

Behavior and physiology of coexistence in two species of *Dascyllus* (Pomacentridae, Teleostei)

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Synopsis

In the Gulf of Aqaba *Dascyllus aruanus* and *D. marginatus*, form distinct populations organised into harems of single males and groups of females, living permanently in *Stylophora* and *Acropora* corals. Each harem consists of 4 sexual casts: dominating males, adult females, sex-changing fish and juveniles. The sexual performance of each adult fish in such social units is controlled by the presence or absence of a dominating male. In corals occupied by mixed groups of both species, only those females spawn that belong to the same species as the dominating male. Direct observation in the sea shows that such situations are produced by indiscriminate settling mechanisms of groups of juvenile fish. Evidence is also presented, demonstrating that dispersion of coral colonies suitable for occupancy and predation by piscivorous fish can modulate such complicated reproduction.

Introduction

Dascyllus aruanus and *D. marginatus* (Pomacentridae) are coral dwelling damsel fish, widely distributed in the Red Sea (Fishelson 1964, 1980, Fishelson et al. 1974, Holzberg 1973, Fricke 1975, 1980). *D. aruanus* is also found in most of the Indo-Pacific. They are usually found among branches of the corals *Stylophora* spp. and *Acropora* spp. which provide refuges, territories and nests for spawning. The number of fishes in such a coral is strongly correlated with the structural complexity of the host (Shpigel 1978, 1982). The inhabitants of each coral demonstrate a hierarchical, harem structure, dominated by a single male. Exceptions include the extremely large and complex coral colonies where 2 or 3 males are able to keep separate harems, or sites where numerous continuous colonies of *Stylophora* extend over many square

meters and here those fish form large populations without detectable subdivisions.

In the Gulf of Aqaba many suitable corals are jointly populated by *D. aruanus* and *D. marginatus*. As demonstrated by various authors, in monospecific colonies one individual is the alpha-male. This male, by special kinds of up and down signal swimming and sound emission, dominates all other fish inhabiting the coral. Since both species use the same microhabitat, various questions arise about their coexistence, that apparently contradict mutual exclusion principles. The question of multi-specific coexistence of fishes in coral microhabitats has been widely discussed (Fishelson et al. 1974, Sale 1972, 1975, 1978b, Thresher 1977, Robertson & Lassig 1980, Sweatman 1983). This study examines the relationships existing within and between *D. aruanus* and *D. marginatus*. Of particular interest was how joint occupancy of a coral colony

influences the numerical and sexual stability of the population of each species.

Methods

One hundred fifty six colonies of the branching corals, *Stylophora* and *Acropora*, populated by *Dascyllus aruanus* and *D. marginatus*, were marked with tags for continuous recognition at the research site near Sharm el Sheikh (Sinai Peninsula). In addition, 160 harems of these fishes were observed at various times on 12 sites along the Gulf of Aqaba. During all the observations the agonistic behavior and signalling, up-and-down swimming display of dominant males, easily enabled their recognition within the groups occurring in separate corals. Twenty experiments were performed in aquaria of the Department of Zoology, Tel Aviv University. Sixteen groups, including 10 of *D. aruanus* and 6 of *D. marginatus*, each consisting of 5 to 10 fish, were used for these laboratory studies. Eight of these groups, of one or the other species, were kept isolated in separate aquaria, while the other eight were maintained under hetero-specific conditions, both species together.

Fishes from 46 harems that served for observations during the field study, were subsequently collected, dissected, and their gonads fixed in Bouin and Carnoy for histological investigations. Sections were stained by Hematoxylin-eosin and Mallory Azan. This was done to determine the relation between the social position of each of the observed fish and its gonadal development. This problem of gonadal histology in sex-changing fish has been intensively studied during the last two decades. The pertinent literature has been summarized in the classical works of Atz (1964), Reinboth (1975), and Shapiro (1984). Studies of *Dascyllus* species from the Red Sea and other regions show that they have a primary ambisexual gonad, in which spermatogonia and oogonia are recognizable in post-metamorphic juveniles. Such gonads, developing in the adult fish, are able to undergo a change from the active female condition, through intersex to the final male stage. Counting the sex-cells along serial histological sections of the investigated gonads en-

abled the determination of sex and physiological state of the fish. After preliminary studies we could distinguish four categories: 1. female (♀) – only oocytes observed; 2. beginning of sex-change (♀♂♀) – female gonad with ‘nests’ of spermatogenesis; 3. pre-ripe male (♂♀♂) – gonad possessing numerous spermatogonia, but few spermatozooids; and 4. ripe male (♂) – testis laden with spermatozoa.

Results

Pattern of distribution of the two species

Sixty-one coral colonies, populated jointly by mixed groups of *D. aruanus* and *D. marginatus* were observed for 10 months near Sharm el Sheikh for: (1) number of fish belonging to each species, and (2) to which species does the dominant male belong. From those colonies forty mixed groups of fish were collected, measured, and sexed. The results of these investigations (Table 1) show that the number of fish of each species in a bispecific group is variable, almost equally divided between the two species. In 18 additional harems taxonomic identity of the alpha-male fish was also found divided almost equally between *D. marginatus* and *D. aruanus* (Table 2). This demonstrates that either

Table 1. Species of *Dascyllus* that outnumbered the other species within a bispecific group of fish.

Number of groups counted	Outnumbered by <i>D. marginatus</i>	Outnumbered by <i>D. aruanus</i>	With equal numbers from both species
40	14	18	8

Table 2. The dominant male of *Dascyllus* in 18 studied bispecific groups.

Number of harems	<i>D. marginatus</i> alpha male	<i>D. aruanus</i> alpha male
18	10	8

species has an equal chance of becoming successful settlers in a coral colony and that neither species has a better chance to gain dominance. As in all these instances, the alpha-male was always one, and constantly the largest fish in the group. Assuming equal survival of both species, it seems that the first sexually mature fish has the best chance of becoming the alpha-male. It shows that extrinsic events, and not intrinsic qualities regulate the sex-allocation in these fishes. To study this possibility, it was important to know the gonadal structures in detail.

The development stages of the gonads

Serial sections of 120 fishes of various ages belonging to 46 harems and holding different social positions in group hierarchies were examined. All preadult individuals begin development as juvenile females, with 95% of the germinative tissue occupied by previtellogenic oögonia of approximately 50 μm in diameter. The dormant male tissue of the gonad can be noted by nests of spermatogonia scattered between the numerous female cells (Fig. 1). As the female gonad ripens and vitellogenesis advances, the growing oocytes reach 400–450 μm in diameter. This results in a decrease of their number in the transects of gonads (Fig. 2). At this stage, the female gonad is at its highest level

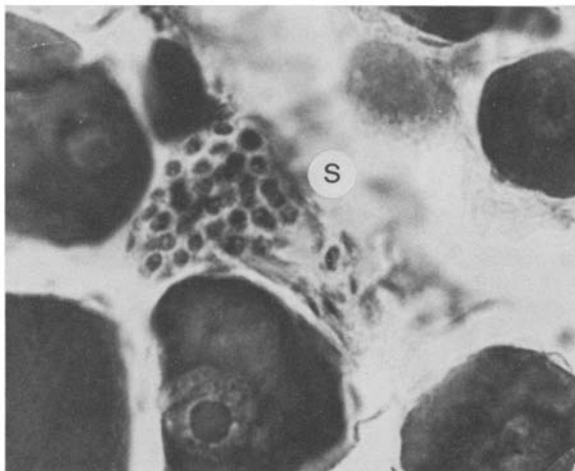


Fig. 1. Islets of dormant spermatogonic tissue (S) among oocytes in an ovary of *Dascyllus marginatus*. Scale 0.01 mm.

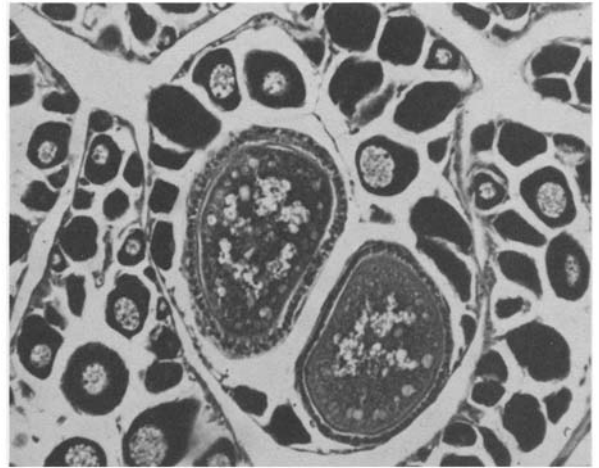


Fig. 2. The ovary of a reproducing female of *Dascyllus marginatus* with large ovulating eggs. Scale 0.1 mm.

of development; the male islets are so minute and pressed aside, that the germinative tissue looks all-female. The third stage in development is an intersexual one, in which spermatogenic activity increases, paralleling the decrease of female function. At this stage, few egg-cells are scattered in the gonad. The germinative layer of the organ is 70–90% male and 10–30% female. Such a transitional gonad is also marked by the absence of yolk, as well as atresia or luteinization of any non-spawned ripe eggs (Fig. 3). As in other fish (Fishelson 1975), at this stage large egg-cells are penetrated by phagocytes and disintegrate. The final stage in the gonadal development of a dominant male is the formation of a ripe testis. At this stage islets of ripe spermatozoa are found throughout the organ, with small scattered rudiments of degenerative ovarian tissue pressed to the tunica exterior (Fig. 4). At a still more advanced stage most female cells disappear.

The quantitative relationship between sexes in mono- and bispecific harems

For this study the gonads of all fish of 32 groups were examined. In 10 harems of *D. aruanus* and in 10 harems of *D. marginatus*, the sex-relationships were alike: 24 to 27% (average 26%) of the fish were males, 62 to 71% (average 64%) females, and

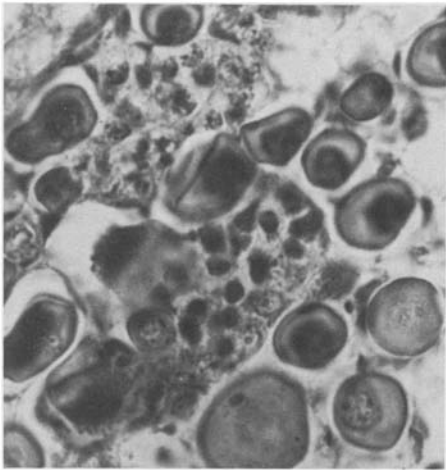


Fig. 3. Multiplication of spermatogonic cells between the lutenised ovocytes, in a developing testis of *Dascyllus aruanus*. Scale 0.01 mm.

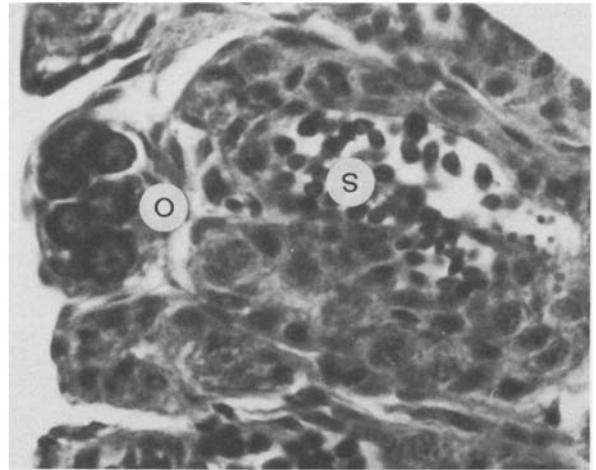


Fig. 4. Spermatogenesis (s) in a ripe and functional testis of male *Dascyllus marginatus*, with a rudimentary group of oocytes (o). Scale 0.01 mm.

4 to 5% (average 2.2%) female intersexes (Table 3). In contrast, in 6 bispecific harems, the males formed only 10 to 13% (average 11.4%) of the population, while 48 to 56% (average 50.2%) were female and 29 to 31% (average 29.8%) pre-ripe intersexes. Among the latter class some fish were in the advanced stages of spermatogenesis, but without ripe spermatozoa. This suggests that the sex-change suppressing influence of the alpha-male, preventing beginning of sex-change from co-existing females, is stronger in a conspecific group than in bispecific groups. This decreased effectiveness of the dominating male to control the group allows an accumulation of initial stages of sex changing fish. Since with the onset of sex-change ovulation terminates, this in turn, reduces the number of egg-

producing females. As intersexual fishes are unable to develop ripe male or female gametes, they do not participate in fertilization, so the genes of sex-changing fish are temporarily 'out of play' and also less fertile eggs are produced. In these instances, only recruitment from postmetamorphic fish can possibly replace a number of new, egg-producing females.

Sale (1975) postulated that recruitment among coral fishes is extremely low. Because of this, we decided to determine if such was the case in the recruitment and settlement in our population of fishes. For this purpose all individuals from twenty harems of *Dascyllus* occurring in isolated corals were anesthetized on the spot under plastic covers, counted and measured. This procedure was carried

Table 3. Ratio of males, females and intersexes in mono- and bispecific groups (n = 140).

Number of groups	Species	Number of fish	Sex Maxima % in group			Average male:female sex ratio
			Male	Female	Intersex	
10	<i>D. marginatus</i>	51	12 (24%)	35 (71%)	4 (5%)	0.342
10	<i>D. aruanus</i>	38	13 (27%)	30 (62%)	5 (11%)	0.435
12	<i>D. marginatus</i> + <i>D. aruanus</i>	51	7 (13%)	29 (56%)	15 (31%)	0.241

out twice: first after the onset and before the mass reproduction in May (most fish adults) and the second time after the reproductive season was almost over in July (juvenile recruits within most of the colonies). All the fish in these groups were divided into 9 categories, based on their total length (TL): Category I was the largest observed and Category IX the smallest and newest recruit. The results of these counts are given in Table 4 and Figure 5. It is apparent that there are significant differences between the reproductive and pre-reproductive stocks of *Dascyllus* in these colonies, especially concerning the Category IX fish. During the reproductive period, the fish numbers increased by almost 12%, of which 60.5% belonged to the Category IX (smallest) and the remainder to the other low-ranking categories of sub-reproducing juveniles. No change was noted in the adult stock of *Dascyllus* during the same period. At this period the newly recruited and settled fish formed almost 50% of the population. As the high-point of the reproductive period terminated, the population gradually returned to its pre-reproductive structure, remaining relatively unchanged for each coral colony (Table 5, Fig. 6). This suggests that despite relatively high recruitment, density increase is limited and a constant portion of the fish disappeared from the colonies, most likely due to mortality (see Discussion).

The following observations provide additional

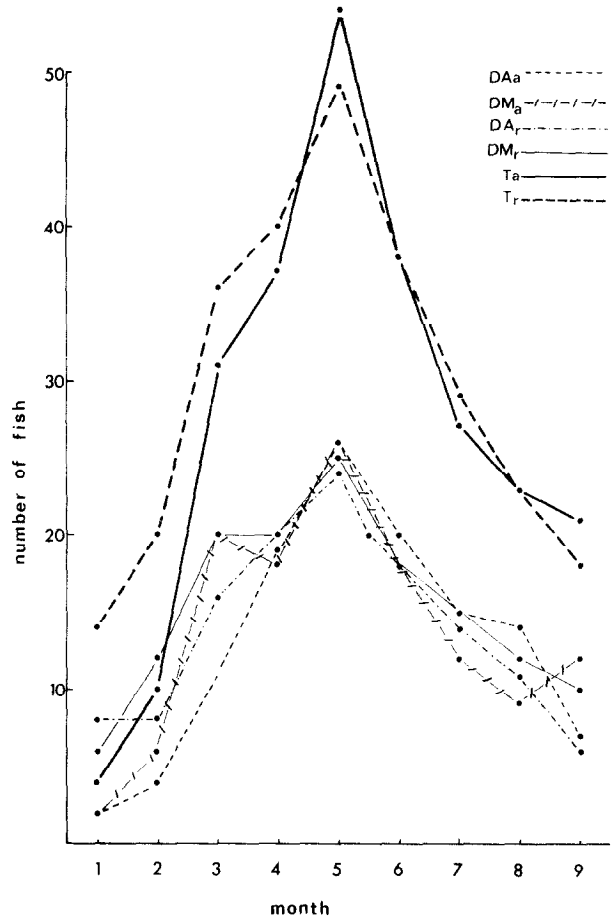


Fig. 5. The total number of adult (Ta) and juvenile (Tr) fish in a group of corals during 9 months of observations. DA = *D. aruanus*; DM = *D. marginatus* (a = adults, r = juveniles).

Table 4. The numbers of recruits in harems of *Dascyllus* at the beginning (May) and advanced (June) months of settling (totals from 20 harems).

Fish Category	TL (in mm)	May			June		
		<i>D. marginatus</i>	<i>D. aruanus</i>	Total	<i>D. marginatus</i>	<i>D. aruanus</i>	Total
I	46	2	2	4	2	3	5
II	41-45	6	4	10	6	7	13
III	36-40	20	11	31	20	16	36
IV	31-35	18	19	37	20	20	40
V	26-30	26	26	52	25	24	49
VI	21-25	18	20	38	20	18	38
VII	16-20	12	15	27	15	14	29
VIII	11-15	9	14	23	12	12	24
IX	10	8	7	15	20	18	38
Total		119	118	237	140	132	272

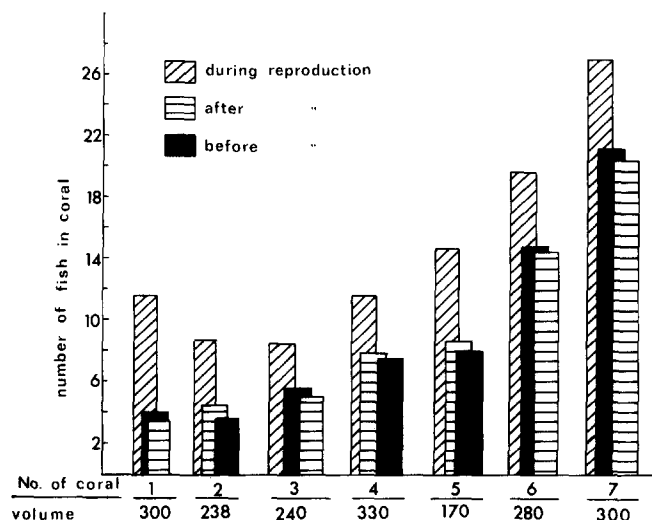


Fig. 6. Composition of *Dascyllus* groups in seven coral colonies of various volume (calculated in $\text{dm}^3 = \text{liters}$).

evidence that recruitment, although high, only produces small stocks of settlers. Schools of post-metamorphic juveniles, measuring about 10 mm TL, were observed actually descending into coral colonies. Most observed settling occurred at late sunset time. Such groups of postmetamorphic juveniles (9.0–11.0 mm TL) included 25–30 fish on several exceptional instances; and on one occasion, such a group of recruits included more than 100 juveniles, all of almost the same dimensions. On the following day only 10–15 of the original arrivals were present; and from those, 8–10 subadult fish

formed the harem. These observations also proved that the juveniles settle as groups and not as single individuals. Additional recruitment data were obtained from 8 colonies during May, approximately one month after the onset of reproduction and with the beginning of settlement of juveniles (Table 5). On this occasion we counted 39 juveniles belonging to Category IX. These were 12% of the total fish population observed and represent 100% of successfully surviving recruits. Table 5 also shows data from June, the high point of reproduction. At that time, the new settlers formed 48.6% of the fish

Table 5. Recruitment of juveniles *Dascyllus* (less than 10 mm TL) in randomly selected colonies (N = 8).

Colony number	Average number of fish per colony at beginning of reproduction	Added number of juveniles		Total	Average number of fish per colony after reproduction
		<i>D. aruanus</i>	<i>D. marginatus</i>		
1	3.80	1	4	5	4.10
2	3.70	3	5	8	3.50
3	20.70	3	3	6	20.70
4	16.75	2	1	3	16.80
5	6.00	—	—	—	7.00
6	5.50	1	2	3	5.25
7	8.65	4	2	6	8.15
8	7.80	1	3	4	7.90
	Total = 72.90	15	20	35	73.40
	X = 9.11 ± 6.26				X = 9.08 ± 6.04

population. But at a later stage, subadults and adults (i.e. fishes greater than 10 mm TL) formed 72.7% of the populations, being almost identical to the 73.4% of the adult stock before the reproductive period. During all those months, increased predation on *Dascyllus* was observed. This again demonstrates that predation on *Dascyllus* is especially devastating during the reproductive season, a time when many fish engage in sexual display outside their colonies and high numbers of recruits settle into them.

Activities of settlement and occupancy of corals

As selective recruitment was postulated for some coral reef fish (Sale et al. 1984) we decided to study this process in *Dascyllus*. Fifteen coral colonies of *Stylophora* situated on a horizontal platform at a depth of 3 m were selected for observations on recruitment: 4 of those colonies were occupied by *D. aruanus*, 4 by *D. marginatus*, 3 by mixed groups of both species of fishes, and an additional 4 were unpopulated coral colonies. As far as form and dimension were concerned, all those corals were alike. The results shown in Table 6 demonstrate that the recruitment of juvenile fish within each of those particular corals has no specificity. This supports the evidence that juveniles of both species of *Dascyllus* settle from plankton wherever possible and not as observed by Sweatman (1983).

How does the alpha male influence the sexual hierarchy in bispecific groups?

Sixteen bispecific fish groups were collected and the gonads histologically examined. The results, shown in Table 7, demonstrate that the species to which the alpha male belongs does not control the taxonomic composition of the harem. As evident from Table 7, the male in coral no. 13 was *D. marginatus* whereas the females belonged to *D. aruanus*. In coral no. 5, the alpha male was *D. aruanus*, with five adult females of *D. marginatus*.

The following provides an additional example: close to the Farasan IS, in the Gulf of Eilat, on one site 34 of 80 coral colonies suitable for settlement were occupied by *Dascyllus*; of these, 18 were oc-

Table 6. Specificity of recruitment of *Dascyllus*-settlers into occupied and nonoccupied corals during two seasons of reproduction (N = 15).

Numbers of colonies observed	Resident species	Settling species
1	<i>D. aruanus</i>	<i>D. aruanus</i>
2	<i>D. aruanus</i>	<i>D. marginatus</i>
3	<i>D. aruanus</i>	<i>D. aruanus</i> + <i>D. marginatus</i>
4	<i>D. aruanus</i>	no recruitment
5	<i>D. marginatus</i>	<i>D. aruanus</i>
6	<i>D. marginatus</i>	<i>D. marginatus</i>
7	<i>D. marginatus</i>	<i>D. marginatus</i> + <i>D. aruanus</i>
8	<i>D. marginatus</i>	no recruitment
9	<i>D. marginatus</i> + <i>D. aruanus</i>	<i>D. aruanus</i>
10	<i>D. marginatus</i> + <i>D. aruanus</i>	<i>D. marginatus</i>
11	<i>D. marginatus</i> + <i>D. aruanus</i>	<i>D. marginatus</i> + <i>D. aruanus</i>
12	Empty coral colony	<i>D. marginatus</i>
13	Empty coral colony	<i>D. aruanus</i>
14	Empty coral colony	<i>D. marginatus</i> + <i>D. aruanus</i>
15	Empty coral colony	no recruitment

cupied by mixed groups of both species; in 10 of them the alpha male was *D. marginatus* and in 8 *D. aruanus*.

Patterns of predation

As long as the harems of *Dascyllus* are among the branches of the host corals, they are protected from the day-active piscivorous fishes. As for crepuscular or night-active predators, most of them are fishes of open waters (Fishelson et al. 1974), and at these hours *Dascyllus* are resting within the coral. Only moray eels seem to be dangerous at this time. During three night-dives *Siderea grisea* (twice) and *Echidna nebulosa* (once) were seen to stick their heads into a coral colony and grasp a *Dascyllus*. This seemed nevertheless to be a rare occurrence, because counting numerous groups of *Dascyllus* before sunset and after sunrise revealed in almost

Table 7. Composition of sexes in bispecific harems of *Dascyllus* (♀♂♀ = initial stage of transition toward maleness; ♂♀♂ – a pre-ripe male) (N = 126).

Group number	Number of fish in the group	Sexual structure								Juvenile recruits
		<i>Dascyllus marginatus</i>				<i>Dascyllus aruanus</i>				
		♂	♀	♀♂♀	♂♀♂	♂	♀	♀♂♀	♂♀♂	
1	14	1	3	1	1	–	4	1	1	2
2	8	1	3	1	–	–	–	2	1	–
3	2	–	–	1	–	–	–	–	1	–
4	2	–	–	–	1	–	1	–	–	–
5	10	–	5	–	–	1	–	4	–	–
6	7	–	–	2	–	1	–	4	–	–
7	20	1	3	1	–	1	6	2	2	4
8	11	1	3	1	–	–	2	–	–	4
9	5	1	2	–	–	–	2	–	–	–
10	5	1	2	1	–	–	1	–	–	–
11	2	1	–	–	–	–	1	–	–	–
12	3	–	2	–	–	1	–	–	–	–
13	5	1	–	–	–	–	3	1	–	–
14	8	1	1	–	–	–	4	1	1	–
15	11	–	1	–	–	1	2	–	–	7
16	13	1	7	–	–	–	4	–	–	1

all cases no change in number. Thus, if heavy predation occurs, this is mainly during the daytime. The most common predators of *Dascyllus* were observed to be: *Paracirrhites fosteri* (Cirrhithidae); *Cephalopholis hemistiktos*, *C. miniatus*, *Epinephelus fasciatus*, *Variola loti* (Serranidae); *Synodus variegatus* (Synodidae); *Fistularia petimba* (Fistulariidae) and *Parapercis hexophthalma* (Parapercidae). Most of these species are bottom fish that lurk in the vicinity and become alert, especially in the afternoons, when the *Dascyllus* emerge from their corals for feeding or to display.

Paracirrhites fosteri and *Synodus variegatus* were frequently observed to lurk close to the coral colonies and suddenly dash into the water column to catch a damselfish that became exposed. As observed by us and also mentioned by Hobson (1978), the alertness of prey changes with time and season. From survival of recruits, we learn that the juvenile fish are the main victims of predation, but among the adults, the alpha male is the most endangered during the reproductive period, because when displaying he swims up and down above the

coral, apparently less alert to the nearby predator and observer. Usually such performing males 'trigger' the alpha males from neighboring harems to initiate the same behavior (Fishelson 1964, Avidor 1976, Fricke 1980) and those are frequently also joined for a while by ripe females. Such are the situations of which the predators take advantage. On 24 occasions individuals of *D. aruanus* and *D. marginatus* were observed to be devoured by a predator fish; of that number 11 were displaying males, 3 were adult reproducing females and 10 were smaller non-reproducing fish.

As soon as a *Dascyllus* group noticed an active predator, the fish dived into the coral. On those occasions the performing males re-enter the last one, commencing their activities immediately as the danger has passed.

Composition of sexes in groups held in captivity

Groups of *Dascyllus* were kept isolated in several aquaria. One experiment included two separate harems, each including one male *D. marginatus*

and four female *D. aruanus*. After 4 months in captivity and frequent spawnings, members of one harem were dissected; and from the second harem the male was isolated and the females left for one month without a male. No sex-change was found in the four dissected animals of the first group of which all were active females, but in the second group of females, one fish started male-like behavior (up and down swimming and sound production) ten days after the removal of the alpha male. These 4 fish were also dissected at the end and the performing 'female' was found to have a testis proliferating with spermatozoa. A second female had ripe eggs in her ovaries, but also an islet of primary spermatids. The remaining two fish showed only ovulating eggs. Thus, as noted in *Anthias squamipinnis* (Fishelson 1975, Shapiro 1984), and experimentally shown in *D. albisella* from Hawaii, and *D. trimaculatus* from Eilat (Fishelson, unpublished), when harems of females are left without alpha males a new male evolves in a relatively short time, and always from the largest female. In Hawaii one of us (LF) was able to produce 3 secondary males of *D. albisella* by simply keeping 6 single females isolated for 12 days.

In 4 additional isolation experiments, single males of *D. aruanus* were each put with four females of *D. marginatus*. Also in these experiments the male dominated non-conspecific females, and the results were the same as in the preceding experiments: new, conspecific males evolved only after the congeneric dominant fish were removed. All experiments were performed in large aquaria with ample coral colonies, thus sufficient area was available for female fish to remain easily apart from the dominant individual. Despite this, the alpha-male invariably succeeded in controlling the sex-situation in his environment.

Sex-development in isolated fish

Histological studies showed that in 9 to 16 mm TL juveniles of *D. aruanus* and *D. marginatus*, the gonads are ambisexual, but having only a few spermatogonia nests and many oogonia, they show a strong tendency toward femaleness. A situation like this was also observed in experimentally iso-

lated juveniles of *Pomacentrus albicaudatus* and *Plectroglyphidodon sulfureus* (Fishelson, unpublished). When such a juvenile *Dascyllus* joins an existing harem of fish, it becomes a female. Is this obligatory or externally regulated? What happens if such an ambisexual juvenile fish settles in a non-occupied coral? To test this, 6 *D. aruanus* 12 to 14 mm TL and 4 *D. marginatus* of the same size, were each separated in small aquaria and kept for 36 days. At the end of this period the fish were of 16 to 18 mm TL. All were dissected and their gonads examined histologically. The gonads were found masculinized in all 10 fish, large parts of them with fields of spermatogonic cells and islets of spermatozoa (Fig. 4). The oocytes in these gonads were degraded and yolk deposition in them was not detected.

These experiments performed in captivity confirm results obtained by histological examinations from natural populations, namely, that in both species of *Dascyllus*, juvenile fish which join a group continue feminization of the gonad. Contrary to this, an isolated individual fish invariably becomes masculinized. From the point of view of fertility and sex-allocation, these female fish are physiologically prepared to enter social groups.

Discussion

The mechanisms whereby fishes regulate their numbers and distribution have been investigated intensively during the last two decades. Especially intriguing has been the research conducted in coral reef habitats, in which hundreds of species of fishes subtly divide or share the environment (see Smith & Tyler 1972, Sale 1975, Fishelson 1980). The damselfishes, which form an important part of these communities, have attracted much attention, especially as concerns sex-allocation, parental care and social hierarchy. With the discovery of socially controlled sex-change in coral reef fish (Fishelson 1970, Robertson 1972) a new dimension was added to those studies. This has been the case also with the species of *Dascyllus*, whose life histories and ecologies have been discussed in numerous papers (Fishelson 1964, Sale 1972, Holzberg 1973, Fricke

1977, Shpigel 1978, 1982). These studies demonstrate that *D. aruanus* and *D. marginatus* are obligatory coral-dwelling fishes. On most sites of their distribution, they live in permanent harems that consist usually of a number of juvenile and adult females, as well as a single dominant male. As in the case of *Anthias squamipinnis* (Fishelson 1970, 1975, Gunderman 1972, Popper & Fishelson 1973, Shapiro & Lubbock 1980) also in *Dascyllus* spp., the sexually active male develops from the adult female condition; he is also the territory-holder over the host coral. But contrary to *Anthias*, that are 'born' with female gonads, the juvenile *Dascyllus* fish are ambisexual, with gonads having both female and male primordial cells. In nature, the development of a female gonad and not a male one from the primordial anlage is channelled by the presence of a dominant fish, in our study a male. In numerous observations on harems of *Dascyllus*, four castes of fish are usually found: juveniles, reproducing females, pre-ripe males in transition toward maleness and the alpha male.

These damsels are able to produce quite different social groupings under different conditions. For example, at Um-Abbak (Dahlak Archipelago of the Southern Red Sea) *D. aruanus* and *D. marginatus* form mixed and continuous groups on undivided coral reef patches of *Stylophora* corals. Such groups show a lek-structure, as described for other fishes (Moyer & Bell 1976, Loiselle & Barlow 1978). In such leks, the ripe females move above and among the courting males, reacting to display and finally diving into a coral and spawning with a selected male. It seems that in such situations only the males show a high grade of fidelity to a given nest-site. In all such cases the paternal care of the egg mass is much greater than that of the female (see Dawkins & Carlisle 1976). The different social groupings – isolated coral-group of females-single male unit, the bispecific-single male unit – appears to have originated from such a primitive lek structure due to the discontinuity of appropriate coral hosts, and possible constraints of predator pressure. As shown by the present study, due to coral colonies dispersions, increased predation acts against movement, therefore the usefulness of grouping and mobility is greatly or totally reduced.

Exogenous constraints could well have produced a mating system in which the female, instead of deserting the male after egg-deposition, remained faithful in the male's domain, forming a part of the multi-female single male harem system. In such situations both sexes receive an increasing payoff: the female survives because she is better protected by the territory of the male and possibly by its territorial behavior, her longevity then increases and she can thus spawn more often (see also Warner 1978). The male holding a harem of females gains increased opportunities to donate his genes to more juveniles, and by caring for them increases the survival of his progeny. Taking into account the small adult size of these fishes and the numerous piscivorous fish of the reef, able to prey on them if they move around, this seems to be an excellent situation of benefit for each single individual. In such small fish that are vulnerable to predation by many fishes, beginning as a female ensures, at least, some gamete-contribution despite the inability to hold a territory.

According to Katzir (1975) and Fricke (1980) harems of *Dascyllus aruanus* and *D. marginatus* occupy separate corals, especially in the northern part of the Gulf of Aqaba. As found by Shpigel (1982) and observed during this study, these two species of fish occur in the same host more frequently than postulated by former investigators. Thus, for example, on one site, on which 34 corals were found populated by *Dascyllus*, 18 were occupied by bispecific harems. On numerous sites such coral colonies with bispecific occupancy were found to be surrounded by numerous empty corals. This partly contradicts certain observations (Fricke 1975, Thresher 1977) that in reef fishes, the size of social units is controlled by the resource abundance. This is not the case with *Dascyllus*. Our investigation has shown that such a condition is the result of a seasonal process, during which early juveniles settle from the plankton and penetrate coral colonies, often in high numbers. As both species of *Dascyllus* have similar life histories, groups of juveniles of both settle in the corals at the same time, in the same manner, and as observed by us, often in the same coral. The final outcome of this settlement will depend on several factors: the

availability of a coral, its degree of occupancy, and by which species. We have shown that on many occasions, settling juveniles are often preyed upon. This means that the fate of the settlers is not decided simply by the dimension of the host coral, as postulated by several authors. As demonstrated by Shpigel (1978) rather its complexity is the determining factor. Actually, as shown in this study, by calculation of volume in cubic decimeters (liters), in some cases, smaller corals are host to more fish than larger ones (Fig. 6). Now, if the complexity of each coral is constant because of slow growth, at least for some years, then one might predict that the groups of fishes in them will also be relatively constant for the same period. It also appears that single fish or pairs of fish, found in corals, are not individuals expelled from existing harems (Fricke 1980), but constitute survivors of larger groups which have been decimated by predation.

During the initial settlement of early juveniles, many of the corals were already occupied by adult fish, the latter being theoretically the possible parents of the immigrants. Sale (1978a) quoting Coats' personal communication, mentioned that agonism against invading conspecifics is much stronger than against other species. This was also observed by Shpigel (1982). This suggests that a recruit *D. aruanus*, settling into an empty coral or a coral occupied by a harem of *D. marginatus* will have a better chance of remaining in the coral, than if he settles into a coral occupied by conspecifics. Thus, it is possible that intraspecific agonism in our damsels can be a factor encouraging the formation of bispecific groups.

After joining such a group, the juvenile develops as a female and becomes an integral part of the social hierarchy that is maintained by recognition and low-level agonistic behavior. The intensity of female-female and female-male encounters, varies with time and season; and it also depends on the momentary spacing of the residents. It appears, therefore, that we are dealing here with some kind of serial territories (Myrberg & Thresher 1974, Thresher 1976) but in this case it is more constant in time than in space.

In bispecific groups the intraspecific and interspecific encounters are of equal strength and fre-

quency (Shpigel 1982). In Pomacentrid fish hybridization was never recorded or observed in nature or captivity; in such groups sex-allocation, parental care and the individual fitness of each fish, relative to gamete-donation, all depend on the specific identity of the alpha male. If in a bispecific group the alpha male is *D. aruanus*, then only the *D. aruanus* females will reproduce, and the *D. marginatus* females will remain arrested from the point of view of fecundity. The opposite will be the case if the alpha male is of *D. marginatus* type: the *D. aruanus* females will then be dormant. As the dominating male directs his agonistic behaviour toward all females in the harem, such conditions actually persisted whenever a male of a different species dominated a mixed harem of females. In such situations, the species that has non-reproducing adults will only be reproductively activated after the alpha male of the opposite species disappears.

An important question that arises is why do the wrong species females not wander off to look for more promising situations? After many years of observation it appears to us that the obvious answer is predation pressure. In numerous experiments we observed that once a fish exposes itself from its coral retreat, it is likely to be quickly captured by predator fish and cannot traverse more than 40–50 cm. During reproduction, as many displaying alpha males are being hunted by predatory fish, situations are formed that enable sex-change and production of new males. In the mono- as well as bispecific groups this produces equal chance for the females to produce a male as well as for those that were until now dormant, to begin reproduction. As most of the agonistic behavior of the male is directed toward the largest females in bispecific groups, sometimes smaller individuals become pre-ripe-males, if their gonads were at the right stage to support this. The same was also observed by Robertson (1974) in larger harems of *Labroides dimidiatus* (i.e., flutter-running).

According to Fricke (1980), the signal jumps of an alpha male attract females of neighboring *Dascyllus*-harems into his own colony. Such immigration of females in nature was never observed by us. Our experiments, performed at the southern reefs, naturally rich in predator fish, show that

predation 'presses' the groups into their coral hosts and changes in the hierarchies are enabled as dominant males are eliminated. Based on data on sex ratios in *Dascyllus*, Fricke (1980) also concluded that predation, by being more severe on males, results in a surplus of females. Although, during the reproductive period, predation is certainly higher on males than on females, 'surplus' of females in *Dascyllus* is a natural phenomenon and results from growth of juveniles. According to the same author, males of *Dascyllus* monopolize the suitable corals and therefore they control access to females. According to him, the females 'wandering, spread over the reef and select for the best male'. This suggestion seems totally unacceptable; first, because during all our observations all harems have successfully developed from earlier settled groups of juveniles, and secondly, wandering *Dascyllus* are never seen in natural habitats of the Gulf. They will be eaten on the spot if they move out from their retreats.

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