Hourigan (1989), (23) Irons (1989), (24) Lasker (1985), (25) Lobel (1978), (26) Motta (1985), (27) Motta pers. comm., (28) Neudecker & Lobel (1978), (29) Okuno (1963), (30) Ormond (1972), (31) Ralston (1981), (32) Reese (1973), (33) Reese (1975), (34) Reese (1977), (35) Reese (1981), (36) Roberts unpublished data, (37) Sano (1989), (38) Sale & Williams (1982), (39) Steene (1978), (40) Sutton (1985), (41) Talbot (1965), (42) Tricas (1985), (43) Tricas (1989), (44) Wood (1979), (45) Holmes (1988).

Species	Sol.	Pair.	Greg.	Territ	Home-Rng	Refs.
Obligate corallivores						
<i>Chaetodon aureofasciatus</i>	++	+			.	10, 33, 34
<i>C. austriacus</i>	o	++		.*		5, 12, 17, 30
<i>C. baronessa</i>		++		.		10, 32, 33, 34, 37
<i>C. collare</i>	+	++			.	2, 22, 29
<i>C. larvatus</i>	++			.*		30
<i>C. multicoloratus</i>		++		.*		9, 20, 25, 33, 42, 43
<i>C. ornatissimus</i>	++			.*		9, 18, 20, 26, 33, 34
<i>C. plebius</i>	+	+			.	10, 33, 34, 37
<i>C. punctatofasciatus</i>		++			.	33, 34, 37
<i>C. rainfordi</i>	+	+			.	10, 33, 34, 38
<i>C. reticulatus</i>	+	++			.	18, 19, 33, 34
<i>C. speculum</i>	o	++			.	10, 33, 37
<i>C. trifascialis</i>	++			.*		10, 12, 17, 23, 33
<i>C. trifasciatus</i>		++		.*		10, 18, 29, 33, 40
Sessile and sedentary invertebrate feeders						
<i>Chaetodon capistratus</i>	+	++	+?	.*	?	4, 13, 14, 24, 28, 45
<i>C. citrinellus</i>	+	++			.	10, 13, 29, 33, 37
<i>C. fremblii</i>			++ ^h	.*		20, 21, 22, 25
<i>C. lineolatus</i>	o	++			.	10, 12, 30, 33
<i>C. melannotus</i>	+	+		.*		1, 10, 11, 17, 33
<i>C. semilarvatus</i>	o	++	o	.*		12, 30, 36
<i>C. ulietensis</i>	+	+	+		.	10, 18, 37
<i>C. unimaculatus</i>	o	++			.*	8, 10, 20, 25, 29, 33
<i>Heniochus intermedius</i>		++	o	.*		12, 17, 30, 36
Motile invertebrate feeders						
<i>Chaetodon aculeatus</i>	++			?		28
<i>Forcipiger longirostris</i>	++	+			.	20, 22, 27, 29, 41
Generalist omnivores						
<i>Chaetodon argentatus</i>		++	o		?	2, 22, 29, 37
<i>C. auriga</i>	+	+	+	.*	.	6, 10, 12, 19, 20, 33
<i>C. ephippium</i>		++			.	6, 10, 18, 19, 33
<i>C. fasciatus</i>	+	++	+	.*	?	5, 12, 17, 30, 36
<i>C. flavirostris</i>	+	+	+		.	10, 22
<i>G. lunula</i>	+	++	+		.	6, 10, 19, 20, 33, 44
<i>C. paucifasciatus</i>		++		.*		12, 17, 36
<i>C. quadrimaculatus</i>	o	++		.*		9, 20, 21, 22, 33, 42
<i>C. vagabundus</i>		++			.	6, 10, 15, 16, 19, 33
<i>Chelmon rostratus</i>	o	++			.	10, 22
<i>Heniochus acuminatus</i>	+	++	o		?	3, 7, 12, 29, 39
Planktivores						
<i>Chaetodon assarius</i>			++	.		39
<i>C. kleinii</i>	o	++			?	10, 20, 31
<i>C. miliaris</i>		++			.	7, 20, 26, 31
<i>Hemitaurichthys polylepis</i>		++			.	18, 20, 37
<i>H. thompsoni</i>		++			.	12, 20
<i>H. zoster</i>		++			.	12
<i>Heniochus diphreutes</i>		++			.	3, 17