Implications of feeding specialization on the recruitment processes and community structure of butterflyfishes

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Synopsis

When settling on coral reefs, fish larvae generally change from zooplanktivory to diverse forms of benthic feeding. Whereas food has not been reported to directly influence settlement, it is hypothesized that food resource might play a major role in the recruitment processes of butterflyfishes. Benthic feeding was found to occur immediatly after settlement, and was related to the degree of specialization of adult diets. Among obligate coral feeders scleractinian polyps were the exclusive diet of new recruits. In non-obligate corallivorous chaetodontids tentacles of sedentarian polychaetes were the preferred prey of juveniles for all the species studied, and represented on average 36.2% of their prey by weight. They formed a transitional food resource for these species which mainly fed on scleratinian polyps when adults (51.6% by weight). Among the chaetodontids studies, some recruited within adult home sites, whereas others exhibited size-specific distributions. The different patterns observed were not closely related to food specialization of the adults. The importance of food resources to the community structure of butterflyfishes on coral reefs is discussed.

Introduction

After a pelagic larval life lasting from one week to several months, with an average of one month (Brothers et al. 1983, Victor 1986a), fish larvae descend to the reef for a more sedentary benthic phase. At this time most species, with the exception of obligate planktivores, change from plankton feeding to benthic feeding. Major factors thought to affect recruitment and early survivorship of newly settled coral reef fishes include the availibility of suitable shelter sites, the density of adults and the encounter rate with predators (Luckhurst & Luckhurst 1977, Williams & Sale 1981, Sale et al. 1984, Shulman 1984, 1985, Victor 1986b). Food resources are not reported to directly influence settlement (Shulman 1984). Even if food is not considered as a limiting factor in recruitment processes questions arise about the way fish cover their energy requirements at settlement, particularly those species exhibiting strong feeding specialization as adults. How and when does the transition take place from the planktonic to the benthic diet? Is the change of diet concomittant with settlement? Is food specialization immediately effective, or is there a transitional diet in juvenile fish? This last hypothesis seems most likely to fit the cases of omnivorous and planktivorous species, but seems irrelevant to highly food selective species. If food specialization occurs immediatly after settlement, the presence of the specific food resource is needed for that particular fish species to recruit, and the distributions of adults and juveniles should coincide. Conversely, the existence of a transitional diet

and different food preferences in juvenile fishes may allow a wider spatial dispersion of the recruits and probably ensure a better survival rate. It would also allow for the colonization of a variety of different habitats by the same species during the course of its ontogenetic development.

The chaetodontid family which has evolved within the coral reef ecosystem (Reese 1977) is particularly suited for the study of these problems. Different types of feeding behaviors and various levels of food specializations, from highly specialized feeders to generalists, are observed within the butterflyfishes. Chaetodontids may be broadly divided into coelenterate predators, carnivores preying upon other benthic invertebrates, omnivores, and plankton feeders (Hiatt & Strasburg 1960, Randall 1967, Hobson 1974, Anderson et al. 1981, Harmelin-Vivien & Bouchon-Navaro 1982, 1983). Coelenterate predators predominate, encompassing 31 to 90% of chaetodontid species on Indo-pacific reefs (Bouchon-Navaro 1985). These often display a high degree of feeding specialization for a particular category of prey (scleractinians, alcyonarians, gorgonians, etc.), in some cases at a generic or even a specific level. Obligate scleractinian feeders are numerous in chaetodontids (15 to 44% of the species), more than in any other reef fish family. Diets of adults have been investigated in a number of species in Hawaii (Hobson 1974, Reese 1977, Ralston 1981), in the Marshall Islands (Hiatt & Strasburg 1960, Reese 1975), on the Great Barrier Reef of Australia (Reese 1975, Anderson et al. 1981), in Okinawa, Japan (Sano et al. 1984), in French Polynesia (Harmelin-Vivien & Bouchon-Navaro 1983, Bouchon-Navaro 1986), in Madagascar (Harmelin-Vivien 1979), in Jordan (Harmelin-Vivien & Bouchon-Navaro 1982) and in the Caribbean (Randall 1967, Birkeland & Neudecker 1981, Gore 1984, Lasker 1985). Nothing is presently known about the food of juvenile chaetodontids, especially during the critical phase of their recruitment on the reef. The only study that refers to ontogenetic food changes in butterflyfishes, was performed on a planktivorous Hawaiian species (Ralston 1981).

This paper is a first attempt to consider these problems and to discuss the implications of feeding specialization on the recruitment and community structure of reef fishes.

Methods

To investigate ontogenetic changes in feeding among chaetodontids, specimens from different geographic areas were studied. Fishes were collected at Tulear (S.W. of Madagascar), Moorea (French Polynesia) and Guadeloupe (French West Indies) in various macrohabitats: lagoonal, reef flat and outer coral reef slope formations (Harmelin-Vivien 1979, Harmelin-Vivien & Bouchon-Navaro 1983).

As most of the chaetodontid species are diurnally active (Hobson 1974, Reese 1975, 1977, Harmelin-Vivien 1979) specimens were sampled during daytime between 0900 to 1600 hours, mainly by spearfishing or rotenone poisoning. Some small specimens were collected with quinaldine anaesthetic and hand nets. Standard length (SL) was measured to the nearest millimeter. Fishes were immediately preserved in a 10% buffered formalin solution with abdominal injection for the largest specimens, and later examined for stomach content. Ten species for which both juvenile and adult specimens were sampled, were taken into account in the present study. A total of 292 fishes with food in their stomach were quantitatively analyzed, 34.6% of them being juveniles. According to the maximum standard length of the various species (Burgess 1978), specimens with SL <40 to 60 mm were considered as juveniles (Table 1). Fishes less than 60 mm SL are expected to be less than 6 months old, if one follows the conclusions reached by Ralston (1976) for *Chaetodon miliaris*. They generally were the smallest size-class distinguished when size was considered for visual counts (Bouchon-Navaro 1979, 1981, Lindquist & Gilligan 1986).

Quantitative analysis of food was conducted on stomach contents as prey were more or less fully digested in the intestine. The main prey items were sorted by systematic groups under a binocular microscope, and then weighted to the nearest 0.1 mg. Relative importance of prey in the feeding was determined by their percentages by wet weight (C_w).

Niche breadth in the utilization of food resources was calculated using the Shannon-Wiener index of diversity

$$H' = \sum_{i=1}^{n} pi \, Log_2 pi,$$

where pi is the proportion by weight of a particular prey category, for n prey categories.

$$\text{Equitability } J' = \frac{H'}{H' \max}$$

was also calculated since this index is independent of n.

In order to determine the similarity of feeding within – and between – species, a cluster analysis using the mean Chi square distances was performed on the data of juvenile and adult diets of all species.

Results

Specialization level

The total number of prey item taxa eaten by a species was generally equal or a little lower in juvenile than in adult chaetodontid fishes, and the mean number of prey found in one specimen did not significantly differ from juveniles to adults for most species (Table 1). The range of food eaten by juveniles and adults were generally very similar except for *Chaetodon lunula* from Tulear (Table 2). The diversity and equitability of diets were similar for the two size-classes in most species.

All the chaetodontid species analyzed in this study were coelenterate predators (Table 2), but they differed greatly in their degree of feeding specialization. Two groups can be readily distinguished: the obligate coral feeders (*C. trifascialis* and *C. trifasciatus*) preying exclusively upon scleractinian polyps, and the non-obligate or facultative coral feeders (*C. auriga, C. citrinellus, C. kleinii, C. lunula, C. madagascariensis, C. vagabundus* and *C. xanthocephalus*) which fed on coral polyps together with many other benthic organisms, from algae to ascidians (Table 2).

Obligate coral-feeders

Food specialization in *C. trifascialis* and *C. trifasciatus* occurred very early in their benthic life history. All the specimens analyzed from 22 mm in standard length to the largest adults, had exclusively fed on scleractinian polyps. The few smallest specimens of *C. trifasciatus* (19 to 21 mm SL) collected on Tulear reefs presented stomach contents composed half of calanoid copepods, half of coral polyp fragments. These specimens were not fully metamorphosed lacking juvenile pigmentation, and still exhibiting the preopercular spines of the tholichthys larval form. Therefore, in the obligate coral feeders such as *C. trifasciatus*, food specialization appears to occur immediatly after the settlement of early juveniles on the reef, and the transition phase from planktonic to benthic food is very short.

Non-obligate coral feeders

In non-obligate coral feeders, benthic feeding also seemed to occur very early, as stomachs from specimens of 19 mm SL (*C. capistratus*), 21 mm SL (*C. auriga*) or 22 mm SL (*C. lunula*) were already full of benthic organisms.

In spite of a food spectrum very similar to the adult one, juveniles of non-obligate coral feeders clearly exhibited distinct food preferences (Table 2). Whatever the geographic area and the species studied, tentacles of sedentarian polychaetes, mainly from serpulid, sabellid and terebellid worms, were a preferred prey of juvenile fishes. An inverse relationship with size in weight percentages of sedentarian polychaete tentacles and scleractinian polyps was observed within all these chaetodontid species (Table 3). The mean proportion of polychaetes in diets of juveniles (36.2%) averaged over all non-obligate coral feeders was significantly higher than in adult ones (8.8%). Conversely, the mean proportion of scleractinian polyps in adult diets (51.6%) far exceeded that found in juveniles (8.2%).

The cluster-analysis performed on the quantitative data of stomach contents defined three main

trophic groups (Fig. 1): group I included only adult size-classes, group II was mainly composed of juvenile size-classes and group III gathered small and large *C. citrinellus*. The last four species were individually very loosely related to the others. Interspecific similarity of feeding was thus higher within each size-class (within adults and within juveniles) than intraspecific similarity between size-classes, *C. citrinellus* excepted.

Distributions of juveniles and adults

Information on the relative distribution of juveniles and adults among chaetodontid populations is sparse in the literature (Table 4). Depending on the species, the patterns of distribution may or may not differ between size-classes. In some species such as *C. paucifasciatus* in the Gulf of Aqaba (Bouchon-Navaro 1979) no difference was observed between juvenile and adult distributions. In others, the different size-classes inhabited different reef zones. Juveniles and sub-adults were generally more abundant in shallow-water areas whether it be coral reefs or seagrass beds, whereas adults predominated in deeper waters (Fricke 1973, Clarke 1977, Bouchon-Navaro 1979, 1981, Lindquist & Gilligan 1986).

Difference or similarity in the distribution patterns of juvenile and adult chaetondontids did not

Table 1. Chaetodontid species studied for ontogenetic change in feeding. Two broad size-classes were distinguished in each species, juvenile individuals (SL <60 mm) and adult individuals (SL >60 mm). Species were collected on Tulear (Madagascar), Moorea (French Polynesia) and Guadeloupe (French West Indies) coral reefs. N = number of specimens analyzed with food in their stomach, XSL = mean standard length of specimens (mm), P = total number of prey types in fish diet. XP = mean number of prey types per individual, s.d. = standard deviation. Significance of t-test was given for the comparison of mean prey per individual (XP) between size-classes in each species (n.s. = non significant, * = p<0.05, ** = p<0.01, *** = p<0.001, – – – = test not calculated, too few data).

Species	Locality	N	XSL (Range)	P	XP (s.d.)
Chaetodon auriga	Tulear	20	39.3 (22–57)	13	3.6 (1.4) n.s.
	Tulear	59	101.4 (65–145)	17	3.5 (1.6)
C. capistratus	Guadeloupe	20	27.5 (19–33)	19	5.3 (1.9) – – –
C. citrinellus	Moorea	5	59.5 (44–60)	9	7.6 (1.2) n.s.
	Moorea	10	84.6 (80–90)	12	7.1 (1.0)
C. kleinii	Tulear	3	35.3 (34–36)	5	3.7 (0.6) – – –
	Tulear	3	57.3 (55–60)	4	2.7 (0.6)
C. lunula	Moorea	4	38.0 (21–60)	9	5.0 (1.4) ***
	Moorea	13	127.8 (106–136)	14	9.0 (1.4)
	Tulear	1	24.0	6	6.0 – – –
	Tulear	4	129.8 (115–135)	2	1.5 (0.6)
C. madagascariensis	Tulear	5	32.4 (25–39)	5	4.7 (0.5) **
	Tulear	10	91.9 (70–131)	4	3.4 (0.5)
C. trifascialis	Tulear	4	40.7 (33–42)	1	1.0 (0.0) n.s.
	Tulear	3	89.3 (84–94)	1	1.0 (0.0)
C. trifasciatus	Moorea	25	38.1 (31–52)	1	1.0 (0.0) n.s.
	Moorea	23	96.3 (78–109)	1	1.0 (0.0)
	Tulear	6	31.2 (19–50)	1	1.0 (0.0) n.s.
	Tulear	35	89.6 (70–106)	1	1.0 (0.0)
C. vagabundus	Moorea	2	43.5 (40–47)	7	6.5 – – –
	Moorea	10	113.8 (104–124)	17	9.4 (1.4)
	Tulear	2	50.1 (43–58)	9	5.5 – – –
	Tulear	13	107.0 (70–130)	15	6.4 (1.3)
C. xanthocephalus	Tulear	4	45.7 (36–60)	7	3.8 (2.5) n.s.
	Tulear	8	129.8 (80–155)	6	3.3 (1.3)

seem to be closely related to their degree of specialization. Distributions were more often similar in highly specialized species, since obligate coral feeders (OCF) and obligate alcyonarian feeders (AL) represented 55.5% of the species with similar patterns, and only 15.8% of the species with different distributions (Table 4). Nevertheless, juveniles of some obligate coral feeders, such as *C. trifascialis* and *C. trifasciatus*, exhibit different patterns of distribution on different reefs.

Discussion

Ontogenetic changes in feeding

The role of larval recruitment in determining the structure and stability of reef fish communities has been often, and sometimes hotly, discussed (Russell et al. 1977, Sale et al. 1980, Williams & Sale 1981, Williams 1983, Victor 1983, 1986b, Eckert 1984, Shulman 1984, 1985, Sale 1985, Doherty & Williams 1988, Mapstone & Fowler 1988, and others). Ecological requirements of larvae and newly settled juveniles generally differ from those of adults, and these differences may explain a number of observed adult distributions (Leis 1986). The importance of shelter, adult density and predation

Table 2. Diets of juveniles and adults in chaetodontids, expressed as weight percentages of prey (Cw) in stomach contents. J = juveniles <60 mm SL, A = adults >60 mm SL, (I) = specimens from 22 to 50 mm SL, (2) = mainly sedentarian polychaete tentacules + juveniles of errant polychaetes, + = Cw <0.1%.

Prey types	C. auriga		C. citri-nellus		C. kleinii		C. lunula		C. lunula		C. madagas-cariensis		C.trifas-scialis		C. trifas-sciatus		C. trifas-sciatus		C. vaga-bundus		C. vaga-bundus		C. xantho-cephalus	
	Tulear		Moorea		Tulear		Moorea		Tulear		Tulear		Tulear		Moorea		Tulear (1)		Moorea		Tulear		Tulear	
	J	A	J	A	J	A	J	A	J	A	J	A	J	A	J	A	J	A	J	A	J	A	J	A
Filamentous algae	12.8	0.1	22.6	34.0	–	–	–	–	–	–	32.5	20.0	–	–	–	–	–	–	1.0	22.5	30.0	+	7.5	7.0
Sponges	–	–	0.4	0.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	13.0	20.0
Hydroids	0.5	0.4	1.0	1.6	25.0	15.5	13.7	0.1	–	–	7.5	–	–	–	–	–	–	–	–	0.8	–	0.1	–	–
Actinians	5.0	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.6	–	–
Scleractinians	0.5	66.2	7.5	15.4	7.5	70.0	2.5	55.7	–	95.0	26.8	55.0	100.0	100.0	100.0	100.0	100.0	100.0	2.0	18.7	10.0	82.5	1.5	6.0
Alcyonarians	0.8	4.7	29.0	27.5	–	–	–	–	–	5.0	–	15.0	–	–	–	–	–	–	–	3.9	–	9.8	3.0	+
Nemerteans	–	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	0.9	–	+	–	–
Polychaetes (2)	57.8	8.6	30.0	12.6	25.0	–	62.3	20.8	7.0	–	30.5	10.0	–	–	–	–	–	–	50.0	21.2	20.0	1.5	43.0	5.0
Sipunculid introverts	7.5	1.4	1.5	5.6	–	–	9.3	4.9	–	–	–	–	–	–	–	–	–	–	–	1.9	–	–	–	–
Opisthobranchs	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10.0	5.2	0.2	0.7	–	–
Gastropods	–	–	–	–	–	–	–	5.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cephalopods	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Molluscan eggs	6.0	14.8	7.6	–	–	–	2.5	4.7	–	–	–	–	–	–	–	–	–	–	30.0	19.9	26.5	1.1	–	–
Cirriped tentacles	–	–	–	–	–	–	–	–	–	–	2.7	–	–	–	–	–	–	–	–	–	–	–	–	–
Calanoid copepods	–	–	–	–	–	–	–	–	10.0	–	–	–	–	–	–	–	–	–	–	–	1.0	–	–	–
Tanaid isopods	–	–	–	+	–	–	–	1.8	20.0	–	–	–	–	–	–	–	–	–	2.0	+	1.8	+	–	–
Amphipods	+	0.1	–	0.1	15.0	4.5	0.7	+	5.0	–	–	–	–	–	–	–	–	–	5.0	+	0.5	+	0.6	–
Decapod shrimps	–	0.2	–	–	–	–	–	1.0	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	–	–
Brachyuran larvae	–	0.1	–	–	–	–	–	2.0	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Echinoid podia	1.8	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Holothurian tentacles	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.3	–	–	–
Pterobranchs	3.3	0.9	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.8	–	–	–
Ascidians	2.1	0.3	–	1.1	27.5	10.0	1.2	–	10.0	–	–	–	–	–	–	–	–	–	–	1.6	–	+	31.4	60.0
Fish eggs	1.9	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	–	–
Mucus + organic matter	–	1.0	–	1.0	–	–	5.0	2.0	48.0	–	–	–	–	–	–	–	–	–	–	2.0	10.0	0.6	–	–
Food niche breadth H'	0.56	1.73	2.30	2.38	1.47	1.30	1.89	2.10	0.92	0.62	1.56	0.83	0.00	0.00	0.00	0.00	0.00	0.00	1.73	2.56	0.64	0.94	1.65	1.58
J'	0.16	0.42	0.72	0.69	0.64	0.65	0.59	0.56	0.37	0.38	0.67	0.36	0.00	0.00	0.00	0.00	0.00	0.00	0.62	0.69	0.19	0.31	0.55	0.68

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Average distance
2.0 1.5 1.0 0.5 0

C.V. TA
C.L. TA
C.K. TA
C.A. TA
C.L. MA
C.V. TJ
C.M. TA
C.L. TJ
C.X. TJ
C.L. MJ
C.A. TJ
C.K. TJ
C.C. MA
C.C. MJ
C.V. MA
C.M. TJ
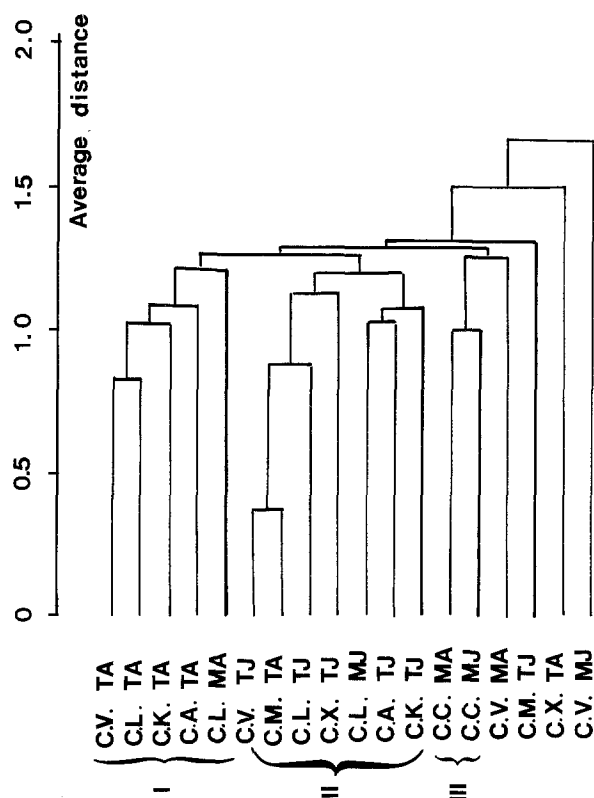C.X. TA
C.V. MJ

I   II   III

Fig. 1. Cluster phenogram of diets of 18 non-obligate corallivo-rous butterflyfishes using average distance coefficients. Group I gathered adult size-classes, group II gathered juvenile size-classes, and group III juveniles and adults of *Chaetodon citrinelus* (C.A. = *Chaetodon auriga*, C.C. = *Chaetodon citrinellus*, C.K. = *Chaetodon kleinii*, C.L. = *Chaetodon lunula*, C.M. = Chaetodon madagascariensis, C.V. = *Chaetodon vagabundus*, C.X. = *Chaetodon xanthocephalus*, T. = Tulear, M = Moorea, A = Adults, J = Juveniles).

has been more thoroughly investigated than the role of the food requirements of early juveniles (Luckhurst & Luckhurst 1977, Williams & Sale 1981, Sale et al. 1984, Shulman 1984, 1985). Based on experiments, Shulman (1984) concluded that food had little effect on recruitment of reef fishes in the Virgin Islands, but did not eliminate 'the possi-bility that prey availability was one of the selective forces involved in settlement site selection by recruits'.

Prey composition diets of larval fishes are very homogeneous and size dominated prey selection patterns. Naupliar through adult stages of cope-pods are the staple food of most marine fish larvae (Hunter 1981). This is probably the case for the diets of chaetodontid larvae, as calanoid copepods were found in the smallest recruits analyzed.

Table 3. Relative importance of polychaetes, mainly tentacles of sedentarian polychaetes andscleractinian polyps in the feeding of juveniles and adults of non-obligate corallivorous chaetodontid species, expressed as weight percentages of the total food ingested. T = Tulear, M = Moorea, G = Guadeloupe, J = juveniles, A = adults, − = no data.

Species	Locality	% Polychaetes		% Scleractinians	
		J	A	J	A
Chaetodon auriga	T	57.8	8.6	0.5	66.2
C. capistratus	G	36.8	−	23.8	−
C. citrinellus	M	30.0	12.6	7.5	15.4
C. kleinii	T	25.0	0.0	7.5	70.0
C. lunula	M	62.3	20.8	2.5	55.7
	T	7.0	0.0	0.0	95.0
C. madagascariensis	T	30.5	10.0	26.8	55.0
C. vagabundus	M	50.0	21.2	2.0	18.7
	T	20.0	1.5	10.0	82.5
C. xanthocephalus	T	43.0	5.0	1.5	6.0
Mean		36.2	8.8	8.2	51.6
s.d.		17.3	8.1	9.6	31.4
Significance of t-test on means		***		***	
		p<0.001		p<0.001	

Change from planktonic to benthic feeding in butterflyfish seems to take place at the very moment of settlement on the reef. The transitional phase between the two life-styles appears to be very short, but needs to be studied more closely. No break in feeding was noticed from the planktonic to the benthic life in the butterflyfish species analyzed, nor in the planktivorous *C. miliaris* studied by Ralston (1981) in Hawaii. In contrast, an interruption in feeding activity during the transformation from the larval to the juvenile state has been observed in other reef fishes such as acanthurids (Randall 1961, Harmelin-Vivien personal observations). For example, during metamorphosis from the acronurus larva, *Acanthurus triostegus* ceases to feed, while largely subsisting on fat reserves stored in its abdominal cavity (Harmelin-Vivien personal observation).

Among chaetodontids, feeding specialization on scleractinian polyps begins at the time of settlement in obligate coral feeders (*C. trifascialis* and *C. trifasciatus*). In these species dietary requirements are probably as important (if not more important) than shelter availability for successful recruitment.

In non-obligate coral feeders, a narrowing of food niche breadth in juveniles, as generally reported for fish (Ross 1986), is hardly noticeable. The food spectrum of the juveniles we studied was similar to that of adults but the relative importance of the main prey eaten differed with size-class. Juveniles of most species took a high proportion of tentacles of sedentarian polychaetes (sabellids, ser-

Table 4. Difference or similarity in the distribution patterns of juvenile and adult chaetodontid fishes. Indication of diets are abbreviated after each species name. OCF = obligate coral feeders, CF = non-obligate coral feeders, AL = alcyonarian feeders, BI = other benthic invertebrate feeders, PK = plankton feeders.

Locality	Similar distributions of juveniles & adults	Different distributions of juveniles & adults	Reference
Guadeloupe		*C. capistratus* (CF)	Bouchon Navaro pers. comm.
Bahamas		*C. capistratus* (CF, BI) *C. ocellatus* (BI) *C. sedentarius* (BI) *C. striatus* (BI)	Lindquist & Gilligan 1986
Jordan (Aqaba)	*C. austriacus* (OCF) *C. paucifasciatus* (CF)	*C. trifascialis* (OCF)	Bouchon-Navaro 1979
Comoro Islands (Anjouan)	*C. melannotus* (AL) *C. trifasciatus* (OCF)	*C. auriga* (CF) *C. kleinii* (BI) *C. trifascialis* (OCF) *C. unimaculatus*	Fricke 1973
Madagascar (Tulear)	*C. blackburni* (AL) *C. guttatissimus* (CF) *C. kleinii* (BI) *C. madagascariensis* (CF) *C. melannotus* (AL) *C. trifascialis* (OCF)	*C. auriga* (CF) *C. lunula* (CF) *C. trifasciatus* (OCF) *C. vagabundus* (CF) *C. xanthocephalus* (BI)	Harmelin-Vivien 1979
Hawaii	*C. miliaris* (PK)		Ralston 1981
French Polynesia (Moorea)	*C. citrinellus* (CF) *C. ornatissimus* (OCF) *C. pelewensis* (CF) *C. quadrimaculatus* (CF) *C. reticulatus* (OCF) *C. trifascialis* (OCF) *C. trifasciatus* (OCF)	*C. auriga* (CF) *C. ephippium* (CF) *C. lunula* (CF) *C. vagabundus* (CF)	Bouchon-Navaro 1981

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pulids, terebellids), whereas adults mainly fed on scleractinians or other sessile invertebrates (alcyonarians, ascidians, sponges). Polychaetes probably are more nutritious than coral tissue, and better supply the higher energy demand of juveniles. The high dietary overlap between juveniles of different species which might result from similar prey preferences does not necessarily imply any competitive interaction, as juvenile density is generally low and their main prey is very abundant on coral reefs. Greater similarity of diets among juveniles than among adults has been observed in other fish species (Duka 1976, Ross 1986), and has been interpreted as a consequence of the exploitation of some abundant types of prey. How prey utilization is related to ontogenetic changes in behavior and/ or morphology of the feeding apparatus has not been determined in this study. In a study of the functional morphology of the feeding apparatus of butterflyfishes, Motta (1988) observed that in many cases the polychaete worms retracted in their tube, and escaped predation faster than fish was able to catch them. A faster jaw protrusion time in juvenile butterflyfish might explain why polychaete worms are mostly preyed upon by juvenile individuals. An alternative hypothesis is that the iron content of the teeth of butterflyfish, which is correlated with their diet (Motta 1987) is much lower in juvenile fishes and prevents them from feeding intensively on hard-bodied prey like corals. In the latter case, the iron content of the teeth caps should be much higher in juvenile specimens of obligate coral feeders than in non-obligate ones. We were unable to investigate this point.

Implication on community structure

The described patterns of butterflyfish communities are based on the distribution and interactions of adult individuals; and generally show a positive relationship between cover of living scleractinians, fish species richness and fish abundance (Bouchon-Navaro 1979, 1981, Anderson et al. 1981, Bell & Galzin 1984, Bell et al. 1985, Bouchon-Navaro et al. 1985, Findley & Findley 1985). Some authors have suggested there is little evidence that butter-

flyfish assemblages are resource-limited (Bell et al. 1985, Findley & Findley 1985). Others, however, have emphasize the possible importance of competitive interactions among chaetodontid species (Reese 1975, Anderson et al. 1981, Bouchon-Navaro 1986).

It is often claimed that reef fishes are relatively site-attached after recruitment (Sale 1980). In fact, the site of settlement and the site of adult-life differ in many reef fish species, and one can notice a differential distribution of size-class cohorts across a reef in the same species (Galzin 1985, Shulman & Ogden 1987). Among chaetodontids, where adults are reported to be highly sedentary (Reese 1975, 1977, 1981), it seems that settlement occurs preferentially in shallow-water habitats for at least half of the species studied (Table 4). The patterns of size-class distribution may vary with geographical areas within the same fish species, and do not seem to be closely related to feeding specialization, contrary to what hypothesized. The importance of shallow waters for reef fish recruits is well known in species such as *Acanthurus triostegus* (Randall 1961, Sale 1969). Particular hydrological conditions, food resources or avoidance of predators are put forward to account for the high rate of fish recruitment observed in shallow waters.

When a fish settles in a reef zone different to that of adults of the same species, its recruitment is independent of local adult density, and no intraspecific overlap in food and microhabitat exists during the early life-history of the species. When recruitment occurs within adult home ranges, differences in food requirements between size-classes reduces the potential intraspecific competition for that resource.

The present study demonstrates that among chaetodontids specific food and spatial requirements of adults and juveniles may range from identical to completely different. Recruitment studies to date have emphasized species with similar juvenile and adult habits. It is suggested that the dynamics of species in which food and habitat requirements differ significantly between juveniles and adults may differ fundamentally from these species. In particular, post-settlement events, especially at times of transition between juvenile and

adult behavior, may be of greater importance in determining recruitment to adult populations than initial densities of post-larvae.

Feeding requirements of juvenile butterflyfishes – and of coral reef fishes in general – need to be thoroughly investigated for a better understanding of post-settlement events. The timing of the transition between planktonic feeding to benthic feeding should be determined by analysis of otoliths and stomach contents for the same individuals. It is necessary to know the food preferences of recruits, and to determine if there is any consistency within fish families or within feeding guilds. The caloric value and chemical composition of prey should be determined, and related to the energetic requirements of juvenile fishes. These analyses should be conducted on syntopic species exhibiting different level of feeding specialization. For species with very specific feeding requirements, distribution and abundance of suitable food resources may greatly restrict the availability of potential settling sizes. The importance of food resources on settlement may be investigated by appropriate experiments where the real specific food resources of recruits are modified.

Acknowledgement

References cited

Anderson, G.R.V., A.H. Ehrlich, P.R. Ehrlich, J.D. Roughgarden, B.C. Russell & F.H. Talbot. 1981. The community structure of coral reef fishes. Amer. Nat. 117: 476–495.

Bell, J.D. & R. Galzin. 1984. The influence of live coral cover on coral reef fish communities. Mar. Ecol. Prog. Ser. 15: 265–274.

Bell, J.D., M.L. Harmelin-Vivien & R. Galzin. 1985. Large scale spatial variation in abundance of butterflyfishes (Chae-

todontidae) on Polynesian reefs. Proc. Fifth Internat. Coral Reef Symp. 5: 421–426.

Birkeland, C. & S. Neudecker. 1981. Foraging behavior of two Caribbean chaetodontids: *Chaetodon capistratus* and *C. aculeatus*. Copeia 1981: 169–178.

Bouchon-Navaro, Y. 1979. Quantitative distribution of the Chaetodontidae on a fringing reef of the Jordanian coast (Gulf of Aqaba, Red Sea). Téthys 9: 247–251.

Bouchon-Navaro, Y. 1981. Quantitative distribution of the Chaetodontidae on a reef of Moorea Island (French Polynesia). J. Exp. Mar. Biol. Ecol. 55: 145–157.

Bouchon-Navaro, Y. 1985. Ecologie des Chaetodontidae des récifs coralliens d'Aqaba (Mer Rouge) et de Moorea (Polynésie française). Diplome EPHE, Paris. 193 pp.

Bouchon-Navaro, Y. 1986. Partitioning of food and space resources by chaetodontid on coral reefs. J. Exp. Mar. Biol. Ecol. 103: 21–40.

Bouchon-Navaro, Y., C. Bouchon & M.L. Harmelin-Vivien. 1985. Impact of coral degradation on a chaetodontid fish assemblage (Moorea, French Polynesia). Proc. Fifth Internat. Coral Reef Symp. 5: 427–432.

Brothers, E.B., D.Mc.B. Williams & P.F. Sale. 1983. Length of larval life in twelve families of fishes at 'One Tree Lagoon', Great Barrier Reef, Australia. Mar. Biol. 76: 319–324.

Burgess, W.E. 1978. Butterflyfishes of the world. T.F.H. publications, Neptune City. 832 pp.

Clarke, R.D. 1977. Habitat distribution and species diversity of chaetondontid and pomacentrid fishes near Bimini, Bahamas. Mar. Biol. 40: 277–289.

Doherty, P.J. & D.Mc.B. Williams. 1988. The replenishment of coral reef fish populations. Oceanogr. Mar. Biol. Annu. Rev. 26: 487–551.

Duka, L.A. 1976. Feeding and food relationships of the larvae and young of the family Labridae. J. Ichtyol. 16: 398–407.

Eckert, G.J. 1984. Annual and spatial variation in recruitment of Labroid fishes among seven reefs in the Capricorn (Bunker Group, Great Barrier Reef). Mar. Biol. 78: 123–127.

Findley, J.S. & M.T. Findley. 1985. A search for pattern in butterflyfish communities. Amer. Nat. 126: 800–816.

Fricke, H.W. 1973. Behaviour as part of ecological adaptation. In situ studies in the coral reef. Helgoländer wiss. Meeresunters. 24: 120–144.

Galzin, R. 1985. Ecologie des poissons récifaux de Polynésie Française: variations spatio-temporelles des peuplements, Dynamique de populations de trois espèces dominantes des lagons nord de Moorea, Evaluation de la production ichtyologique d'un secteur récifo-lagonaire. Ph. D. Dissertation, Univ. Sciences et Technique du Languedoc, Montpellier. 195 pp.

Gore, M.A. 1984. Factors affecting the feeding behavior of a coral reef fish, *Chaetodon capistratus*. Bull. Mar. Sci. 35: 211–220.

Harmelin-Vivien, M.L. 1979. Ichtyofaune des récifs coralliens de Tuléar (Madagascar): Ecologie et relations trophiques. Ph. D. Dissertation, Univ. Aix-Marseille II, Marseille. 165 pp.

Harmelin-Vivien, M.L. & Y. Bouchon-Navaro. 1982. Trophic

relationships among chaetodontid fishes in the Gulf of Aqaba (Red Sea). Proc. Fourth Internat. Coral Reef Symp. 2: 537–544.

Harmelin-Vivien, M.L. & Y. Bouchon-Navaro. 1983. Feeding diets and significance of coral feeding among chaetodontid fishes in Moorea (French Polynesia). Coral Reefs 2: 119–127.

Hiatt, R.W. & D.W. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30: 65–127.

Hobson, E.S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. U.S. Fish. Bull. 72: 915–1031.

Hunter, J.R. 1981. Feeding ecology and predation of marine fish larvae. pp. 33–77. In: R. Lasker (ed.) Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries, University of Washington Press, Seattle.

Lasker, H.R. 1985. Prey preferences and browsing pressure of the butterflyfish Chaetodon capistratus on Caribbean gorgonians. Mar. Ecol. Prog. Ser. 21: 213–220.

Leis, J.M. 1986. Ecological requirements of Indo-Pacific larval fishes: a neglected zoogeographic factor. pp. 759–766. In: T. Uyeno, R. Arai, T. Taniuchi & K. Matsuura (ed.) Indo-Pacific Fish Biology: Proc. Second Internat. Conf. Indo-Pacific Fishes, Ichtyol. Soc. of Japan, Tokyo.

Lindquist, D.G. & M.R. Gilligan. 1986. Distribution and relative abundance of butterflyfishes and angelfishes across a lagoon and barrier reef, Andros Island, Bahamas. Northeast Gulf Science 8: 23–30.

Luckhurst, B.E. & K. Luckhurst. 1977. Recruitment patterns of coral reef fishes on the fringing reef of Curaçao, Netherlands Antilles. Can. J. Zool. 55: 681–689.

Mapstone, B.D. & A.J. Fowler. Recruitment and the structure of assemblages of fish on coral reefs. TREE 3: 72–77.

Motta, P.J. 1987. A quantitative analysis of ferric iron in butterflyfish teeth (Chaetodontidae, Perciformes) and the relationship to feeding ecology. Can. J. Zool. 65: 106–112.

Motta, P.J. 1988. Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. Env. Biol. Fish. 22: 39–67.

Ralston, S. 1976. Age determination of a tropical reef butterflyfish utilizing daily growth rings of otoliths. U.S. Fish. Bull. 74: 990–994.

Ralston, S. 1981. Aspects of the reproductive biology and feeding ecology of Chaetodon miliaris, a Hawaiian endemic butterflyfish. Env. Biol. Fish. 6: 167–176.

Randall, J.E. 1961. A contribution to the biology of the convict surgeon fish of the Hawaiian Islands, Acanthurus triostegus sandvicensis. Pac. Sci. 15: 215–272.

Randall, J.E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. 5: 665–847.

Reese, E.S. 1975. A comparative field study of the social behavior and related ecology of reef fishes of the family Chaetodontidae. Z. Tierpsychol. 37: 37–61.

Reese, E.S. 1977. Coevolution of corals and coral feeding fishes of the family Chaetodontidae. Proc. Third Internat. Coral Reef Symp. 1: 267–274.

Reese, E.S. 1981. Predation on corals by fishes of the family Chaetodontidae: implications for conservation and management of coral reef ecosystems. Bull. Mar. Sci. 31: 594–604.

Ross, S.T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia 1986: 352–388.

Russel, B.C., G.R.V. Anderson & F.H. Talbot. 1977. Seasonality and recruitment of coral-reef fishes. Aust. J. Mar. Freshw. Res. 28: 521–528.

Sale, P.F. 1969. Pertinent stimuli for habitat selection by the juvenile manini, Acanthurus triostegus sandvicensis. Ecology 50: 616–623.

Sale, P.F. 1980. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Ann. Rev. 18: 367–421.

Sale, P.F. 1985. Patterns of recruitment in coral reef fishes. Proc. Fifth Internat. Coral Reef Symp. 5: 391–396.

Sale, P.F., P.J. Doherty & W.A. Douglas. 1980. Juvenile recruitment strategies and the coexistence of territorial pomacentrid fishes. Bull. Mar. Sci. 30: 147–158.

Sale, P.F., W.A. Douglas & P.J. Doherty. 1984. Choice of microhabitats by coral reef fishes at settlement. Coral Reefs 3: 91–100.

Sano, M., M. Shimizu & Y. Nose. 1984. Changes in structure of coral reef fish communities by destruction of hermatypic corals: observational and experimental views. Pac. Sci. 38: 51–79.

Shulman, M.J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. J. Exp. Mar. Biol. Ecol. 74: 85–109.

Shulman, M.J. 1985. Recruitment of coral reef fishes; effects of distribution of predators and shelter. Ecology 66: 1056–1066.

Shulman, M.J. & J.C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish Haemulon flavolineatum. Mar. Ecol. Prog. Ser. 39: 233–242.

Victor, B.C. 1983. Recruitment and population dynamics of a coral reef fish. Science 219: 419–420.

Victor, B.C. 1986a. Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). Mar. Biol. 90: 317–326.

Victor, B. 1986b. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol. Monogr. 56: 145–160.

Williams, D.Mc.B. 1983. Daily, monthly and early variability in recruitment of a guild of coral reef fishes. Mar. Ecol. Prog. Ser. 10: 231–237.

Williams, D.Mc.B. & P.F. Sale. 1981. Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within One Tree Lagoon, Great Barrier Reef. Mar. Biol. 65: 245–253.