

Habitat partitioning between species of the genus *Cephalopholis* (Pisces, Serranidae) across the fringing reef of the Gulf of Aqaba (Red Sea)

Muki Shpigel*, Lev Fishelson

Department of Zoology, Tel Aviv University, Tel Aviv, Israel

ABSTRACT: Spatial partitioning of sympatric fish species of the genus *Cephalopholis* (Serranidae, Teleostei) was studied on the coral reef of the southern part of the Gulf of Aqaba. Data obtained from observations on 290 individuals over 3000 m² of transects in 4 reef formations demonstrated partitioning related to substrate, depth and time. The studied groupers occupy species-specific habitats over the reef: *C. argus* (Bloch and Schneider) was found to dominate the shallow reef tables and reef wall; *C. miniata* (Forsskal) dwells on coral knolls and up to depths of 10 to 30 m; *C. hemistiktos* (Rüppell) is common on flat bottom and coral rubble areas; and *C. sexmaculata* (Rüppell) dominated at depths exceeding 30 m. All 4 species are diurnal fish, although *C. sexmaculata* is active nocturnally in shallow water and diurnally in deeper water. On sites where the territories of the various species overlap, agonistic behaviour and a size-related dominance hierarchy was observed.

INTRODUCTION

Coral reefs, which provide a wide range of ecological niches, harbor some of the most diverse species assemblages known (Fishelson et al. 1974, Ehrlich 1975, Sale 1980, Waldner & Robertson 1980). Various modes of space and food utilization and social specialization enable fishes inhabiting reefs to generate complex patterns of resource partitioning and energy flow (Jones 1968, Smith & Tyler 1972, 1973, 1975, Fishelson et al. 1985). According to the resources utilization, all coral reef fish species can be grouped into generalists, that utilize diverse sets of the available resources (Bardach 1958, Russell et al. 1974, Sale & Dybdahl 1978, Fishelson 1980, Myrberg et al. 1988), and specialists, adapted to very specific resources within a narrow range of habitats (Fricke 1973, 1977, Smith 1977, Thresher 1977, Fishelson 1980, Shpigel & Fishelson 1986).

Several theories have been suggested to explain these types of space utilization and coexistence of reef fishes (Smith & Tyler 1972, 1975, Smith 1977, Sale 1980, Waldner & Robertson 1980, Kaufman & Ebersole

1984). Despite the fact that many coral fishes are predators (Goldman & Talbot 1976), only a few studies deal with the distribution and interactions of predators dwelling in coral reefs (Odum & Odum 1955, Bardach & Menzel 1957, Harmelin-Vivien & Bouchon 1976, Fishelson 1977, Nagelkerken 1981, Bouchon-Navaro 1986). Groupers (Serranidae) are one of the most dominant and abundant predators along the Virgin Islands (Randall 1963), Curaçao (Nagelkerken 1979), and other warm water regions. Despite this, only sparse information has been gathered on their ecology, distribution and habitat use (Moe 1969, Hobson 1974, Munro 1974, Thompson & Munro 1978, Nagelkerken 1981). In the Gulf of Aqaba (Red Sea) the most common groupers are *Cephalopholis miniata* attaining 320 mm total length (TL), *C. argus* of 400 mm max TL, and *C. hemistiktos* of 250 mm TL. Two rare species that also occur here are *C. oligosticta* (Randall & Ben-Tuvia 1983) (350 mm TL) and *C. sexmaculata* (300 mm TL). All these species, except *C. oligosticta*, occur in the shallow water coral habitat and partly overlap in their distribution (Shpigel 1985). The 3 common species live in well-defined social units, each consisting of up to 12 adult individuals, of which 1 is the dominating male. Each unit occupies a specific area and throughout its entire life is dominated by 1 territorial male (Shpigel 1985).

This study was initiated in order to investigate inter-

* Present address: Israel Oceanographic and Limnological Research Institute, National Center for Mariculture, Eilat, Israel

specific interactions of the sympatric species and to determine how these predators divide resources in the coral reef, both in space and time.

METHODS

Four types of habitats were defined on the shore of Sinai Peninsula in the southern part of the Gulf of Aqaba, in which a total of 290 *Cephalopholis* fish were observed:

(1) The fore-reef wall: steep coral walls form the seaward side of the coral platforms. The wall begins in the subtidal zone (1 m deep) and plunges to a depth of 30 m. These sites are especially species-rich on exposed reefs, where strong water motion maintains high oxygen levels and low sedimentation. Seventy-five individual groupers were counted here.

(2) Coral knolls: formations which occur as submerged splint islands, isolated from other coral formations by sandy bottom flats. Their dimensions are 100 m² or more, and their height ranges from 4 to 10 m above the sea bottom. Forty individual groupers were found in this habitat.

(3) Open areas: open sandy flats at a depth of 2 to 10 m on which small coral heads of 2 to 5 m² are found. Such areas can be horizontal or slightly sloping. Seventy-five groupers were observed here.

(4) Shallow-water complex: usually a back reef in shallow water with small coral heads and platform like reef tables, interspersed with sandy patches. One hundred groupers dwelled in this habitat.

In the 4 habitats, 3 sites of 400 m² each, were selected for observations. Line transects were swum within these habitats according to the technique described by Loya (1972) and Chave & Ekert (1974). Subsequently each of the habitats was further subdivided. The reef wall and the open area were divided into to 3 depth zones: 0–10 m, 10–20 m and 20–30 m. In the shallow water complex, the subdivision was made into reef table, reef wall, shallow open area, and knolls.

Censuses and observations of groupers were carried out by a group of 5 investigators swimming parallel to each other. Using SCUBA gear, 25 randomly delineated transects of 15 × 2 m were surveyed within each subhabitat, with observations on each transect lasting 3 min. This provided a total of 75 min and 750 m² area of observation per subhabitat, or 300 min over 3000 m² for all 4 sites. Such censuses were carried out in the morning hours, 07:00 to 09:00; mid-day, 11:00 to 13:00; and in the afternoon, 15:00 to 18:00. All data were analysed by one-way ANOVA (Sokal & Rohlf 1969).

Activity patterns of fishes were studied at 6 sites:

(A) Two sites were in the shallow water complex, 1 with *Cephalopholis miniata* only (3 groups, each with 1

male and 6, 5, and 4 females, respectively), and a second harboring *C. miniata* (1 male and 4 females) together with *C. argus* (1 male and 2 females) and *C. hemistiktos* (2 pairs).

(B) Two sites were situated on the reef wall, 1 occupied by *Cephalopholis argus* alone (2 groups, each with 1 male and 2 and 4 females, respectively) and the second by *C. argus* (1 male and 2 females) together with *C. miniata* (1 male and 4 females) and *C. hemistiktos* (2 pairs).

(C) Two sites were selected in the open area, with *Cephalopholis hemistiktos* (3 male-female pairs) only.

In each of the sites, 80 observations of 3 min each, were made, providing a total of 240 min species⁻¹. Observations on times of activity were conducted from selected permanent points, between 06:00 and 20:00 h, with 10 observations every 2 h. Sporadic observations were also carried out at night, from 20:00 to 04:00 h. For each appearance of a moving fish, whether hunting, courting or engaged in agonistic interaction, the species was identified and recorded as time of activity, according to the definition used by Smith & Tyler (1972). The total activities of individuals from each species was calculated in percent of this taxon activity in the total activity noted in 1 h of observation. These activity data were analyzed by the Kruskal Wallis 1-way ANOVA (KW) and Mann and Whitney U-test (MW). This enabled the identification of similarity or nonsimilarity patterns in the activity of the various species.

Behavioral observations such as interaction between fish, were made sporadically for 3 yr in zones with overlapping distribution of *Cephalopholis argus*, *C. miniata* and *C. hemistiktos*.

RESULTS

Distribution

The fore-reef wall

This wall in its shallow parts (0–10 m) was predominantly populated by *Cephalopholis argus* and *C. miniata*, that form almost 71 and 14% respectively of all the *Cephalopholis* observed (Fig. 1). When caves were present, the 2 species were also joined by *C. sexmaculata*. At a depth of 20 m, *C. miniata* groups were more numerous, forming over 90% of the population. At 30 m, *C. hemistiktos* and *C. miniata* were joined by *C. sexmaculata* and occasionally by an additional rare species (*C. oligosticta*). Thus *C. argus* dominated from 0–10 m ($F = 3.541$, $p < 0.01$), and *C. miniata* from 10 to 20 m ($F = 5.2$, $p < 0.01$). The average number of *Cephalopholis* per transect of the reef-wall is given in Table 1.

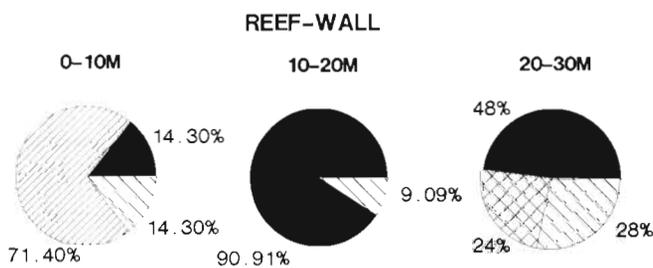


Fig. 1. *Cephalopholis* species. Relative abundance of the various species on the reef-wall: filled = *C. miniata*; hatching = *C. argus*; sparse hatching = *C. sexmaculata*; cross hatching = *C. hemistiktos*

Table 1. *Cephalopholis* species. Average number per transect of reef-wall ($\bar{x} \pm SD$). For a depth $n=25$. *C. sexmaculata* found in coral undercuts and caves. N.S. = not significant

Species	Depth (m)		
	0-10	10-20	20-30
<i>C. miniata</i>	0.08 ± 0.27	0.80 ± 1.52	0.48 ± 1.06
<i>C. argus</i>	0.40 ± 0.91	-	-
<i>C. hemistiktos</i>	-	-	0.24 ± 0.64
<i>C. sexmaculata</i>	0.08 ± 0.40*	0.08 ± 0.40*	0.28 ± 0.79*
Cumulative average	0.56	0.88	1.00
	F = 3.54	F = 5.2	N.S.
	p < 0.05	p < 0.05	p > 0.05

* In caves

Open area

The high dominance of *Cephalopholis hemistiktos* in this area extended from the shallowest water to a depth of 30 m (Fig. 2) ($F = 4.17, 5.17, 3.55$ in 0-10, 10-20 and

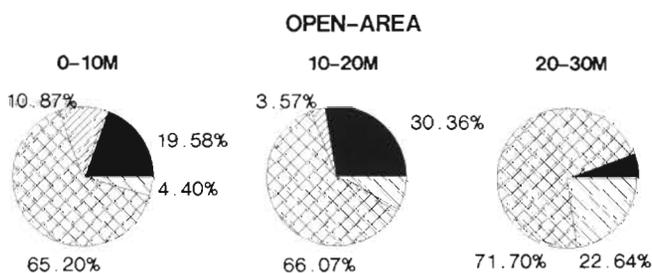


Fig. 2. *Cephalopholis* species. Relative abundance in the open area; symbols as in Fig. 1

20-30 m, respectively; $p < 0.05$). These fish were found in pairs within the small coral knolls and at densities of up to 7 pairs 30 m^{-2} . Occasionally, at such high densities 2 females occurred with 1 male. Sparsely distributed *C. sexmaculata* and a very few *C. oligosticta* were observed at depths greater than 30 m. The average number of *Cephalopholis* per transect of open area is given in Table 2.

Table 2. *Cephalopholis* species. Average number per transect in open area ($\bar{x} \pm SD$); $n=25$ for each depth

Species	Depth (m)		
	0-10	10-20	20-30
<i>C. miniata</i>	0.20 ± 0.70	0.36 ± 0.96	0.04 ± 0.20
<i>C. argus</i>	0.12 ± 0.33	0.04 ± 0.02	-
<i>C. hemistiktos</i>	0.60 ± 0.91	0.76 ± 1.01	0.40 ± 0.87
<i>C. sexmaculata</i>	0.04 ± 0.20*	-	0.12 ± 0.06
Cumulative average	0.96	1.16	0.56
	F = 4.17	F = 5.17	F = 3.55
	p < 0.01	p < 0.01	p = 0.05

* In caves

Knolls

Coral knolls (Fig. 3) are sub-habitats in which all 4 common species of *Cephalopholis* were observed, with a high dominance of *C. miniata* (75.94%) ($F = 3.72, p < 0.05$). Groups of the different species maintain perma-

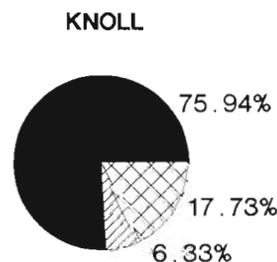


Fig. 3. *Cephalopholis* species. Relative abundance on the knolls; symbols as in Fig. 1

nent sites on the knoll, protecting these from alien groupers. Individuals of *C. argus* moved more than the others over the knolls and adjacent sites; individuals of *C. miniata* were situated on the central portions and *C. hemistiktos* along the base of it. Table 3 provides the number of *Cephalopholis* observed per transect of knolls.

Table 3. *Cephalopholis* species. Average number fish per transect on the knolls ($\bar{x} \pm SD, N=25$)

Species	Knoll
<i>C. miniata</i>	1.20 ± 1.78
<i>C. argus</i>	0.40 ± 0.11
<i>C. hemistiktos</i>	0.28 ± 0.792
Cumulative average	1.88
	F = 3.72
	p < 0.05

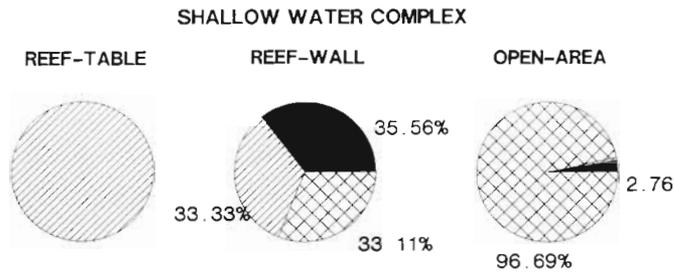


Fig. 4. *Cephalopholis* species. Relative abundance in the shallow water formation; symbols as in Fig. 1

Shallow complexes

The reef flats and the upper fore-reef fringe are dominated exclusively by *Cephalopholis argus*, that formed 100% of the resident groupers (Fig. 4); *C. miniata* dominated on the shallow knolls (76%) and *C. hemistiktos* dominated in small cavities and on small coral heads (97%). Table 4 shows the number of *Cephalopholis* fish counted per transect of the shallow complex. In this habitat, individuals of *C. argus* had the largest home ranges and they were seen moving over the reef table, fore-reef, knolls, and coral heads. On some sites this brought them into close proximity with other species of the same genus.

Activity time

Cycles of activity were censused every 2 h and were found almost identical on the reef wall and the open site for *Cephalopholis argus*, *C. miniata*, and *C. hemistiktos*. These species exhibited 2 activity peaks, 1 during the morning and the second during the afternoon (Fig. 5). In the morning hours, a complete overlap of their activity was observed, whereas in the afternoon activity of different species peaked at only slightly

Table 4. *Cephalopholis* species. Average number per transect of shallow water complex ($\bar{x} \pm SD$); n=25 for each complex; S = significant; N.S. = not significant

Species	Location		
	Reef table	Reef-wall	Open area
<i>C. miniata</i>	-	0.16 ± 0.61	0.04 ± 0.20
<i>C. argus</i>	0.24 ± 0.59	0.16 ± 0.61	0.04 ± 0.20
<i>C. hemistiktos</i>	-	0.16 ± 0.54	1.40 ± 1.10
<i>C. sexmaculata</i>	-	0.04 ± 0.21*	-
Cumulative average	0.24	0.52	1.48
	S	N.S.	F = 13.46 p < 0.01

* In caves

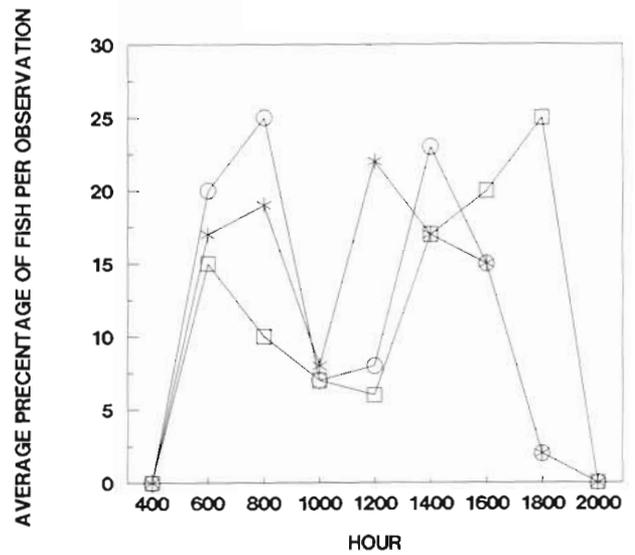


Fig. 5. *Cephalopholis* species. Temporal activity of 3 common species. □: *C. argus* (n = 8); ○: *C. miniata* (n = 18); *: *C. hemistiktos* (n = 6); from a total of 80 observations per species

different times: *C. hemistiktos* from 12:00 to 15:00 h, *C. miniata* from 15:00 to 17:00 h and *C. argus* from 15:00 to 18:00 h. This mode of action persists on sites where the distributions of the 3 species overlaps or even when they occur alone. As all the counts were performed in accordance with the lunar calendar, no correlation was found between activity cycles and tidal ranges. The behaviour of *C. sexmaculatus* is different; at depths of 30 m and more, these fish were active all day long. In shallow water, however, on sites where they overlap with the other congeners, they become nocturnal, remaining hidden in caves within the reef during the day

Interspecific encounters

During their various activities, the *Cephalopholis* fishes often meet, and as a result of this their behaviour changes accordingly. In 265 of 300 observations (85%) of congeneric encounters between males or females, which usually occurred in the overlapping parts of their territories, the loser was the smaller fish. Losers usually changed their coloration to pale-whitish with pale vertical bars, resembling the camouflage color adopted by these species while hunting (Shpigel & Fishelson 1989).

In 34 encounters (11.33%), when, because of similar size, the hierarchy of the 2 fish was dubious, they oriented themselves in an antiparallel position, their colors became darker, and the pale bars on their bodies repeatedly appeared and disappeared. This kind of 'color fight' has been described by Barlow (1963). The outcome of such encounters was peaceful if 1 of the

participants adopted the pale, submissive color and swam away to its territory. In 11 encounters (3.66%) aggressive fights were observed. In 5 of these encounters *Cephalopholis argus* dominated *C. miniata*, while in the remaining 6 encounters larger *C. miniata* dominated smaller *C. argus*. In 200 encounters involving the smaller *C. hemistiktos*, this fish was always dominated by *C. argus* or *C. miniata*.

DISCUSSION

Since Gause (1934), it has been generally assumed that the closer 2 taxa are in evolutionary relationship and physiology, the more subtle are differences in their ecological niches. Such differences can be based on partitioning of space, food or time (Schoener 1974, Fishelson 1980). In coral reef fishes, there are numerous examples of such resource partitioning, such as the distribution of pomacentrids across the reefs (Fishelson et al. 1974, Fricke 1977), the diurnal-nocturnal change-over of various reef fishes (Smith & Tyler 1972), and partitioning of food and space (Bouchon-Navaro 1986). All these instances dealt with taxa, which occur permanently on well defined, small parts of the habitat. In these subtle relationships the individuals are able to learn the qualities of their actual environment, and as a result form specific phenotypic qualities. Thus, for example, in coral bush dwelling damsel fish, gobies and pseudochromids, the actual dimensions of the fish living in various types of coral, reflects the form and quality of the host coral (Shpigel & Fishelson 1986, Fishelson 1989).

The same ideas of plasticity seem to apply to species of *Cephalopholis* within the Red Sea coral reefs. In the groupers studied, partitioning of space and food as well as slight differences in time of activity, possibly enables their more peaceful coexistence and more efficient utilization of existing resources. This is also supported by the clear hierarchy observed among the species in overlapping areas. Here, and as in the damsel fish (Shpigel & Fishelson 1986), the larger fish species always dominate the smaller ones, which thus reduces aggression and creates well-balanced behavioral partitioning.

In addition to habitat and time partitioning, the diets of each of the species also differ (Shpigel & Fishelson 1989), as each of them utilizes a different dominant food source in the habitat. From dissections of over 590 fish, we learned that *Cephalopholis miniata*, frequenting the knoll, feeds predominantly on *Anthias squamipinnis*, schools of which hover over this habitat (Popper & Fishelson 1975); *C. argus*, living on the platforms, feeds heavily on surgeonfish *Acanthurus nigrofuscus*, which grazes there in groups (Fishelson et

al. 1987); and *C. hemistiktos*, living over open bottoms, hunts a variety of invertebrates. As the predominant prey of *C. argus* and *C. miniata* are diurnal fishes, the activity of these predators was moulded accordingly. Even the bimodality observed in the feeding activities of the prey fish (Popper & Fishelson 1975, Montgomery et al. unpubl.) is followed by the bimodal activity pattern of hunting in *Cephalopholis*.

Such distinct species-specific niche partitioning in coral reef utilization by groupers was also documented by Nagelkerken (1981) from the Antilles Islands. The questions that remain open for further study are, do *Cephalopholis* species have a specific prey search image and does the specific prey search finally lead to the 'decision' of where to establish the 'hunting' ground, or, because of the primary fidelity to specific habitats, do they focus on food items found there?

Ecological plasticity is shown by *Cephalopholis sexmaculata*. On sites where this species overlaps with *C. argus* and *C. miniata*, it is a nocturnal fish, hiding during the day in coral reef caves and crevices. Contrary to this, on sites where the 2 competitors are absent as, for example in deeper water, *C. sexmaculata* is active during the day, living exposed between the corals and showing a diurnal activity cycle.

In deep water we observed also the rarest species, *Cephalopholis oligosticta*. This occurrence of rarest forms in deeper waters appears to confirm the postulation of Randall (1963), that when 2 species are of similar size, one is likely to be rare and the other common.

Acknowledgements. The authors thank all those volunteers who helped out during the field studies. Thanks are also due to Dr D. Popper, Dr A. Diamant (Eilat), to Prof. M. L. Montgomery (Flagstaff, Arizona), and anonymous referees for important and critical remarks on the manuscript. Part of the funding for the research was provided by the Israeli Society for Nature Protection and Tel Aviv University.

LITERATURE CITED

- Bardach, J. E. (1958). On the movement of certain Bermuda reef fishes. *Ecology* 39: 139-140
- Bardach, J. E., Menzel, D. W. (1957). Field and laboratory observations on the growth of some Bermuda reef fish. *Proc. Gulf Caribb. Fish. Inst.* 9: 106-112
- Barlow, G. W. (1963). Ethology of the Asian teleost *Badis badis*: motivation and the signal value of the color patterns. *Anim. Behav.* 11: 97-105
- Bouchon-Navaro, Y. (1986). Partitioning of food and space resources by chaetodontid fishes on coral reefs. *J. exp. mar. Biol. Ecol.* 103: 21-40
- Chave, E. H., Eckert, D. G. (1974). Ecological aspects of the distributions of fishes at Fanning Island. *Pacif. Sci.* 28: 297-317
- Ehrlich, P. R. (1975). The population biology of coral reef fishes. *Rev. Ecol. Syst.* 6: 211-247
- Fishelson, L. (1977). Sociobiology of feeding behavior of coral

- fish along the coral reef of the Gulf of Eilat, Red Sea. Israel J. Zool. 26: 114–134
- Fishelson, L. (1980). Partitioning and sharing of space and food resources by fishes. In: Bardach, J. E., Magnuson, J. J., May, R. C., Reinhart, J. M. (eds.) Fish behavior and its use in the capture and culture of fishes. International Center for Living Aquatic Resources Management, Manila, Philippines ICLARM Conf. Proc. 5: 415–445
- Fishelson, L. (1989). Why so many little fish in tropical regions? Senckenbergiana Maritima, Frankfurt (in press)
- Fishelson, L., Montgomery, W. L., Myrberg, A. A., Jr (1985). A unique symbiosis in the gut of herbivores surgeon-fish (Acanthuridae, Teleostei) from the Red Sea. Science 229: 49–51
- Fishelson, L., Montgomery, W. L., Myrberg, A. A., Jr (1987). Biology of the surgeon-fish *Acanthurus nigrofasciatus* with emphasis on change-over in diet and annual gonadal cycle. Mar. Ecol. Prog. Ser. 39: 37–47
- Fishelson, L., Popper, D., Avidor, A. (1974). Biosociology and ecology of pomacentrid fishes around the Sinai peninsula, northern Red Sea. J. Fish Biol. 6: 119–133
- Fricke, H. W. (1973). Ecologie und Sozialverhalten des Korallenbarsches *Dascyllus trimaculatus* (Pisces, Pomacentridae). Z. Tierpsychol. 32: 225–256
- Fricke, H. W. (1977). Community structure, social organization and ecological requirements of coral reef fish (Pomacentridae). Helgoländer wiss. Meeresunters. 30: 412–426
- Gause, G. F. (1934). The struggle for existence. Williams and Wilkins, Baltimore
- Goldman, B., Talbot, F. H. (1976). Aspects of the ecology of coral reef fishes. In: Jones, O. A., Endean, R. (eds.) The biology and geology of coral reefs. Academic Press, New York, p. 128–154
- Harmelin-Vivien, M. L., Bouchon, C. (1976). Feeding behavior of some carnivorous fishes (Serranidae and Scorpaenidae) from Tulear (Madagascar). Mar. Biol. 37: 329–340
- Hobson, E. S. (1974). Feeding relationship of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull. U.S. 72: 915–1031
- Jones, R. S. (1968). Ecological relationships in Hawaiian and Johnston Island Acanthuridae (Surgeonfishes). Micronesica 4: 309–361
- Kaufman, L. B., Ebersole, J. P. (1984). Microtopography and the organization of two assemblages of coral reef fishes in the West Indies. J. exp. mar. Biol. Ecol. 78: 253–268
- Loya, Y. (1972). Community structure and species diversity of hermatypic corals at Eilat, Red Sea. Mar. Biol. 13: 100–123
- Moe, M. A., Jr (1969). Biology of the red grouper *Epinephelus morio* (Val.), from the eastern Gulf of Mexico. Prof. Pap. Ser. mar. Lab. Fla. 10: 1–95
- Munro, J. L. (1974). The biology, ecology, exploitation and management of Caribbean reef fishes. Vb. Serranidae (hinds and groupers). Res. Rep. zool. Dep. Univ. W. Indies 3: 1–82
- Myrberg, A. A., Jr., Montgomery, W. L., Fishelson, L. (1988). The reproductive behavior of *Acanthurus nigrofasciatus* and other surgeonfish (Acanthuridae) off Eilat, Israel (Gulf of Aqaba, Red Sea). Ethology 79: 31–61
- Nägelkerken, W. P. (1979). Biology of the Graysby, *Epinephelus cruentatus*, of the coral reef of Curaçao. Stud. Fauna Curaçao 60: 1–118
- Nägelkerken, W. P. (1981). Distribution and ecology of the groupers (Serranidae) and snappers (Lutjanidae) of the Netherlands Antilles. Natural History Series. No. 3. Foundation Science Research in Surinam and Netherlands Antilles. Utrecht, Holland
- Odum, H. T., Odum, E. P. (1955). Trophic structure and productivity of a windward coral reef community of Eniwetok. Atoll. Ecol. Monogr. 25: 230–291
- Popper, D., Fishelson, L. (1975). Ecology and behavior of *Anthias squamipinnis* in the coral habitat of Eilat (Red Sea). J. exp. Zool. 184: 409–424
- Randall, J. E. (1963). An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Caribb. J. Sci. 3: 31–47
- Randall, J. E., Ben-Tuvia, A. (1983). A review of the groupers (Pisces: Serranidae, Epinephelinae) of the Red Sea, with description of a new species of *Cephalopholis*. Bull. mar. Sci. 33: 373–426
- Russel, B. D., Talbot, F. H., Domm, S. (1974). Patterns of colonization of artificial reefs by coral reef fishes. Proc. 2nd int. Symp. coral Reefs 1: 207–215 [Cameron, A. M. et al. (ed.) Great Barrier Reef Committee, Brisbane]
- Sale, P. F. (1980). The ecology of fishes on coral reefs. Oceanogr. mar. Biol. A. Rev. 18: 367–421
- Sale, P. F., Dybdahl, R. (1978). Determinants of community structure for coral reef fishes in isolated coral heads at lagoonal and reef slope sites. Oecologia 34: 233–243
- Schoener, T. E. (1974). Resource partitioning in ecological communities. Science 185: 27–38
- Shpigel, M. (1985). Aspects of the biology and ecology of the Red Sea groupers *Cephalopholis* (Serranidae, Teleostei). Ph.D. dissertation, Tel Aviv Univ., Tel Aviv (In Hebrew with English summary)
- Shpigel, M., Fishelson, L. (1986). Behavior and physiology of coexistence in two species of *Dascyllus* (Pomacentridae, Teleostei). Envir. Biol. Fish. 17: 253–265
- Shpigel, M., Fishelson, L. (1989). Food habits and prey selection of three species of groupers of the genus *Cephalopholis* (Serranidae, Teleostei). Envir. Biol. Fish. 24 (1): 67–73
- Smith, C. L. (1977). Coral reef fish communities – order or chaos. Proc. 3rd int. Symp. coral Reefs 1. 21–22
- Smith, C. L., Tyler, J. C. (1972). Space resource sharing in a coral reef fish community. Contr. Sci. 14: 125–170
- Smith, C. L., Tyler, J. C. (1973). Direct observation of resource sharing in coral reef fish. Helgoländer wiss. Meeresunters. 24: 264–275
- Smith, C. L., Tyler, J. C. (1975). Succession and stability in fish communities and the species equilibrium theory in insular biogeography. J. Biogeogr. 6: 49–62
- Sokal, R. R., Rohlf, F. J. (1969). Biometry. W. H. Freeman Co., San Francisco
- Thompson, R., Munro, J. L. (1978). Aspects of the biology and ecology of Caribbean reef fishes: Serranidae. J. Fish Biol. 12: 115–146
- Thresher, R. E. (1977). Ecological determinants of social organization of reef fishes. Proc. 3rd int. Symp. coral Reefs 1. 551–557
- Waldner, R. E., Robertson, D. R. (1980). Patterns of habitat partitioning by eight species of territorial Caribbean damselfishes (Pisces Pomacentridae). Bull. mar. Sci. 30: 171–186

This article was submitted to the editor

Manuscript first received: April 4, 1989

Revised version accepted: August 4, 1989