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COHABITATION OF COMPETING TERRITORIAL DAMSELFISHES ON A CARIBBEAN CORAL REEF[1]

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Abstract. Individual adults of three Caribbean damselfishes defend feeding areas that do not overlap with those of conspecific adults. The feeding areas of adults of the two smaller species, *Stegastes dorsopunicans* and *S. planifrons,* do not overlap interspecifically. However, feeding areas of adults of the largest species, *Microspathodon chrysurus,* are superimposed on feeding areas of adults and juveniles of the two *Stegastes* species. The large species aggressively dominates its smaller interspecific cohabitants. Cohabitant individuals of each species eat the same types of benthic microalgae. *M. chrysurus* has the same daily cycle of feeding activity as the two small species, uses the same feeding microhabitats as they do, and feeds almost exclusively in their feeding areas. Cohabitants defend their feeding areas against the same set of other herbivorous fishes, but *M. chrysurus* is involved in defensive actions much less frequently than is either of its small cohabitants. *M. chrysurus* also is much less effective at such defense than at least one cohabitant, *S. dorsopunicans. S. dorsopunicans* on a reef from which *M. chrysurus* were removed increased their body mass more and had larger fat deposits than conspecifics on a control reef. Thus adults of *M. chrysurus* appear to be dependents that use their size-based dominance ability to obtain food from their cohabitants. Juveniles of *M. chrysurus* and *S. dorsopunicans* exhibit small-scale habitat segregation and segregated use of feeding substrates in a shared microhabitat, which may facilitate the recruitment of both species.

Key words: Caribbean; coexistence; cohabitation; coral reef fishes; damselfishes; food competition; herbivory; territoriality.

Introduction

Assemblages of fishes that live on coral reefs are among the most speciose known. Given the possibility of interspecific competition and competitive exclusion it is of theoretical interest to determine the types and importance of different mechanisms that maintain the composition of those assemblages. The traditional view of such mechanisms emphasizes the minimization of interspecific competition through resource partitioning. This view has come to be challenged by studies that have found that behavior indicative of interspecific interference competition commonly occurs, and that groups of species with similar resource requirements often co-occur (for reviews see Sale 1977, 1980, Talbot et al. 1980, Williams 1980, Anderson et al. 1981).

It now seems evident that both intra- and interspecific competition for food are common among herbivorous fishes that live on coral reefs in a variety of locations. Assemblages of herbivorous reef fishes typically contain many species and high densities of individuals, and sympatric herbivores often exhibit a high degree of overlap in their diets (Hiatt and Strasburg 1960, Randall 1967, Jones 1968, Robertson et al. 1979). Many herbivores establish feeding territories that are defended not only against conspecifics but also against a broad range of other fishes that have similar diets. The literature has emphasized how those territorial herbivores usually attempt to exclude from their feeding areas any fishes that try to use food resources contained therein (Low 1971, Myrberg and Thresher 1974, Robertson et al. 1976, Ebersole 1977, Itzkowitz 1977, Sale 1977, Williams 1978, Robertson et al. 1979, Mahoney 1981, Losey 1982). Recently, however, Robertson and Polunin (1981) have described a relationship between different species of highly territorial herbivores that share and defend a common food supply. Here I describe in detail a similar relationship between pairs of algivorous damselfishes (Pomacentridae) which was briefly discussed by Waldner and Robertson (1980). The species are *Microspathodon chrysurus* (Cuvier), which cohabits with *Stegastes* (=*Eupomacentrus,* Emery and Allen 1980) *dorsopunicans* (Poey) and *S. planifrons* (Cuvier). All three species are abundant on shallow reefs throughout the Caribbean Sea (Bohlke and Chaplin 1968, Randall 1968, Emery 1973, Clarke 1977, Itzkowitz 1977, Waldner and Robertson 1980). Most attention is given to the relationship between *M. chrysurus* and *S. dorsopunicans* because these two species reach their greatest abundance in shared habitat. Although overlap in habitat use by *M. chrysurus* and *S. planifrons* is not as marked as with *M. chrysurus* and *S. dorsopunicans,* the relationship between *M. chrysurus* and *S. planifrons* is also discussed because it illustrates the importance of size-based dominance abilities in these cohabitation relationships.

To define the nature of the relationships between each pair of species I present observational and experimental data on the spatial distributions of each species, their population densities and standing crops, and the degree of partitioning of food resources in space and time. I also present data on their territorial relations with conspecifics, with their cohabitants, and with

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other species, and the effort each cohabitant contributes to the defense of shared areas. Finally, I describe an experiment that identifies a net cost to the relationship for one of the cohabitants.

The Study Species and Study Area

Microspathodon chrysurus, which is one of the largest Caribbean pomacentrids (Bohlke and Chaplin 1968), reached a mass of 155 g in the study area. The two *Stegastes* species are considerably smaller; the largest *S. dorsopunicans* and *S. planifrons* that I collected from unmanipulated populations weighed 25 and 55 g, respectively.

Data were collected between October 1976 and September 1982 on shallow reefs off Punta de San Blas, on the Caribbean coast of Panama. Waldner and Robertson (1980) present a general description of those reefs. Data on cohabitant *M. chrysurus* and *S. dorsopunicans* were collected on the top of the eastern tip of Aguadargana reef in a shallow (<2 m deep) habitat composed mostly of a mixture of dead and live elkhorn coral, *Acropora palmata,* and coralline rock, with scattered clumps of *Millepora* hydrocorals. Data on cohabitant *M. chrysurus* and *S. planifrons* were obtained from fishes living in a slightly deeper habitat (3–6 m depth) composed of live and dead corals, principally *Agaricia agaricites* and *Acropora cervicornis.* This habitat was located on the sides of Aguadargana reef.

Observations

Methods

To determine the degree of habitat overlap by the three species on the main study reef I counted the numbers of individuals of each that had feeding areas in 5 m long segments of a 5 m wide belt transect. The transect was run from the lower limit of coral growth on one side of Aguadargana reef, up across the top of the reef and down to the lower limit of coral growth on the other side.

I determined overlap in feeding areas as follows. In the center of the habitat in which *M. chrysurus* and *S. dorsopunicans* co-occurred I mapped the feeding areas of all adults of both species present in a 10 × 10 m plot, using the location of bites taken by each individual. *S. dorsopunicans,* which has small feeding areas and feeds at a high rate (see Results) was observed for 10 min/fish. *M. chrysurus,* which also feeds at a high rate but has larger feeding areas, was observed for 30 min/fish. Similar sets of observations were made on *M. chrysurus* and *S. planifrons* in a 15 × 10 m plot in their shared habitat. The feeding area of each adult *M. chrysurus* resident in that plot was mapped, using the locations of the bites it took during three discontinuous 15-min periods. I also mapped the locations of all *S. planifrons* of three size-classes: large fish (>20 g), medium fish (8–20 g), and small fish (4–7 g). Adult and subadult *S. planifrons* defend small mats of algae from which they obtain virtually all of their substrate-derived food (Robertson et al. 1981). Those mats, which have a characteristic appearance (Brawley and Adey 1977, Kaufman 1977), were used to determine the locations of the fish. Overlap in the feeding areas of adult *M. chrysurus* with those of the *S. planifrons* living inside the boundary of the *M. chrysurus'* feeding areas was determined by recording how many bites each of 20 *M. chrysurus* took inside vs. outside *S. planifrons'* feeding areas during a 15-min period.

Densities and standing crops

Population densities were determined from counts of the numbers of residents in the 100 m^2 and 150 m^2 plots (see above). Each individual whose feeding area was only partly in those plots was assigned a score that reflected the percentage of its feeding area that was in the plot. I calculated the standing stock of each species using these density figures and the mean masses of a series of cohabitant individuals of each species that I speared in the study habitats.

Agonistic relations of the cohabitants

Observations were made on a series of individuals of each species, for periods of 10–20 min for the *Stegastes* spp., and 15–60 min for *M. chrysurus.* During each period I recorded all agonistic interactions the study animal had, noting the species and size of the opponent, which fish initiated the encounter, and which fish was overtly aggressive (threatened with fin spreading and moved toward, rushed at, and/or chased the other).

Partitioning of food resources by adult cohabitants

Cohabitants could partition food resources by eating different types of food items, by obtaining the same food items from different microhabitats or, if the food was renewed very rapidly, by consuming the same food items at different times of the day. These alternatives were assessed as follows.

Diets

Stomach contents of a series of sets of cohabitants were analyzed to assess the similarity of the cohabitants' diets. Each set consisted of an *M. chrysurus* and an adult *Stegastes* sp. cohabitant living in the center of that *M. chrysurus'* feeding area. Pairs of fishes were speared, killed immediately, and dissected within 60 min of capture. The stomach contents of each fish were preserved in 5% neutral buffered formaldehyde in seawater. The relative abundances of items present in each stomach were determined by placing an aliquot of each sample on a glass slide, and noting (using a microscope) what items were present under 100 randomly distributed points on a grid superimposed on that slide. The relative abundances of different diatom genera were determined separately, using the same method.

Use of different feeding microhabitats

The habitat shared by *M. chrysurus* and *S. dorsopunicans* is topographically complex, due mainly to the growth form of *Acropora palmata.* Nine substrate microhabitats were defined, taking into account the nature of the substrate (e.g., live coral, "dead" rock), its degree of exposure, its inclination, and its physical accessibility to each cohabitant.

Two observers simultaneously noted the feeding activity of sets of cohabitants in each of these microhabitats. Each observer watched an individual of a different species and recorded the number of bites it took from each microhabitat during a specified period. One observer collected data on a *M. chrysurus* for 1 h while the other collected data on 3–6 *S. dorsopunicans* (10–20 min per fish) living in that *M. chrysurus'* area. Then the observers switched species and the data collection was repeated on the same cohabitant individuals. The entire 2 h of observations were combined to calculate a mean percentage of bites taken by each cohabitant species in each microhabitat.

Daily feeding activity

All three damselfishes are diurnally active fishes that become relatively inactive at night (D. R. Robertson, *personal observations*). Daily cycles of feeding activity of adults of each species were determined as follows. For each species a series of 10-min observations on at least 12 different individuals was made during each hour of the day. During each 10-min period the number of bites taken from the substrate by the study fish was recorded. Each series of observations was used to calculate a mean bite rate during each hour. No observations were made when the fishes were feeding intensively on plankton.

Relations between juveniles of M. chrysurus *and* S. dorsopunicans

Juveniles of *M. chrysurus* are known to feed heavily on *Millepora* hydrocorals (Ciardelli 1968). Since, on cursory inspection, those juveniles appeared largely to be restricted to patches of such hydrocorals in San Blas, the spatial distributions of juveniles of both *M. chrysurus* and *S. dorsopunicans* were examined in relation to *Millepora* patches growing in habitat shared by adults of those fishes. In addition, the degree of partitioning of feeding microhabitats by juveniles of both species living in *Millepora* patches and their territorial relations were examined.

On a 50 × 2 m belt transect that was run across shared habitat on Aguadargana reef I noted the location of each juvenile of both damselfishes relative to *Millepora* patches. These data were used to compare the abundances of juveniles of each species in and out of *Millepora* patches.

To determine the relative amounts of feeding in different microhabitats by each species I made a series of 20–30 min observations on different juveniles of each species living in *Millepora* colonies. During each observation period I recorded the type of substrate from which each bite was taken by the fish.

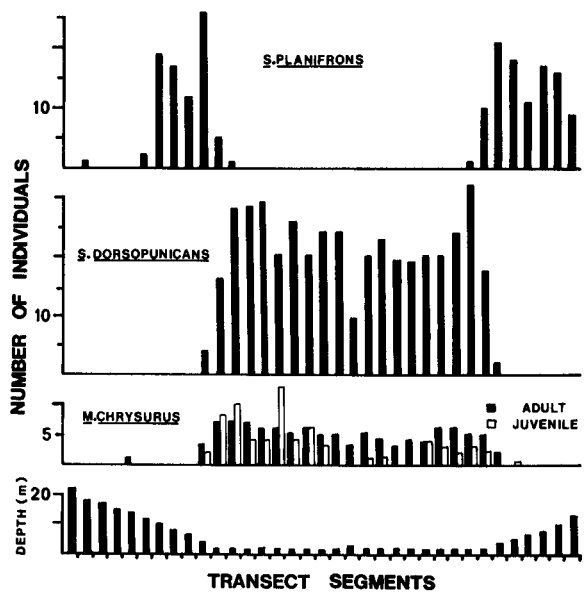

FIG. 1. Distributions of three damselfishes along a belt transect. Number of individuals of each species in each 5 × 5 m segment of the 165 m long transect; *Stegastes planifrons* and *S. dorsopunicans* total, *Microspathodon chrysurus* adults and juveniles separated. Depth = depth in center of each transect segment.

To assess territorial relations between juveniles of the two species I determined the degree of overlap of the feeding area of each study fish with the feeding areas of other juveniles of *M. chrysurus* and *S. dorsopunicans* and recorded agonistic interactions between such space sharers.

RESULTS

Spatial distributions

Habitat distributions.—*M. chrysurus* and *S. dorsopunicans* found in at least four widely separated Caribbean sites typically share the same habitats, and each species reaches its greatest population density and greatest relative abundance of large adults in shared habitat (Emery 1973, Clarke 1977, Itzkowitz 1977, Waldner and Robertson 1980). In the main study area the coincidence of the distributions of these species was very striking (Fig. 1). Habitat sharing between *S. planifrons* and *M. chrysurus* was less pronounced (e.g., Fig. 1), and habitat that characteristically supported large adults of *S. planifrons* contained very few *M. chrysurus* (Waldner and Robertson 1980, D. R. Robertson, *personal observations*).

Feeding area overlaps.—In all three species, feeding areas were occupied by single individuals of either sex. There was virtually no overlap between the feeding

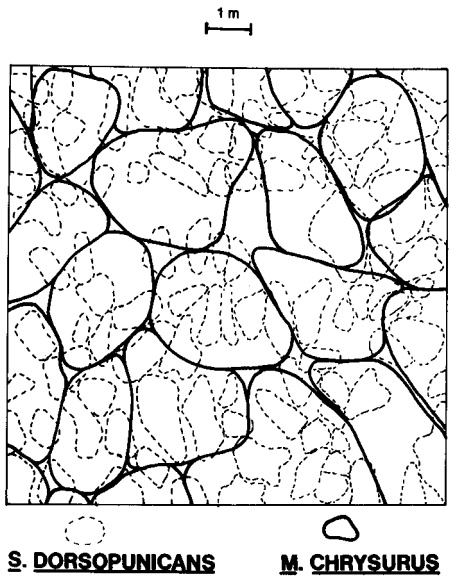

FIG. 2. Map of the feeding areas of adult *Microspathodon chrysurus* and adult *Stegastes dorsopunicans* in a randomly chosen 10 × 10 m plot. Each *M. chrysurus* was observed for 30 min, and each *S. dorsopunicans* for 10 min.

areas of adult conspecifics. Only 1.8% of 3075 bites by 24 adult *M. chrysurus* (observation time 30 min/fish) were taken from overlap areas, as were 0.2% of 3876 bites taken by 102 adult *S. dorsopunicans* (10 min/fish) and 0.4% of 3796 bites taken by 31 adult *S. planifrons* (20 min/fish).

In contrast, the feeding areas of adult *M. chrysurus* typically overlapped those of *S. dorsopunicans* of all size classes, although there was no tendency for borders of the two species' areas to coincide (Fig. 2). All of the substrate feeding by 24 adult *M. chrysurus* that were each observed for 30 min occurred within the feeding areas of their *S. dorsopunicans* cohabitants.

The presence or absence of overlap in the feeding areas of small *M. chrysurus* and *S. dorsopunicans* was related to some extent to the relative sizes of the individual fishes involved. Each of 25 medium-sized juveniles of *M. chrysurus* overlapped feeding areas with *S. dorsopunicans* individuals that were less than half the size of the *M. chrysurus*. However, each of those *M. chrysurus* also had at least one noncohabitant neighboring *S. dorsopunicans* that was >75% of the *M. chrysurus* size.

The feeding areas of adult *M. chrysurus* frequently overlapped completely with the smaller feeding areas of *S. planifrons*. However, this overlap only involved *S. planifrons* that were smaller than about half the maximum size reached by the species. I speared the largest *S. planifrons* individual that shared its feeding area with each of 20 adult *M. chrysurus*; those *S. planifrons* had a mean mass of 19 ± 2 g (95% CI), while the smallest noncohabitant *S. planifrons* neighbor of each of those *M. chrysurus* that I collected had a mean mass of 23 ± 3 g. Those noncohabitant *S. planifrons* usually had feeding areas located outside the edge of an *M. chrysurus'* area. However, some noncohabitant *S. planifrons* had feeding areas that were inside and completely surrounded by an *M. chrysurus'* feeding area. In the habitat in which I examined space sharing by these two species, only about half the *S. planifrons* adults and subadults shared their feeding areas with *M. chrysurus* (Table 1). In the 150-m^2 study plot in that habitat there was a negative association between the spatial distributions of *M. chrysurus* adults and large *S. planifrons*: although the *M. chrysurus'* feeding areas occupied 59.5% of that plot, only 11 of 83 large *S. planifrons* were found inside them ($\chi^2 = 73.7$, $P < .001$). However, there was a positive association of *M. chrysurus'* feeding areas with those of smaller *S. planifrons*, since disproportionately large numbers of medium (41 of 53, $\chi^2 = 7.1$, $P < .01$) and small (72 of 100, $\chi^2 = 6.5$, $P < .05$) *S. planifrons* were found inside *M. chrysurus'* feeding areas (Fig. 3).

Twenty *M. chrysurus* adults took a mean of 94.1% (SE = 1.0) of their substrate bites from within the feeding areas of their cohabitant *S. planifrons*.

Population densities and standing crops.—In the habitat in which *M. chrysurus* and *S. dorsopunicans* were both abundant and represented by many large adults, *M. chrysurus* was much less dense than *S. dorsopunicans*, and the average adult *M. chrysurus* feeding area encompassed the feeding areas of about six adult *S. dorsopunicans* (Table 1). However, due to the great difference in mean sizes of the adults of these two species the standing crop of *M. chrysurus* was ≈50% higher than that of *S. dorsopunicans* (Table 1).

Adult *M. chrysurus* living in habitat they shared with *S. planifrons* were considerably smaller than adult *M. chrysurus* living with *S. dorsopunicans* (Table 1). Consequently, even though individual *M. chrysurus* adults

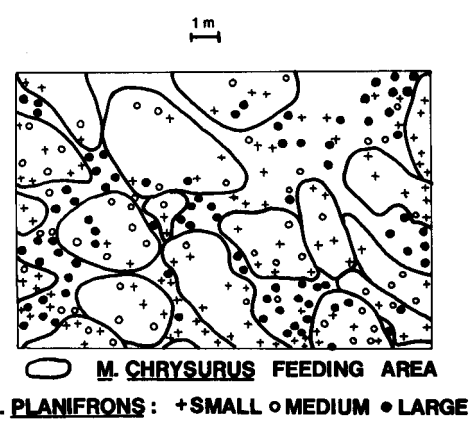

FIG. 3. Distributions of different-sized *Stegastes planifrons* relative to the feeding areas of adult *Microspathodon chrysurus*. *S. planifrons*: large ≥20 g, medium 8–19 g, small 4–7 g.

TABLE 1. Population densities and standing crops of cohabitant damselfishes. Data are $\bar{x}$ and 95% CI. *M. ch.* = *Microspathodon chrysurus, S. dp.* = *Stegastes dorsopunicans, S. pl.* = *S. planifrons.*

	Cohabitants		Cohabitants	
	M. ch.	*S. dp.*	*M. ch.*	*S. pl.*
1. No. *Stegastes* sp. individuals per *M. chrysurus* adult feeding area		6.01 ± 0.5 (adults)		5.9 ± 0.7 (adults + large juveniles)
No. *M. chrysurus* feeding areas observed		34		28
2. Mass (g) of adult cohabitants	109 ± 4	13 ± 1	60 ± 2	10 ± 2
No. fish measured	34	79	15	33
3. Percentage of *Stegastes* sp. individuals that cohabit with adult *M. chrysurus* in shared habitat		100		52.5*
No. *Stegastes*		200 (adults)		236 (adults + large juveniles)
4. No. adults/m²	0.17	0.90	0.15	1.27
No. *M. chrysurus* feeding areas observed	24		18	
5. Estimated standing crop of adults (g/m²)†	19	12	9	13

* In habitat in which cohabitation is commonly observed.
† Derived from 2 and 4 above.

in each habitat had about the same number of *Stegastes* sp. cohabitants and about the same population densities (Table 1), the standing crop of *M. chrysurus* in *S. planifrons* habitat was only half that of conspecifics in *S. dorsopunicans* habitat and was ≈30% less than that of the cohabitant *S. planifrons* (Table 1).

Agonistic relations of the cohabitants

Intraspecific relations.—Adults of each species were strongly intraspecifically territorial and attacked and largely excluded conspecific adults from their feeding areas. This attempted exclusion was also directed at juvenile conspecifics and, although a minority of juveniles (2 of 14 *M. chrysurus* juveniles and 22 of 114 *S. dorsopunicans* juveniles in the 10 × 10 m study plot) did live inside conspecific adults' feeding areas, they (and juveniles living just outside the adults' feeding areas) were harrassed by those adults.

Relations between cohabitants.—Although there were agonistic interactions between adult *M. chrysurus* and their adult *S. dorsopunicans* cohabitants, individuals of each species were involved in such interactions much less frequently than they were involved in intraspecific territorial interactions (Table 2). Interactions between *M. chrysurus* and both cohabitant and noncohabitant *S. planifrons* occurred much more frequently than interactions between *M. chrysurus* and *S. dorsopunicans* (Table 2). Juvenile *M. chrysurus* interacted with adult conspecifics and with noncohabitant adult *S. dorsopunicans* at about the same frequency, which was greater than that of interspecific interactions between cohabitant adults of the two species (Table 2).

S. dorsopunicans and *S. planifrons* initiated about half of their agonistic encounters (54% of 24 and 227 encounters, respectively) with their cohabitant *M. chrysurus.* In contrast, noncohabitant *S. planifrons* adults initiated almost all (97% of 146) of their encounters with neighboring adult *M. chrysurus.* None of the interactions between juvenile *M. chrysurus* and either adult conspecifics or noncohabitant adult *S. dorsopunicans* was initiated by the juvenile *M. chrysurus.*

Interactions between juvenile *M. chrysurus* and both

TABLE 2. Frequencies of intraspecific and interspecific agonistic interactions among territorial individuals of the three damselfishes. Data are $\bar{x}$ and 95% CI. Sample sizes are given in parentheses.

Type of interaction	No. interactions/h involving adults of:		
	M. chrysurus	*S. dorsopunicans*	*S. planifrons*
Between an adult and conspecific adults	In *S. dorsopunicans* habitat 8.0 ± 1.6 (39 fish × 30 min) In *S. planifrons* habitat 3.5 ± 1.1 (65 fish × 15 min)	5.8 ± 2.2 (74 fish × 10 min)	7.0 ± 1.4 (79 fish × 10 min)
Between an adult *M. chrysurus* and cohabitant *Stegastes*		0.4 ± 0.3	9.4 ± 2.7
noncohabitant *Stegastes*		0 (58 fish × 30 min)	4.3 ± 1.1 (65 fish × 15 min)
Between a juvenile *M. chrysurus* and noncohabitants	5.2 ± 1.8 (50 fish × 30 min)	4.3 ± 1.9 (48 fish × 30 min)	No data

TABLE 3. Attacks on other fishes by cohabitant *M. chrysurus* and *Stegastes* spp. *M. ch.* = *M. chrysurus*, *S. dp.* = *S. dorsopunicans*, *S. pl.* = *S. planifrons*.

	No. of attacks:				
	By each cohabitant during same observation period		By *M. ch.* after removal of *S. dp.*	By each cohabitant during same observation period	
Receiver of attacks	*M. ch.*	*S. dp.*		*M. ch.*	*S. pl.*
Algivores*					
Scarus iserti	3	731	427	9	191
Sc. vetula	0	95	9	0	0
Sparisoma viride	2	103	37	9	76
Sp. rubripinne	0	75	12	0	0
Sp. aurofrenatum	0	84	12	0	51
Sp. chrysopterum	0	19	5	0	0
Acanthurus bahianus	1	193	245	0	4
A. coeruleus	3	87	56	0	0
A. chirurgus	0	1	34	0	0
Kyphosus sectatrix	0	1	0	0	0
Abudefduf saxatilis	0	0	0	6	21
Total	9	1389	837	24	346
Carnivores*					
Chaetodon capistratus	0	45	0	0	31
C. striatus	0	1	0	0	0
Pomacanthus paru	0	0	0	0	1
Halichoeres maculipina	1	8	0	0	7
H. radiatus	0	2	0	0	2
H. bivittatus	0	2	0	0	6
H. garnoti	0	0	0	0	6
Thalassoma bifasciatum	0	44	2	3	74
Bodianus rufus	0	0	0	0	1
Petrometopon cruentatum	0	2	0	0	0
Lutjanus apodus	1	1	7	0	0
Aulostomus maculatus	0	4	0	0	1
Haemulon spp.	0	4	0	3	19
Pempheris schomburgki	0	1	0	0	0
Canthigaster rostrata	0	0	0	0	7
Hypoplectrus spp.	0	0	0	0	4
Total	2	114	9	6	161
Hours observation	34		16	14	

* For diets see Randall 1967.

adult conspecifics and noncohabitant *S. dorsopunicans* consisted of attacks on the juvenile *M. chrysurus* by those fishes. During interactions between adult *M. chrysurus* and cohabitant *S. dorsopunicans*, the *M. chrysurus* invariably were overtly aggressive, whereas the *S. dorsopunicans* were overtly aggressive during only half of 24 encounters. The *M. chrysurus* adults also invariably were overtly aggressive towards cohabitant *S. planifrons* during interactions. However, *S. planifrons* cohabitants were overtly aggressive towards the *M. chrysurus* more often (77% of 227 encounters) than *S. dorsopunicans* were with their *M. chrysurus* cohabitants ($\chi^2 = 66.6$, $P < .001$). During interactions between *M. chrysurus* adults and noncohabitant *S. planifrons*, the noncohabitant *S. planifrons* were overtly aggressive more often (97% of 146 encounters, $\chi^2 = 33.8$, $P < .001$) than were cohabitant *S. planifrons* were with their *M. chrysurus*.

Relations with other species

Types of species attacked.—The great majority of each cohabitant's attacks were directed at algivorous fishes, and the frequency with which different species were attacked by *S. dorsopunicans* varied considerably (Table 3). Nonherbivores that cohabitants attacked included mainly consumers of sessile and mobile benthic invertebrates, as well as some fish predators.

Individual *M. chrysurus* adults attacked noncohabitant fishes much less frequently than did individual *Stegastes* spp. cohabitants in those *M. chrysurus'* feeding areas, and the combined frequency of attacks by all *Stegastes* individuals resident in an *M. chrysurus* area was, on average, 13–74 times as great as that of the *M. chrysurus* resident (Table 4).

Partitioning of food resources by adult cohabitants

Stomach content analyses.—All of the sampled material ingested by 10 sets of *M. chrysurus* and *S. dorsopunicans* cohabitants consisted of microalgae. The most abundant items in the stomachs of both species were diatoms, which represented two-thirds of the algae eaten by each species. In addition, the second and third most abundant items were the same for both

TABLE 4. Frequency of attacks on other herbivorous fishes by cohabitants living in each *M. chrysurus'* feeding area. Data are $\bar{x}$ and 95% CI.

Attacker		No. attacks/h on other herbivores
M. chrysurus		0.6 ± 0.4
S. dorsopunicans	(a) total by all individuals in an *M. chrysurus'* area	44.5 ± 19.8
	(b) average/individual	7.3* (24 *M. chrysurus* feeding areas†)
M. chrysurus		1.8 ± 1.1
S. planifrons	(a) total by all individuals in an *M. chrysurus'* area	24.6 ± 11.4
	(b) average/individual	4.2* (28 *M. chrysurus* feeding areas†)

* Calculated from $\bar{x}$ no. adult *S. dorsopunicans* and adult + subadult *S. planifrons/M. chrysurus* area; see Table 1.
† Each *M. chrysurus* feeding area was observed for 30–60 min.

species (Table 5). Together these three items made up >90% of the material in the stomach samples of each species. Thirty-two genera of diatoms were present in the stomachs of one or both species, and the relative abundance of the different genera in the stomach samples from *M. chrysurus* was positively correlated with their relative abundance in the stomach samples from *S. dorsopunicans* (Table 6).

Diatoms constituted >80% of the stomach contents of 10 *M. chrysurus* and 10 adult *S. planifrons* cohabitant in the *M. chrysurus'* feeding areas (Table 5), and there was a positive correlation between the relative abundance of the different genera in the stomach samples from *M. chrysurus* and those from each of the *Stegastes* species (Table 6). Most items other than diatoms were present in only small quantities in the stomachs of one of the other damselfish species. The only exception was the bluegreen alga *Microcoleus lyngbyaceus,* which was better represented in *S. planifrons'* stomachs than in those of *M. chrysurus.* Animal material was uncommon in the stomachs of both species.

Differential use of feeding microhabitats by M. chrysurus *and* S. dorsopunicans *adults.*—Observations on the feeding activity of adult *M. chrysurus* and adult cohabitant *S. dorsopunicans* in different microhabitats show that although there was segregated use, this segregation was slight (Table 7). Over 80% of the bites taken by each species were from microhabitats that

TABLE 5. Stomach contents of two sets of cohabitant damselfishes. Data are $\bar{x}$ ± SE. Algae: BG = bluegreen, G = green, B = brown, R = red.

Item	Cohabitants		Cohabitants	
	M. chrysurus	*S. dorsopunicans*	*M. chrysurus*	*S. planifrons*
Algae	Percentage of each species' stomach contents represented by each item			
Diatoms	66.6 ± 6.4	68.8 ± 8.4	89.1 ± 1.8	81.0 ± 4.3
Microcoleus lyngbyaceus (BG)	18.6 ± 7.5	15.4 ± 4.7	1.6 ± 0.9	14.3 ± 4.6
Polysiphonia sp. (R)	5.2 ± 1.7	8.3 ± 3.9	2.4 ± 1.1	0
Taenioma nanum (R)	2.9 ± 2.0	0.2 ± 0.2	0.8 ± 0.4	0
Ceramium sp. a (R)	2.3 ± 1.1	2.0 ± 1.2	0	0.6 ± 0.6
Ceramium sp. b (R)	1.6 ± 0.6	0	0.1 ± 0.1	0.2 ± 0.2
Gelidium sp. (R)	1.5 ± 1.5	0	0	0
Dictyota sp. (B)	0.8 ± 0.4	0	0	0.1 ± 0.1
Giffordia sp. (B)	0.3 ± 0.3	0	0	0
Wurdemania miniata (R)	0.1 ± 0.1	0.5 ± 0.3	0.1 ± 0.1	0.5 ± 0.3
Bryopsis sp. (G)	0	1.8 ± 1.5	0.3 ± 0.2	0
Cladophora sp. (G)	0	1.6 ± 0.9	0.7 ± 0.5	0
Hypnea sp. (R)	0	1.4 ± 0.9	0.5 ± 0.5	0.2 ± 0.2
Laurencia sp. (R)	0	0.6 ± 0.6	0	0
Sphacelaria sp. (B)	0	0.4 ± 0.4	0.8 ± 0.6	0
Ectocarpus sp. (B)	0	0	1.9 ± 1.4	0
Unidentified 1 (R)	0	0	0.9 ± 0.9	0
Unidentified 2 (R)	0	0	0.6 ± 0.6	0.5 ± 0.5
Enteromorpha sp. (G)	0	0	0	0.6 ± 0.6
Jania sp. (R)	0	0	0	0.4 ± 0.4
Centroceras clavulatum (R)	0	0	0	0.1 ± 0.1
Crustaceans	0	0	0.2 ± 0.2	1.5 ± 1.0
No. fish	10	10	10	10

TABLE 6. Relative abundance of different genera of diatoms in the stomach contents of two sets of cohabitant damselfishes. Data are $\bar{x} \pm$ SE. Spearman rank correlation coefficients (considering genera that constituted $\bar{x} \geq 1\%$ of diatoms in at least one of each pair of cohabitants): *M. chrysurus* and *S. dorsopunicans*, $n = 14$, $r_s = 0.85$, $P < .001$; *M. chrysurus* and *S. planifrons*, $n = 16$, $r_s = 0.70$, $P < .005$.

Diatom genus	Cohabitants		Cohabitants	
	M. chrysurus	*S. dorsopunicans*	*M. chrysurus*	*S. planifrons*
	Percentage of diatoms that belonged to each genus			
Synedra	20.5 ± 2.3	13.4 ± 2.1	16.0 ± 3.4	18.6 ± 4.8
Hantzschia	19.6 ± 2.4	12.7 ± 1.7	14.4 ± 2.5	12.0 ± 4.2
Amphora	16.2 ± 1.9	6.1 ± 1.3	8.0 ± 2.0	3.5 ± 0.8
Asterionella	11.1 ± 4.0	26.2 ± 4.3	24.3 ± 8.9	31.3 ± 7.3
Acnanthes	7.8 ± 1.5	5.1 ± 1.1	0.4 ± 0.2	0.4 ± 0.2
Coconeis	6.9 ± 1.5	8.4 ± 1.8	3.1 ± 1.2	3.7 ± 0.8
Licmophora	4.2 ± 0.6	12.6 ± 2.5	3.0 ± 1.1	2.2 ± 0.7
Mastogloia	3.4 ± 0.8	2.5 ± 1.2	8.6 ± 1.9	3.1 ± 0.6
Navicula	3.2 ± 0.5	2.4 ± 0.4	2.9 ± 0.6	2.2 ± 0.7
Pleurosigma	1.6 ± 0.6	1.2 ± 0.3	0.5 ± 0.2	0.5 ± 0.3
Orthoneis	1.5 ± 0.9	0.2 ± 0.2	2.9 ± 1.0	1.1 ± 0.3
Biddulphia	1.0 ± 0.8	4.8 ± 2.2	2.8 ± 1.9	8.9 ± 4.0
Rhopalodia	1.0 ± 0.4	0.3 ± 0.1	4.0 ± 1.5	1.1 ± 0.6
Rhoicosigma	0.6 ± 0.5	0.3 ± 0.2	0.1 ± 0.1	0
Nitzschia	0.5 ± 0.3	0.3 ± 0.2	2.6 ± 1.0	1.9 ± 1.1
Campylodiscus	0.4 ± 0.2	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1
Actinocyclus	0.3 ± 0.1	0	1.6 ± 0.7	1.8 ± 0.7
Surirella	0.3 ± 0.1	0	0.4 ± 0.2	0.3 ± 0.1
Cyclophora	0.3 ± 0.2	0.4 ± 0.3	0	0.3 ± 0.3
Grammatophora	0.2 ± 0.1	0.9 ± 0.5	1.5 ± 0.6	1.0 ± 0.4
Trachyneis	0.2 ± 0.1	0	0.3 ± 0.2	0
Striatella	0.2 ± 0.1	0	0.1 ± 0.1	0
Diploneis	0.2 ± 0.2	0	0.7 ± 0.3	0.6 ± 0.3
Campylostylus	0.1 ± 0.2	0	0.1 ± 0.1	0
Podocystis	0.1 ± 0.1	1.0 ± 0.4	0.3 ± 0.2	1.8 ± 0.5
Rhabdonema	0.1 ± 0.1	0.3 ± 0.1	0.4 ± 0.2	2.0 ± 0.6
Stauroneis	0.1 ± 0.1	0.6 ± 0.3	0.1 ± 0.1	0.5 ± 0.3
Anorthoneis	0.1 ± 0.1	0	0	0
Coscinodiscus	0.1 ± 0.1	0.3 ± 0.3	0	0
Opephora	0.1 ± 0.1	0	0.3 ± 0.2	0.1 ± 0.1
Gyrosigma	0	0.8 ± 0.1	0	0
Climacosphenia	0	0.2 ± 0.2	0	0.2 ± 0.2
Triceratium	0	0	0.8 ± 0.8	0.5 ± 0.3
Tropidoneis	0	0	0.6 ± 0.3	0.2 ± 0.2
Caloneis	0	0	0.2 ± 0.2	0
Fragilaria	0	0	0.2 ± 0.2	0.1 ± 0.1
Anaulus	0	0	0.2 ± 0.1	0
Auricula	0	0	0.2 ± 0.1	0
Plagiograma	0	0	0.1 ± 0.1	0
Diatoma	0	0	0.1 ± 0.1	0.2 ± 0.2
Tabellaria	0	0	0	0.1 ± 0.1
No. fish	10	10	10	10

were not used differently. Three of the four microhabitats for which there were statistically significant differences in usage were regularly used by both species. *S. dorsopunicans* took very few of its bites from sites that were physically inaccessible to *M. chrysurus* (Table 7).

Daily feeding cycles.—Adults of all three species exhibited essentially the same diel pattern of variation in feeding activity. Those fishes became active about 10–20 min before sunrise. Their bite-rates were low initially, rose slowly through the morning, and reached a peak in early to late afternoon. Their bite-rates declined sharply shortly before the fishes took shelter, ≈10–20 min after sunset (Fig. 4).

Relations between juveniles of M. chrysurus *and* S. dorsopunicans

Small-scale habitat segregation.—Such segregation was evident among juvenile *M. chrysurus* and *S. dorsopunicans* in habitat where adults of both species cohabited. Of 33 *M. chrysurus* juveniles, all were found in *Millepora* patches, while most *S. dorsopunicans* juveniles (96 of 117, $\chi^2 = 151.6$, $P < .001$) were located outside such hydrocoral patches.

Feeding-microhabitat segregation in Millepora *patches.*—There was distinct segregation in use of feeding substrates by the juveniles of the two species. *M. chrysurus* took over half their bites from live *Millepora* and live corals. *S. dorsopunicans* rarely fed on those

substrates; they fed almost exclusively on other substrates from which *M. chrysurus* juveniles took only about one-third of their bites (Table 8).

Agonistic relations.—Juvenile *M. chrysurus* were weakly territorial towards both conspecific juveniles and juvenile *S. dorsopunicans*. Although juvenile *M. chrysurus* did defend feeding areas to some extent, each individual ($n = 40$) shared its feeding area with a mean of 2.4 (SE = 0.29) other conspecific juveniles, and with 1–4 *S. dorsopunicans* that were smaller than it.

Juvenile *S. dorsopunicans* living in *Millepora* patches also were rather weakly territorial, and, instead of maintaining exclusive feeding areas, they typically shared feeding space with other juveniles. Each of 20 *S. dorsopunicans* juveniles living in *Millepora* patches shared at least part of its feeding area with a mean of 1.8 (SE = 1.0) conspecific juveniles, plus a mean of 1.3 (SE = 0.3) juvenile *M. chrysurus* (including a mean of 0.47 individuals that were smaller than the *S. dorsopunicans* juvenile).

TABLE 7. Use of different feeding microhabitats by cohabitant *M. chrysurus* and *S. dorospunicans*. $n = 8$ sets of cohabitants, each set = 1 *M. chrysurus* + 3–6 *S. dorsopunicans*.

Substrate microhabitat	Percentage of bites taken in each microhabitat: By *M. chrysurus* $\bar{x} \pm$ SE		By *S. dorsopunicans* $\bar{x} \pm$ SE
On exposed flat horizontal	42.8 ± 3.3		42.1 ± 4.0
On exposed flat vertical	22.5 ± 2.1		22.2 ± 2.6
In exposed concavity	10.7 ± 1.8		6.5 ± 1.4
On exposed convexity	10.6 ± 1.3	*	6.0 ± 1.8
In large crevice	6.0 ± 0.9		5.8 ± 0.4
On live coral or gorgonian	3.7 ± 0.9		4.8 ± 1.3
At entrance of small cave	2.7 ± 0.5	*	5.2 ± 0.8
Inside small cave	1.0 ± 0.2	*	3.2 ± 0.9
In small crevice†	0	*	4.2 ± 1.5

* $P < .05$, remainder not significant, Wilcoxon Signed Ranks Test.

† The only microhabitat physically inaccessible to *M. chrysurus*.

EXPERIMENTS

1. *Size-based dominance relations and noncohabitation of certain classes of* M. chrysurus *with* S. dorsopunicans *and* S. planifrons

Methods.—Adults of *M. chrysurus* aggressively dominated and cohabited with much smaller individuals of both *Stegastes* spp. However, adult *S. dorsopunicans* aggressively dominated *M. chrysurus* that were about the same size or smaller than the *S. dorsopunicans*, and such sets of individuals did not share feeding areas. A similar relationship existed between large *S. planifrons* adults and small *M. chrysurus* adults. To determine whether the *Stegastes* individuals in such situations were preventing the *M. chrysurus* from feeding in the *Stegastes'* feeding areas I performed the following experiments. In each replicate I observed an *M. chrysurus* for 1 h and recorded the locations of all its substrate bites relative to the feeding area of each noncohabitant *Stegastes*. I then speared the noncohabitant *Stegastes* sp. individuals that aggressively dominated the *M. chrysurus* and repeated the 1-h observation of the *M. chrysurus'* feeding activity. Juvenile *M. chrysurus* responded much more rapidly than conspecific adults did to the removal of noncohabitant *Stegastes* neighbors. Consequently, in experiments examining the effects of adult *S. dorsopunicans* on juvenile *M. chrysurus*, the postremoval observations were begun 1 h after the removal, while in experiments dealing with *S. planifrons* and adult *M. chrysurus*, postremoval observations were begun ≈24 h after the removal of the *S. planifrons*. In control areas I made similar sets of observations without removing the *Stegastes*. I compared the rates of feeding by the *M. chrysurus* in the feeding areas of the noncohabitant *Stegastes* before and after the removal of the latter.

Results.—The removal of adult *S. dorsopunicans* and large adult *S. planifrons* led to greatly increased feeding in those fishes' feeding areas by noncohabitant juvenile and adult *M. chrysurus*, respectively. There were virtually no changes in the feeding activity of control fish (Table 9). Thus *Stegastes* spp. individuals do aggressively exclude small noncohabitant *M. chrysurus* from their feeding areas.

2. *Lack of food partitioning indicated by temporal stability of agonistic relations among cohabitants.*

Methods.—Agonistic interactions between an *M. chrysurus* and its cohabitant *S. dorsopunicans* occur much less frequently than do intraspecific interactions between individuals of either species. This situation applies to a stabilized relationship, in which individual cohabitants presumably have been living together for some time. If, however, interactions between cohabitant individuals that have only just begun to live together occur more frequently than do interactions among individuals in a stabilized relationship, then cohabitant individuals may, through such agonistic interactions, achieve a subtle partitioning of food resources immediately after they begin living together. To explore this possibility I performed the following experiments. In each replicate I observed an *M. chrysurus* for 1 h, during which I noted all interactions between it and its cohabitant *S. dorsopunicans*. Then I speared either the *M. chrysurus* or all its cohabitant *S. dorsopunicans*. Postremoval observations of the same duration were begun 1 h after the removals in one set of experiments and ≈24 h later in another set. I used these two different time periods because, although *S. dorsopunicans* individuals typically began moving into a cleared area within 30 min of the clearing, *M. chry-*

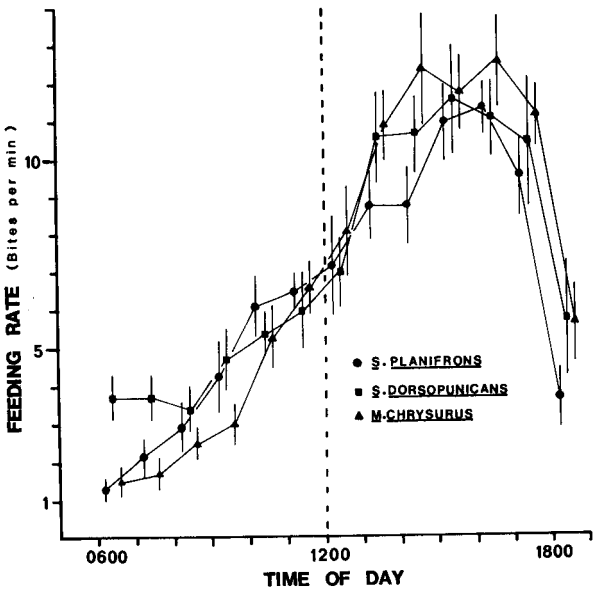

FIG. 4. Diel feeding activity of three damselfishes. Symbols with bars represent $\bar{x}$ and 95% CI for each species. Each point represents ≥20 10-min observation periods of ≥12 different individuals.

surus adults usually did not begin moving in until several hours after a territory vacancy was created. In control areas I made the two sets of observations but did not spear any fishes. Comparisons were made between the frequencies of interactions among the cohabitants before and after the removals.

Results.—The removal of *S. dorsopunicans* did not lead to increases in the frequency of interactions between the "old" resident *M. chrysurus* and the "new" resident *S. dorsopunicans,* which began moving into the cleared area <0.5 h after the removal (Table 10). The removal of *M. chrysurus* did lead to increases in the frequency of interspecific interactions in one set of experiments (Table 10). However, those increases occurred in only two of the eight replicates, and all the postremoval interactions involved only 3 of the 47 adult *S. dorsopunicans* resident in the eight experimental areas. Those three fish, which were speared after the data collection period, were ripe males that may have been guarding eggs. Thus, interactions between "old" residents of one species and "new" residents of the other species typically occur no more frequently than interactions between "old" residents of both species.

3. *Relative contributions to defense of shared feeding areas by cohabitants*

Methods.—*M. chrysurus* and its two *Stegastes* cohabitants defend their feeding areas against the same species of herbivorous fishes, principally parrotfishes and surgeonfishes. However an *M. chrysurus* attacks such herbivores much less frequently than its *Stegastes* cohabitants do. To determine if these differences in attack frequencies reflect differences in the contribution that each species makes to the defense of the shared feeding area, I performed the following set of experiments with *M. chrysurus* and *S. dorsopunicans.* In each replicate I observed an *M. chrysurus* feeding area for 1 h and recorded all attacks on other fishes by the *M. chrysurus* and all of its *S. dorsopunicans* cohabitants. In addition, every 30 s I made a count of the noncohabitant herbivores (=intruders) feeding in the *M. chrysurus'* area. I then speared all individuals of one species of cohabitant, waited 0.5 h and made a 1-h postremoval set of similar observations. Two similar sets of observations were made in control areas, from which fishes were not removed. Comparisons were made between (a) the mean numbers of intruders present before and after the removals, and (b) the frequency of attacks on intruders by the unmanipulated species of cohabitant before and after the removal of the other species of cohabitant.

Results.—The removal of *M. chrysurus* did not result in changes in either the frequency of intrusions by other herbivores or the frequency of attacks on those herbivores by the resident *S. dorsopunicans* (Table 11). Conversely, the removal of *S. dorsopunicans* did lead to large increases in both the frequency of intrusions into shared feeding areas by feeding individuals of other herbivores and the frequency of attacks on those herbivores by *M. chrysurus* (Table 11). The frequency of attacks on each species of herbivore by *M. chrysurus* after the removal of *S. dorsopunicans* (Table 3) was positively correlated with the postremoval frequency of intrusions by those species ($r_s = 0.78$, $n = 10$ species of intruders, $P < .01$; data from all experimental replicates were pooled). In those same eight areas there was a positive correlation between the preremoval frequency of attacks on each species of intruder by the resident *S. dorsopunicans* and the preremoval frequency of intrusions by those species ($r_s = 0.98$, $P < .001$; data from all replicates were pooled).

4. *Effects of the presence of* M. chrysurus *on the body size and fat reserves of cohabitant* S. dorsopunicans

Methods.—The observations and results of the experiments on the contribution of cohabitants to the defense of shared feeding area prompted the following hypothesis. Because an *M. chrysurus* contributes little to the defense of the competitively limiting food supply it shares with its cohabitant *S. dorsopunicans,* the presence of an *M. chrysurus* in a *S. dorsopunicans'* feeding area is detrimental to the *S. dorsopunicans.* To test this possibility I performed the following experiment. On a small isolated reef I mapped the feeding areas of all *S. dorsopunicans* resident in five separate 2 × 2 m plots. Then I estimated the lengths of those fish by holding a measuring device near each individual. That device consisted of lengths of plastic set in a fine wire frame

at the end of a wire pole. Each fish was assigned to one of four standard-length (SL) classes: juveniles (≤51 mm SL), and small (52–62 mm SL), medium (63–69 mm SL) and large adults (≥70 mm SL). Based on the length/mass relations of specimens I had collected previously, those length classes corresponded to mass classes of <6 g, 6–12 g, >12–18 g, and >18 g, respectively. After the fish counts I speared 68 of the 69 adult, and 45 of the 46 juvenile *M. chrysurus* on the reef. One year after the removals of the *M. chrysurus* I made a postremoval set of size estimations and maps of feeding areas for the *S. dorsopunicans* in those plots. Concurrent with the two sets of measurements on the experimental reef I made two sets of counts and size estimations of *S. dorsopunicans* in similarly sized plots in the same type of habitat on an unmanipulated control reef ≈0.7 km from the experimental reef. After the sets of postremoval observations were completed I made a collection of fish ≥60 mm SL from both the experimental and control reefs. Each fish was dissected while fresh and was scored as belonging to one of four classes in terms of the amount of fat in its gut mesenteries: (1) fat present in strips of a thickness equal to about half the diameter of the intestine; (2) half the amount of fat of (1); (3) only scattered traces of fat visible; (4) no fat visible. Comparisons were made between (a) the changes in abundance of different-sized *S. dorsopunicans* on the experimental and control reefs, and (b) the relative abundances of experimental and control fish having different amounts of fat.

Results.—The removal of *M. chrysurus* led to changes in the size distribution of *S. dorsopunicans* on the experimental reef that were different from those that occurred on the control reef. There were increases in the number of larger sized fish on the experimental reef, but not the control reef (Table 12). In addition, males and females of *S. dorsopunicans* collected from the experimental reef at the end of the experiment had significantly larger deposits of fat in their gut mesenteries than did fish collected on the control reef (Table 13).

TABLE 8. Use of different substrates for feeding by juveniles of *M. chrysurus* and *S. dorsopunicans* living in patches of *Millepora* hydrocorals. Live corals were *Acropora palmata* and *Porites porites*. Bites on *Millepora* constituted 87.4% of this class of bites by *M. chrysurus* juveniles.

Species	Substrate type: Live *Millepora* and live corals	Substrate type: Dead coral and algae
	Median percentage of bites taken	
M. chrysurus $n = 26$ observation periods	60.8 *	35.5 *
S. dorsopunicans $n = 20$ observation periods	1.8	99.4

* $P < .001$, Mann-Whitney U test.

TABLE 9. Effects of the removal of two *Stegastes* spp. on the feeding of noncohabitant *M. chrysurus* in those *Stegastes'* feeding area. Data are $\bar{x}$ and 95% CI.

Treatment	No. bites/h by *M. chrysurus* in *Stegastes* sp. feeding area: Before removal	After removal
Remove *S. dorsopunicans* adults to determine reactions of juvenile *M. chrysurus* $n = 6$	2 ± 2	151 ± 94
Controls $n = 6$	2 ± 3	3 ± 2
Remove *S. planifrons* large adults to determine reactions of small adult *M. chrysurus* $n = 5$	0	190 ± 74
Controls $n = 5$	0	0.6 ± 2.2

DISCUSSION

There is extensive overlap in the habitat distributions of *M. chrysurus* and *S. dorsopunicans* at widely separated sites in the Caribbean, and populations of both species contain the greatest proportions of large adults in shared habitat. To a lesser degree *M. chrysurus* adults also share habitat with other territorial *Stegastes* species, notably *S. planifrons*, but also *S. diencaeus*, *S. variabilis*, and *S. partitus* (D. R. Robertson, *personal observations*). *M. chrysurus* is the largest of the common, permanently territorial damselfishes in the Caribbean. The only damselfishes I have seen that are capable of aggressively excluding adult *M. chrysurus* from their feeding areas are large adults of *S. planifrons* and *S. diencaeus* (which can reach 60 g), although egg-guarding males of other damselfishes appear to be able to keep *M. chrysurus* away from their nests. Consequently, it seems likely that *M. chrysurus* adults are aggressively excluded from only small proportions of a restricted set of habitats by other competitors, and that the high abundance of this species in the habitat it shares with *S. dorsopunicans* reflects an active preference for that habitat.

Although there is virtually no intraspecific overlap in the feeding areas of adults of *M. chrysurus*, *S. dorsopunicans*, and *S. planifrons*, the feeding areas of *M. chrysurus* overlap with those of adults of the two *Stegastes* species, and *M. chrysurus* adults feed almost exclusively in the feeding areas of their cohabitants. Adult *M. chrysurus* and their cohabitant *Stegastes* concentrate their feeding in the same microhabitats and ingest similar proportions of the same types of benthic microalgae. The three cohabitants all have essentially the same daily cycles of feeding activity. Taborsky and Limberger (1980) have suggested that this type of cycle, which they and others have observed in various blen-

TABLE 10. Effects of removal of one species of cohabitant on the frequency of agonistic interactions between cohabitant *S. dorsopunicans* and *M. chrysurus*. Data are $\bar{x}$ and 95% CI. In short-term experiments post-removal observations were begun within 1 h after removal. In long-term experiments post-removal observations were begun 24 h after removal.

	No. agonistic interactions/h			
	Short-term experiments		Long-term experiments	
Treatment	Before removal	After removal	Before removal	After removal
S. dorsopunicans removals	0	0	0.6 ± 0.4	0.1 ± 0.1
No. of 1-h observations	8		9	
Controls	0	0	0	0
No. of 1-h observations	6		6	
M. chrysurus removals	No data (See Lack of Food Partitioning, Methods)		0	1.9 ± 1.1
No. of 1-h observations			8	

nies (Nursall 1981) and damselfishes (Montgomery 1980), represents a response to diel changes in the quality of algal food. There is no evidence of any fine-scale partitioning of feeding space by cohabitant *M. chrysurus* and *S. dorsopunicans* that results from agonistic interactions between them, because interactions occur no more frequently between "naive" cohabitants than between cohabitants that have lived together for some time. Thus, there is no evidence that partitioning of food resources could account for the intimate cohabitation of pairs of species that appear to compete for food with both conspecifics and a number of other fishes.

The cohabitants defend food against fishes that feed actively in *Stegastes* spp. feeding areas when their owners are removed (Table 11, and Robertson et al. 1976). Differences in the frequency of attacks on different species of intruders by both cohabitant *M. chrysurus* and *S. dorsopunicans* are related primarily to rates of intrusion into feeding areas by the other species rather than interspecific selectivity on the part of the territory holders. All three damselfishes also are aggressive to some extent towards carnivores. This response could be due to (a) an attempt to evict piscivores that could eat them, (b) an attempt to evict fishes that could eat eggs (which are stuck to the substrate and guarded by male damselfishes), or (c) an attempt to protect the algal mat from carnivores that feed on benthic invertebrates. (Other workers [Randall 1967, Emery 1973, Lobel 1980] have recorded substantial amounts of animal material of benthic origin in the stomach contents of the three cohabitants considered here.)

The burden of the defense of shared food against other herbivores falls largely on the *Stegastes* spp. cohabitants. They are much more active than *M. chrysurus* in this defense, and the experimental removals

TABLE 11. Number of intruding herbivorous fishes feeding in a *M. chrysurus* territory and frequency of attacks on them by resident cohabitants, before and after removal of each species of cohabitant. Feeding intruders included five parrotfishes (Scaridae), three surgeonfishes (Acanthuridae) and one damselfish. Counts of intruders are $\bar{x}$ and 95% CI, determined from counts made every 30 s over a 1-h period.

	Replicate no.	*S. dorsopunicans* removals		Controls		*M. chrysurus* removals	
		Before	After	Before	After	Before	After
No. feeding intruders present in a *M. chrysurus* feeding area	1	1.2 ± 0.3	2.9 ± 0.7	0.6 ± 0.1	0.9 ± 0.2	0.7 ± 0.1	0.7 ± 0.1
	2	0.6 ± 0.2	10.8 ± 0.6	2.2 ± 0.3	2.0 ± 0.3	0.3 ± 0.1	0.2 ± 0.1
	3	1.3 ± 0.3	19.9 ± 1.3	0.3 ± 0.9	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.1
	4	1.8 ± 0.3	24.4 ± 1.1	6.2 ± 0.9	4.8 ± 0.8	3.8 ± 0.6	1.4 ± 0.2
	5	1.0 ± 0.3	41.8 ± 1.6	2.6 ± 0.6	2.8 ± 0.9	4.4 ± 0.6	4.8 ± 0.7
	6	1.3 ± 0.2	25.0 ± 2.2	3.0 ± 0.5	2.9 ± 0.5	2.9 ± 0.4	3.4 ± 0.4
	7	2.2 ± 0.3	32.3 ± 1.2	...	...	...	...
	8	1.4 ± 0.5	17.5 ± 1.5	...	...	...	...
Grand $\bar{x}$		1.4	21.8 *	2.5	2.3 NS	1.9	1.8 NS
$\bar{x}$ no. of attacks/h on intruders By *M. chrysurus*		0.3	87.0 *	0.3	0 NS	0.5	...
By *S. dorsopunicans*		74	...	42	40 NS	31	26 NS

* $P < .01$, NS = not significant; Wilcoxon Paired-Sample Test.

of *M. chrysurus* and *S. dorsopunicans* demonstrate that *M. chrysurus* is much less competent than *S. dorsopunicans* at inhibiting the feeding of intruders in the shared areas.

The hypothesis that the presence of *M. chrysurus* adults is detrimental to their *Stegastes* spp. cohabitants is supported by the experiment which showed that removal of *M. chrysurus* leads to increases in the size of *S. dorsopunicans* cohabitants, and that *S. dorsopunicans* living without *M. chrysurus* have larger fat deposits than those living with *M. chrysurus*. Since fecundity generally is a positive function of body size within a species of fish (Weatherley 1972) individual *S. dorsopunicans* probably pay a price for living with *M. chrysurus*, a price that is likely to be high, since the standing crop of *M. chrysurus* exceeds that of *S. dorsopunicans*. In the relationship between *M. chrysurus* and *S. planifrons* the cost to an *S. planifrons* presumably is lower than that to an *S. dorsopunicans*, since the standing crop of *M. chrysurus* is lower in *S. planifrons* habitat than *S. dorsopunicans* habitat.

It seems likely that the basis of the ability of an *M. chrysurus* to cohabit with the *Stegastes* spp. is that the *M. chrysurus* adults' great advantage in size enables them to dominate aggressively the much smaller *Stegastes*. The *M. chrysurus* adults invariably are aggressive towards, and are not dominated by their cohabitants when they interact agonistically with them. Small *M. chrysurus* that lack a sufficient size advantage are dominated by and excluded from the feeding areas of individuals of both *Stegastes* spp., as well as those of adult conspecifics. *M. chrysurus* adults that live in *S. planifrons* habitat are smaller than those living with *S. dorsopunicans*, and large *S. planifrons* can actively prevent such *M. chrysurus* gaining access to their feeding areas. Although differences in the relationship that *M. chrysurus* has with each *Stegastes* species are due in part to differences in the mean size of adult *M. chrysurus* in each habitat and differences in maximum size achieved by the two *Stegastes* species, differences in the aggressiveness of the two *Stegastes* species probably also have a role. The frequency of interactions between an *M. chrysurus* and its cohabitant *S. planifrons* is much higher than that between an *M. chrysurus* and its cohabitant *S. dorsopunicans*. This is not attributable to differences in the number of individuals of each *Stegastes* species that an *M. chrysurus* lives with. Nor is it a reflection of differences in the tendency of an individual of each *Stegastes* species to interact with neighboring conspecifics, since the frequency with which a fish interacts with such neighbors is about the same in both *Stegastes* species. Thus, an *S. planifrons* probably is more liable than an *S. dorsopunicans* to attack its cohabitant *M. chrysurus*, because *S. planifrons* is a more aggressive species than *S. dorsopunicans*. The frequency of agonistic interactions between an *M. chrysurus* and its *S. dorsopunicans* cohabitants is much lower than the frequencies of intraspecific interactions that each species normally experiences. This lack of continual resistance by *S. dorsopunicans* may be because such activity is not cost effective.

The potential for competition for living space or food between juveniles of *M. chrysurus* and *S. dorsopunicans*, which might present a problem for the recruitment of either species, seems slight. Juveniles of the two species partition living space, and partition feeding substrates in situations in which there is overlap in microhabitat use. Further, the weak territoriality of juveniles of both species in the microhabitat to which juveniles of *M. chrysurus* are restricted may facilitate the recruitment of *M. chrysurus* juveniles to that microhabitat.

Although it is evident that *M. chrysurus* do rely on cohabitant *S. dorsopunicans* to defend food for the former species, it remains to be determined whether this relationship is obligatory or facultative for *M. chrysurus*. Long-term removals of *S. dorsopunicans* could demonstrate how competently an *M. chrysurus* can defend a territory by itself. Although an *M. chrysurus* may be able to defend its own food supply, the

TABLE 12. Effects of the removal of *M. chrysurus* on the size distribution of *S. dorsopunicans*. Null hypothesis: the change in size distribution of experimental animals is not different from the change in size distribution of control animals. $\chi^2 = 14.76$, $P < .005$.

Treatment	No. *S. dorsopunicans* in each size class			
		Adults		
	Juveniles	Small	Medium	Large
Experiment				
Before removal	12	12	7	7
After removal	9	10	13	9
Control				
Before removal	15	10	4	1
After removal	11	14	3	1

TABLE 13. Sizes of fat deposits in the gut mesentery of adult *S. dorsopunicans* living on a reef from which the *M. chrysurus* were experimentally removed, and those living on a control reef. For details of fat deposit classes, see Experiments 4: effects of the presence of *M. chrysurus*.

Amount of fat	Number of individuals with different amounts of fat			
	Males		Females	
	Experimental	Control	Experimental	Control
1 ↑	4	0	8	0
2 Increasing	7	2	4	0
3	11 *	10	22 *	9
4	6	11	3	25

* $P < .05$ in both cases; Mann-Whitney U test: males: $Z = 2.86$, females: $Z = 5.60$.

TABLE 14. Comparison of two cohabitation relationships.

	Caribbean cohabitants (this paper)	Indo-Pacific cohabitants (Robertson and Polunin 1981)
Dependent species =	1 large damselfish	1 small damselfish
Host species =	2 small damselfishes	2 large surgeonfishes
Ratio of body mass of small species to body mass of large species	1:6.0–8.4	1:4.9–13.5
Ratio of standing crop of dependent species to standing crop of host species	1.58–0.69:1	0.09–0.07:1
Population density (fish/m^2)		
Of large species	0.17–0.15	0.11–0.14
Of small species	0.90–1.27	0.06–0.16

effectiveness of *S. dorsopunicans* defense may be so much greater that cohabitation permits the population density and/or size and reproductive output of individual *M. chrysurus* to reach levels that could not otherwise be attained.

There are both distinct similarities and pronounced differences between the relationship described here and that described by Robertson and Polunin (1981) for some Indo-Pacific reef fishes (Table 14). In both cases the cohabitants differ greatly in size, there is great overlap in food use, and the relationship appears to involve a host and a "dependent." However, in one case the large species is the dependent species, while in the other the small species is dependent. In the case described here the cost is likely to be quite high for the host species, whereas in the other case it probably is very low; this may be due largely to differences in the ratios of standing crops of dependent and host in each case. In the system described here the dependent is able to maintain its presence by being able to dominate the host aggressively. In the system described by Robertson and Polunin (1981) the dependent species' small size enables it to take refuge in holes in which it is inaccessible to the host; this, combined with the apparent low cost of the relationship to the host, may make it uneconomical for the host to attempt to exclude the dependent. While the population densities of the large species are low in both cases, the densities of the small species differ greatly (Table 14). Not only the costs and benefits of cohabitation to each species, but also the role (dependent or host) that each species has in the relationship may depend primarily on the population densities of each.

Here I have considered cohabitation relationships between pairs of species (see also Robertson and Polunin 1981). However, cohabitation systems may sometimes be much more complex and involve more than two species. The herbivorous blenny *Ophioblennius atlanticus* is abundant on many Caribbean reefs (Randall 1968, Bohlke and Chaplin 1968). This small fish ($\bar{x}$ mass of adults = 5.5 g, D. R. Robertson, *personal observations*) commonly shares habitat with *S. dorsopunicans* and *M. chrysurus* in San Blas and elsewhere. Like the damselfishes, individuals of this blenny defend feeding territories, and their feeding areas are superimposed on those of *S. dorsopunicans* and *M. chrysurus* (D. R. Robertson, *personal observations,* and Nursall 1981). My observations indicate that the blenny is strongly intraspecifically territorial, interacts agonistically to some extent with both its cohabitant damselfishes, but is very weakly territorial towards other herbivores (see also Nursall 1981). *O. atlanticus* also eats many of the microalgae that its cohabitant damselfishes eat (Randall 1967). Consequently this blenny may be a dependent of *S. dorsopunicans,* a dependent that the damselfish cannot economically exclude because the blenny's small size and slender shape enable it to use refuges that are inaccessible to the damselfish. Other Caribbean blennies and gobies have diets that include much benthic microalgae (Randall 1967) and I have seen individuals of some of those species living inside the feeding areas of territorial damselfishes. Thus, interspecific cohabitation that involves sharing of competitively limiting resources may be common among reef fishes. Such relationships may contribute significantly to maintaining high species diversity on the within-habitat scale. It will be necessary to determine the degree to which these relationships are obligatory rather than facultative for the dependent species, in order to establish whether they are important to maintaining such diversity on a larger scale, i.e., at the species level.

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