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Trophic relationships of reef fishes in Tuléar (Madagascar)

Fishfauna
Coral reefs
Trophic relationships
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Ichtyofaune
Récifs coralliens
Relations trophiques
Madagascar
Océan Indien

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ABSTRACT

Trophic relationships of reef fishes in Tuléar (Madagascar) were studied by quantitative analysis of stomach contents of 142 fish species. Feeding behaviours vary according to size of individuals, time and biota. Diurnal and nocturnal sets of species were sampled. The diurnal group including 60% of species and 63% of individuals is both more numerous and more diversified than the nocturnal one.
The consumption of prey by reef fishes differ in quality and in quantity with time and biota. The main prey are Brachyurans (29% by weight), Fishes (19%) and Algae (16%). Prey consumption is higher by day (63%) than by night (37%). Fishes adjust their feeding to the diversity level of the benthic communities. Biomass of prey in communities and in fish feeding fluctuate in the same way, but no direct proportionality was observed between the two values. The various reef zones furnish different energy resources to the fishfauna. Two cycles of organic matter are present in the food webs of a coral reef. Low trophic levels are exclusively consumed by day whereas high trophic levels are used in same quantities by day and by night. At least 5 trophic levels were recorded in the coral reefs of Tuléar.

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RÉSUMÉ

Relations trophiques des poissons
dans les récifs coralliens de Tuléar (Madagascar).

Le rôle de l'ichtyofaune dans les réseaux trophiques des récifs coralliens a été étudié à Tuléar (Madagascar) grâce à l'analyse quantitative des régimes alimentaires de 142 espèces. L'alimentation des espèces varie selon la taille des individus, la période de récolte et le milieu. Deux populations actives, l'une diurne, l'autre nocturne, ont été séparées en fonction du rythme d'activité des espèces. La population diurne comprenant 60% des espèces et 63 % des individus est plus importante et plus diversifiée que la population nocturne.
La consommation des proies par les poissons récifaux varie en qualité et en quantité dans le temps et dans l'espace. Elle est dominée par les Brachyoures (29 % en poids), les Poissons (19 %) et les Algues (16 %) et est plus importante le jour (63 %) que la nuit (37 %). On observe une adaptation de la diversité de l'alimentation des poissons à la diversité des peuplements benthiques. Les biomasses des proies dans le milieu et dans l'alimentation des poissons varient dans le même sens sans qu'il y ait proportionnalité directe entre les deux. Les différents biotopes récifaux offrent des sources d'énergie différentes à l'ichtyofaune. Il existe deux cycles de la matière fonction du rythme jour-nuit. Les niveaux trophiques les plus bas sont consommés exclusivement le jour, tandis que les niveaux les plus élevés sont utilisés avec des rendements à peu près identiques le jour et la nuit. Il existe au moins 5 niveaux trophiques dans les récifs coralliens de Tuléar.

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INTRODUCTION

The structure of trophic food webs of a coral reef was studied in different ways by Sargent and Austin (1954), Odum and Odum (1955), Hiatt and Strasburg (1960), Talbot (1965), Bakus (1969), Pérès and Picard (1969), Smith and Tyler (1972), Vivien (1973), and Goldman and Talbot (1976), all of them emphasizing the complexity of such a structure. Most of the time this problem is approached by the analysis of feeding behaviours of reef fishes (Hiatt, Strasburg, 1960; Randall, 1967; Hobson, 1968; 1974; Vivien, 1973). Other papers give basic information on the food of particular families pointing out the relations between fishes and their prey (Randall, Brock, 1960; Talbot, 1960; Jones, 1968; Hobson, Chess, 1976; 1978; Vivien, Peyrot-Clausade, 1974; Vivien, 1975; Harmelin-Vivien, Bouchon, 1976).

This paper is part of a more important study on the feeding behaviour and ecology of the reef ichthyofauna in Tuléar (Madagascar) (Harmelin-Vivien, 1979), where different fish faunas occurring in various reef biota were described along with diurnal and nocturnal fish populations which take turns according to a nycthemeral rhythm. The present paper summarizes the main conclusions on the distribution of the various feeding patterns on reefs, on the consumption of prey by fishes and on the food webs of a tropical coral reef.

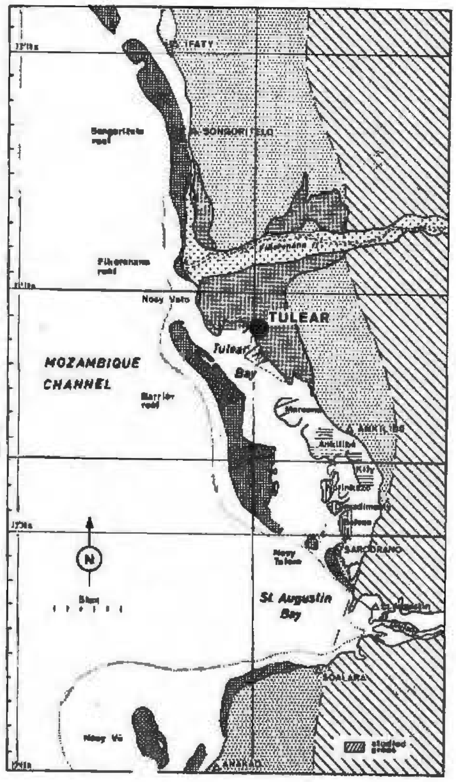

Figure 1

Coral reefs of Tuléar region (SW coast of Madagascar). The main studied areas are located on the barrier reef, the "Grand Récif".

Récifs coralliens de la région de Tuléar (SW Madagascar). Les secteurs étudiés principalement (zones hachurées) sont situés sur le « Grand Récif » qui barre la baie de Tuléar.

Location

Since 1961, intensive reef studies have been conducted in the vicinity of Tuléar on the south west coast of Madagascar. The morphology of coral reefs has been detailed by Clausade *et al.* (1971) and Pichon (1978). Around Tuléar, tides are of semi-diurnal type. Their maximum range is of 3.2 m during spring periods which induce the emergence of reef flats at each low spring tide.

The studied area runs from Ifaty in the North to Sarodrano in the South but most observations were developed on the "Grand Récif", a 18 km long and 980 to 3000 m wide barrier reef which closes Tuléar Bay (Fig. 1). Different morphological features can be distinguished on the barrier reef from the open sea to the lagoon: the outer reef slope divided into a lower coral flagstone and a spur and groove system, the outer reef flat, the boulder tract, the inner reef flat, the sandy accumulation which is sometimes covered by seagrasses and the lagoon slope (Fig. 2).

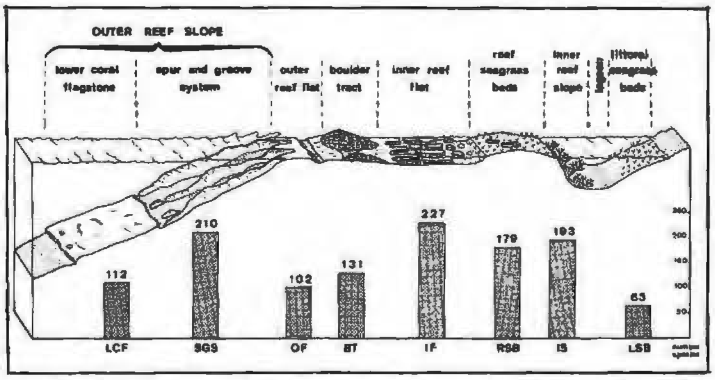

Figure 2

Transversal section across the various biota of the barrier reef with numbers of fish species censued.

Coupe transversale du Grand Récif montrant les divers biotopes prospectés, et les nombres d'espèces de poissons observés dans chaque milieu.

Methods

Observations and sampling were conducted from the shore down to 55 m on the deep border of the lower coral flagstone from September 1969 to November 1972. A total of 130 samples (102 by day and 28 by night), most of them collected with rotenone were made in all biota. Only 22 samples were made with explosive on the slopes where no nocturnal sampling were conducted. Randall (1963 *a*) and recently Russell *et al.* (1978) have reviewed techniques for sampling reef fishes, but all represent a more or less broad selectivity.

The quantitative study of stomach contents was carried out according to the analysis method described by Vivien (1973) taken from Hureau (1970).

RESULTS

Feeding behaviours

The fish fauna of Tuléar is rich and diversified. In this area more than 700 species were censused by Maugé (1967); 552 species belonging to 71 families were recorded for the present study. A total of 8 370 individuals belonging to 142 species were analysed for stomach contents. These species are the commonest ones on the reef as they represent 84% of the 19 900 specimens collected. All are Teleosteans which constitute the main part of the reef ichthyofauna and belong to 37 families (Table 1). List of fishes and feeding behaviours are detailed in Harmelin-

Table 1

List of reef fish families studied for analysis of feeding behaviours on Tuléar reefs: number of species studied; A_1, relative abundance in sample analyzed; A_2, relative abundance in total fish fauna collected; main diets of species studied; activity rhythm (H_1, herbivorous grazers on short algae; H_2, herbivorous browsers on large fleshy algae; O, omnivorous species; C_B; carnivorous browsers on sessile invertebrates; C_M, predators on motile invertebrates; C_{PK}, zooplankton feeders; C_S, carnivores feeding on sandy bottoms; P, piscivorous fishes; D, species active during the day; N, species active during the night).

Liste des familles étudiées pour l'analyse des régimes alimentaires des poissons récifaux à Tuléar ; nombre d'espèces étudiées par famille; A_1, abondance relative des espèces étudiées; A_2, abondance relative des familles par rapport à la totalité des prélèvements; principaux régimes alimentaires des espèces étudiées; rythme d'activité de ces espèces (H_1, herbivores broutant le gazon algal; H_2, herbivores broutant de grandes algues molles; O, omnivores; C_B, carnivores broutant des invertébrés sessiles; C_M, prédateurs d'invertébrés vagiles; C_{PK}, carnivores planctonophages; C_S, carnivores fouillant le sable; P, piscivores; D, espèces actives le jour; N, espèces actives la nuit).

Families	N° species studied	A_1	A_2	Main diets	Activity rhythm
Moringuidae	1	0.6	0.6	C_M	D+N
Muraenidae	3	1.8	2.2	C_M	D+N
Congridae	1	0.7	0.8	P(+C_M)	D+N
Ophichthidae	2	0.2	0.4	C_S	D ?
Synodontidae	2	0.7	0.6	P	D(+N)
Gobiesocidae	1	0.6	0.5	C_M	D
Ophidiidae	1	0.7	0.7	C_M	D+N
Holocentridae	3	2.2	2.2	C_{PK}, C_M	N
Syngnathidae	3	1.8	1.7	C_M	D
Scorpaenidae	8	1.9	1.9	C_M(+P)	D+N
Platycephalidae	1	0.1	0.2	P	D+N
Serranidae	6	0.9	2.4	P, C_M	D+N
Grammistidae	1	0.1	0.1	C_M(+P)	D+N ?
Pseudochromidae	1	0.3	0.3	C_M	D
Pseudogrammidae	1	0.2	0.2	C_M	D(+N ?)
Plesiopidae	1	3.7	3.1	C_M	N
Apogonidae	11	15.1	13.5	C_{PK}, C_M	N
Lutjanidae	3	1.9	2.1	C_S(+C_M)	N
Pomadasyidae	1	0.1	0.2	C_M(+C_S)	N
Lethrinidae	3	0.8	0.7	C_S	D
Mullidae	2	0.5	0.5	C_S	D
Pempheridae	1	2.4	2.1	C_{PK}	N
Chaetodontidae	9	1.9	2.0	C_B	D
Pomacentridae	19	27.3	25.9	{O, C_{PK}, C_M(+C_B)}	D
Labridae	16	10.0	9.5	C_M	D
Scaridae	4	1.7	1.7	H_1, H_2	D
Blenniidae	9	7.9	7.1	O, H_1, P	D
Congrogadidae	1	2.5	2.2	C_M	D
Tripterygiidae	1	0.3	0.8	C_M	D
Callionymidae	1	0.1	0.1	C_M	D
Gobiidae	8	5.6	6.6	O, C_M	D
Acanthuridae	3	2.6	2.6	H_1, H_2	D
Siganidae	1	0.5	0.5	H_2	D
Bothidae	1	0.3	0.2	C_S	D(+N)
Balistidae	6	0.8	0.9	C_B, C_M, 0	D
Ostracionidae	1	0.1	0.1	O	D(+N ?)
Tetraodontidae	5	1.0	0.9	O, C_B C_M	D N

Vivien (1979). Relative abundances of families (Table 1), relative importances of diurnal and nocturnal species and those of various kinds of diets are similar in sample analysed and in total fish fauna. Results achieved can be considered as representative of the whole ichthyofauna on Tuléar reefs, except for the outer reef slope where piscivorous species were underestimated.

The three main groups of feeding behaviour (herbivores, omnivores and carnivores) were divided into several categories according to type of prey, active period and feeding strategy which are summarized on Table 2. Smith (1978) conducted a comparison between classifications of feeding strategies established by Hiatt and Strasburg (1960), Randall (1967), Smith and Tyler (1973), Vivien (1973) and Hobson (1975) that differ somewhat according to the area in which they worked and the species analysed. But all classifications emphasize the great diversity of feeding strategies occurring among carnivorous fishes.

In Tuléar, herbivorous reef fishes represent 9% of the species number, omnivorous fishes 17% and carnivorous fishes 74%. Proportions in number of individuals are a little different (Table 3). Studies conducted in different areas by Randall (1963*b*; 1967), Talbot (1965), Bakus (1967) and Goldman and Talbot (1976) also pointed out the low percentages of species and individuals of herbivorous fishes on coral reefs which is opposed to the conclusion of Odum and Odum (1955). The distribution of feeding categories varies across the reef according to the biota. Herbivores increase in number of individuals on the outer reef flat and on the boulder tract, carnivores on the outer reef slope and seagrass beds while omnivores are more or less regularly distributed in all biota (Table 4). Among carnivorous species (Table 5), plankton feeders are dominant on the reef slopes. The importance of piscivorous fishes seems rather constant but is greater on the outer slope. Predators feeding on hard substrates are numerous on the front part of the reef and predators feeding on soft bottoms increase on the inner reef flat and the lagoon.

In all reef zone the fish fauna includes a diurnal and a nocturnal set of species. The diurnal group is much more varied than the nocturnal one since 60% of species are active during the day compared with 32% at night and 8% are active by day as well as by night. It is also more numerous since 63.5% of the individuals are diurnally active. The feeding strategies are also more diversified by day. The diurnal population includes all the herbivorous species, all the omnivores and 46% of the carnivorous species. All the nocturnal fishes are carnivores.

Table 2

Classification of feeding guilds in Tuléar reef fishes based on both diets and activity rhythms.

Classification des éthologies alimentaires des poissons récifaux à Tuléar en fonction des régimes et des rythmes d'activité.

HERBIVOROUS (all diurnal)
- Grazers on short algae (=algal turf)
- Browsers on large fleshy algae and seagrasses

OMNIVOROUS (all diurnal)

CARNIVOROUS
- Diurnal carnivores
  - § preying on invertebrates
    - = zooplankton feeders
    - = benthophagous fishes
      - + feeding on hard substrates
        -) browsers on sessile invertebrates
        -) predators on motile invertebrates
      - + feeding on soft bottoms
    - = ectoparasite feeders
  - § piscivorous fishes
- Nocturnal carnivores
  - § preying on invertebrates
    - = zooplankton feeders
    - = benthophagous fishes
  - § piscivorous fishes
- Carnivores indifferently active by day and by night (mainly piscivorous)

Table 3

Importance of herbivorous, omnivorous and carnivorous fishes on several coral reefs (% W = weight percentages; % N = numerical percentages; % S = percentages in number of species).

Importance des poissons herbivores, omnivores et carnivores dans différents récifs coralliens (% W = pourcentages en poids; % N = pourcentages en nombre d'individus; % S = pourcentages en nombre d'espèces).

	Randall (1963) Virgin Islands	Randall (1967) Puerto Rico	Talbot (1965) East African coast	Harmelin-Vivien (1979) Madagascar		Bakus (1967) Enewetak		Goldman and Talbot (1976) One Tree I. Great Barrier Reef	
	% W	% S	% W	% S	% N	% S+W	% W		% W
Herbivores	24	11	19	9	11	22	16	Browsers ([a])	18
								Plankton feeders	10
Omnivores	16	15	20	17	26	9	14	Predators on benthic invertebrates	18
Carnivores	60	74	61	74	63	69	70	Piscivorous fishes	54

([a]) Goldman and Talbot (1976) include herbivores and coral feeders in the "Browsers".

Table 4

Distribution and relative importance of the three main feeding guilds in the various biota of the barrier reef near Tuléar (Madagascar) (% S = percentages in species number; % N = percentages in number of individuals).

Distribution et importance relative des trois grandes catégories d'éthologie alimentaire dans les différents biotopes du récif barrière de Tuléar (Madagascar) (% S = pourcentages en nombre d'espèces; % N = pourcentages en nombre d'individus).

	Lower coral flagstone		Spur and groove system		Outer reef flat		Boulder tract		Inner reef flat		Reef seagrass beds		Inner reef slope		Littoral seagrass beds	
	% S	% N	% S	% N	% S	% N	% S	% N	% S	% N	% S	% N	% S	% N	% S	% N
Herbivores	8.0	2.1	12.3	7.5	16.6	24.2	8.4	27.2	8.8	7.6	6.0	4.9	7.2	1.9	4.8	2.2
Omnivores	17.8	12.4	13.3	24.7	18.6	18.5	22.1	25.8	19.7	31.2	17.0	20.7	19.1	25.7	15.9	29.8
Carnivores	74.1	85.5	74.4	67.8	64.7	57.3	69.5	47.0	71.5	61.2	77.0	74.4	73.7	72.4	79.4	68.0

Table 5

Distribution of the different carnivorous fish categories across the barrier reef near Tuléar (Madagascar) (specific and numerical percentages are calculated with respect to the whole carnivorous population in each biota).

Distribution des grands groupes de poissons carnivores dans les différents biotopes des récifs de Tuléar (Madagascar) (les pourcentages en nombre d'espèces et d'individus ont été calculés par rapport à la population totale de poissons carnivores dans chaque zone).

	Lower coral flagstone		Spur and groove system		Outer reef flat		Boulder tract		Inner reef flat		Reef seagrass beds		Inner reef slope		Littoral seagrass beds	
	% S	% N	% S	% N	% S	% N	% S	% N	% S	% N	% S	% N	% S	% N	% S	% N
Piscivorous fishes	21.8	4.7 ([a])	8.9	2.9 ([a])	9.1	2.1	6.6	1.5	9.2	3.8	12.1	8.2	6.3	7.8	6.0	4.7
Zooplankton feeders	12.0	71.7	14.6	42.6	12.1	7.6	6.6	5.5	7.4	26.3	6.4	4.2	15.4	55.4	4.0	0.4
Predators of invertebrates on soft bottoms	12.0	3.4	11.5	4.8	1.5	0.1	20.8	3.7	22.1	6.9	41.4	48.6	25.2	4.8	74.0	75.7
Predators of invertebrates on hard substrates	54.2	20.2	65.0	49.7	77.3	89.9	65.9	89.4	61.3	62.9	40.1	39.0	53.1	32.0	16.0	19.2

([a]) Broad underestimation due to sampling.

Consumption of prey by reef fishes

Qualitative and quantitative differences occur in the consumption of prey by reef fishes during day and night. A minimum estimation of the consumption of prey by reef fishes was calculated on the barrier reef of Tuléar from the results of stomach contents analysis of 142 species which formed 84 % of the total number of fish collected.

Quantitative data on the consumption of food by reef fishes in Tuléar, expressed as percentages by weight, are summarized on Table 6. Crustaceans, especially Brachyurans and shrimps, are the main group of prey ingested by reef fishes. They represent 40 % of the total weight of food. Fishes take the second place with 19 % and Algae the third with 16 %. Polychaetes form only

Table 6

Consumption of the main food categories by the 142 more numerous fish species in Tuléar reefs by day, by night and the two periods combined, expressed as percentages of total weight of food for each period (+percentages <0.1 %).

Consommation des principaux groupes de proies par les 142 espèces de poissons les plus abondantes sur les récifs coralliens de Tuléar. Les consommations diurne, nocturne et globale sont exprimées en pourcentages du poids total de nourriture consommée à chaque période (+pourcentages <0,1 %).

Preys	Day %W	Night %W	Total (day → night) %W
Algae	25.6	0.2	16.1
Seagrasses	1.4	0.9	1.2
Sponges	3.5	0.9	2.5
Coelenterates	5.7	0.2	3.6
Polychaetes	4.4	12.5	7.5
Molluscs	6.2	1.9	4.6
Crustaceans	26.8	62.1	40.0
Echinoderms	4.6	+	2.9
Ascidians	2.8	+	1.7
Fishes	17.7	20.6	18.8
Miscellaneous	1.3	0.7	1.1
Total weights	1 151.8 g	690.5 g	1 842.3 g

7.5 % of all the food ingested and all of the other kinds of prey less than 5 %.

Diurnal and nocturnal food intake

Consumption of prey is higher by day than by night: 62.5 % of total weight of food are ingested by fishes during the day and only 37.5 % by night. The relative importance of diurnal and nocturnal fish populations is equal to this ratio (63.5 % of individuals are active by day and 36.5 % by night). So, its appears that, in Tuléar reefs, the feeding efficiency of diurnal and nocturnal fish populations is similar and that the feeding rate of fishes is proportional to their number. The food is more diversified by day than by night: 54 major groups of food organisms were recognized in fishes collected by day and only 41 in fishes collected by night.

Three kinds of prey are dominant in the food ingested during the day: filamentous algae (22 %), fishes (17 %) and brachyurans (16 %). The other prey ingested in some importance are corals (5 %), polychaetes (4 %), large fleshy algae (4 %), sea urchins (4 %), sponges (4 %), shrimps (4 %), gastropods (3 %) and ascidians (3 %). All other food types form less than 15 % of the weight of diurnal food. Some food categories are mainly or exclusively ingested during the day (Table 6): algae and seagrasses, sessile invertebrates (sponges, coelenterates, barnacles, bryozoans, ascidians), molluscs (except cephalopods), small crustaceans (ostracods, copepods, cumaceans, tanaids, isopods, amphipods, small hermit crabs), echinoderms, larvaceans, fish eggs and organic matter.

During the night, fishes prey upon four main food categories: brachyurans, including porcellanids, representing 51 % of food weight ingested at night, fishes 21 %, polychaetes 13 % and shrimps 7 %. All the other prey form only 8 % of the food. The organisms caught mainly at night are polychaetes, cephalopods, shrimps, galatheans, brachyurans and hemichordates.

Prey consumption according to reef zone

The consumption of prey by reef fishes was calculated for each reef zone according to mean number of individuals of species analysed. Variations in consumption of the main food categories by fishes across the reef expressed as percentages by weight of prey in each zone are shown in Figure 3. It appears that the food is well diversified on the lower coral flagstone, the spur and groove system, the inner reef flat and the inner reef slope, but is dominated by a single category of prey in other biota. Algae form 46 % of the food ingested by fishes on the outer reef flat and 58 % on the boulder tract; 58 % of prey are brachyurans in reef seagrass beds and 74 % in littoral seagrass beds.

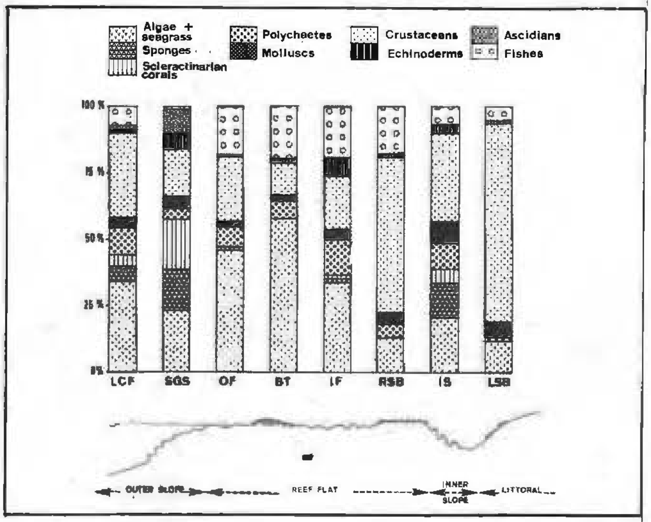

Figure 3

Variations of the consumption of the main prey categories by fishes in the various biota of the barrier reef of Tuléar, expressed as weight percentages.

Variations de la consommation, en poids, des principaux groupes de proies par les poissons sur une coupe du Grand Récif.

If we now consider the total consumption of each of the main food categories, it appears that they are utilized in different quantities in various reef zones (Table 7). Algae are mainly browsed on the boulder tract (33 %) and in lesser amount on the inner reef flat (17 %), the outer reef flat (13 %) and the inner reef slope (12 %). But filamentous and large fleshy algae are not grazed in the same proportions in all zones. Algal turf (filamentous and short algae) growing on dead corals is mainly grazed on the outer reef flat, the boulder tract, the inner reef flat and in seagrass beds where epiphytic algae are numerous. On the contrary, large fleshy algae are browsed on the lower coral flagstone and the reef slopes. Sessile invertebrates like sponges, coelenterates and ascidians are browsed in the spur and groove zone and on the inner slope (Table 7). Polychaetes are mainly preyed upon on the inner flat (30 %), inner slope (24 %), boulder tract (14 %) and reef seagrass beds (12 %). Molluscs, especially shelled gastropods, are consumed in greater quantities in calm areas: inner slope (28 %), reef seagrass beds (18 %), littoral seagrass beds (14 %) and inner reef flat (13 %). Nudibranchs are eaten more on the seagrass beds and inner reef flat, amphineura on the boulder tract, pelecypods on the inner reef flat and spur and groove zone, cephalopods on the inner reef flat. Molluscs come

Table 7
Variations of the consumption of each of the main food organisms in the various reef zones (percentages of the total weight of each food type).
Variation de la consommation des principaux groupes de proies dans les différentes zones du récif (pourcentages par rapport au poids total de chaque type de proie).

	Lower coral flagstone % W	Spur and groove system % W	Outer reef flat % W	Boulder tract % W	Inner reef flat % W	Reef seagrass beds % W	Inner reef slope % W	Littoral seagrass beds % W
Algae + seagrasses	3.7	8.7	12.5	33.4	17.4	8.2	12.2	3.9
Sponges	3.9	37.2	+	0.1	4.0	0.1	54.7	–
Corals	3.5	60.6	3.9	0.4	5.2	0.4	25.9	–
Polychaetes	4.6	5.4	8.7	14.3	29.5	12.0	24.0	1.5
Molluscs	2.3	12.2	4.0	8.9	12.6	17.9	28.3	13.8
Crustaceans	2.9	5.7	5.6	6.7	9.1	32.3	16.9	20.7
Echinoderms	1.0	27.2	1.1	10.9	40.2	2.6	17.0	+
Ascidians	5.3	67.2	3.7	2.2	4.5	8.6	3.9	4.5
Fishes	1.9([a])	0.6([a])	11.6	25.7	22.9	26.0	7.9	3.3

([a]) Broad underestimation due to the selectivity of sampling method.

mainly from sandy bottoms in protected areas and from hard substrates in windward biota.

About 70% of all crustaceans come from three biota: reef seagrass beds (32%), littoral seagrass beds (21%) and inner reef slope (17%). But the situation is a little different for each crustacean group. Calanoid copepods and crustacean larvae are mainly ingested on the reef slopes, stomatopods on seagrass beds and inner reef flat; galatheans from inner reef flat and hermit crabs from inner slope and boulder tract. Brachyurans are mainly caught on seagrass beds (47% from the reef, 25% from the littoral) and in lower quantities on the boulder tract (7%), the inner reef flat (6%) and the outer reef flat (6%). 40% of echinoids come from the inner reef flat, 27% from the spur and groove zone, 17% from the inner slope.

Most fishes were captured on the reef flat, but this does not reflect the reality because of the selectivity of the sampling methods. It is likely that, as in other reefs, fishes are caught in greatest quantities on the reef slope, more particularly in the spur and groove zone.

Predator-prey relationships

Close relationships, dependent on time and biota, exist between reef fishes and their prey. Davis and Birdsong (1973), Hobson (1974; 1975), Vivien and Peyrot-Clausade (1974), Hobson and Chess (1976; 1978), Robertson and Howard (1978) and Harmelin-Vivien (1979) studied some aspects of predator-prey relationships among reef fishes. Consumption of a prey by a predator is generally determined by its availability during the active period of the predator; but this is not a rule. Prey with permanent accessibility are generally caught during the day. Thus holo- and meroplankton are eaten essentially during the day by diurnal plankton feeders. In the same way, sessile or motile invertebrates which are always available at the surface of reef buildings or sandy bottoms are preyed upon by day for their greatest part. Motile invertebrates sheltered in sand or in reef crevices are caught during the day by fishes which exhibit behavioural or morphological adaptations to take them out of their cover. Prey which display changes in behaviour or habitat generally have different predators by day and by night, and then are more regularly used by fishes. Organisms which emerge at night from the reef are caught by nocturnal plankton feeders or by nocturnal benthic predators. Distribution and time and space variations of demersal reef zooplankton were studied by Porter and Porter (1977), Porter *et al.* (1977), Alldredge and King (1977), Sale *et al.* (1978).

Bakus (1964; 1966; 1969) concluded that the low number of sessile invertebrates available on the reef, corals expected, as well as defensive structures of many benthic organisms are the results of predation pressure from fishes. But Hobson (1974) pointed out that if "predation pressure lead to defensive adjustments in prey, these in turn stimulate further offensive modifications in predators".

Diversity and importance of prey in fish feeding

Consumption of prey by reef fishes varies in quality and quantity according to reef zone. To relate these variations to the diversity and importance of prey on the reef, we have first compared Shannon indices of diversity (H′) of benthic communities and fish feeding (Fig. 4). Diversity indices were calculated from data of Peyrot-Clausade (1977) and Peyrot-Clausade *et al.* (in press) for motile reef cryptofauna and from Thomassin (1978) for soft bottom communities. Shannon indices were also compared to the number of coral species given by Pichon (1978) for the various biota (Fig. 4). It appears that the diversity of fish feeding fluctuates in accordance with diversity of the various benthic communities. Specific diversity of benthic communities is maximum in the spur and groove zone, on the inner reef flat and inner reef slope, zones where consumption of prey by fishes is the most diversified. On the contrary, one or two kinds of prey are dominant on the outer reef flat, the boulder tract and the seagrass beds, zones where the specific diversity of benthic communities decreases. Then the diversity of fish feeding is adaptated to the diversity of reef communities.

Importance of prey in fish feeding was also compared to the biomass or number of reef invertebrates in the benthic communities on Tuléar reefs from the results of Peyrot-Clausade (1977) and Thomassin (1978). It was concluded that there is no direct proportionality between quantities

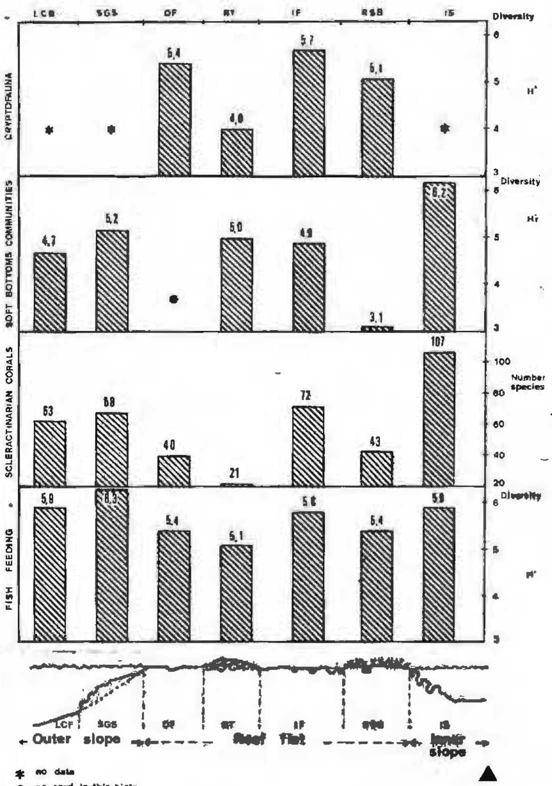

Figure 4
Relationships between diversity of prey in benthic communities and diversity of fish feeding in the various biota of the barrier reef in Tuléar (data from Pichon, 1978, for Scleractinians, from Thomassin, 1978, for soft bottoms communities and from Peyrot-Clausade, 1977, for the motile cryptofauna).

Relations entre la diversité des proies dans les communautés benthiques et la diversité de l'alimentation des poissons dans les principaux biotopes du Grand Récif de Tuléar (données tirées des travaux de Pichon, 1978, pour les Scléractiniaires, de Thomassin, 1978, pour les sédiments et de Peyrot-Clausade, 1977, pour la faune cavitaire vagile).

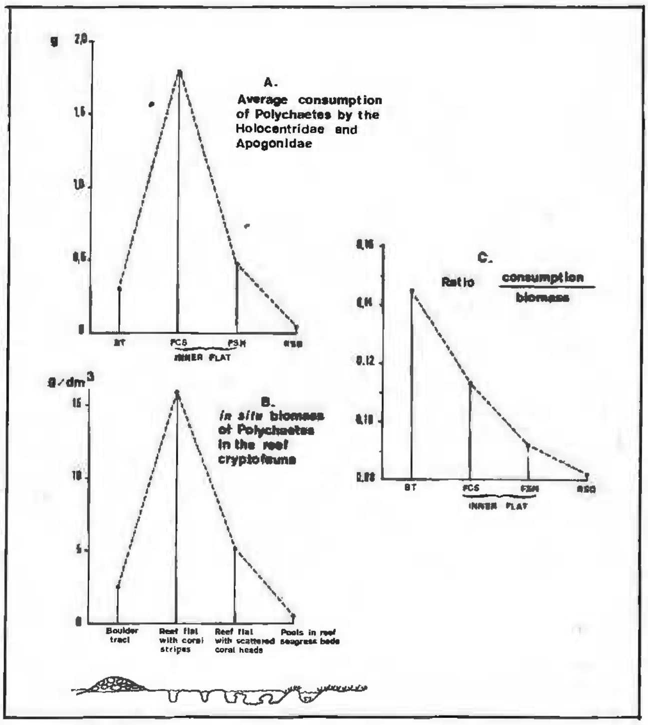

Figure 5
Relationships between in situ *biomass of Polychaetes of the reef cryptofauna (data from Peyrot-Clausade, 1977) and their consumption by Apogonid and Holocentrid reef fishes. The two values fluctuate in accordance but are not directly proportional as indicated by the variations of the ratio consumption/biomass.*
Relation entre la biomasse des Polychètes *in situ* dans les milieux cavitaires (données de Peyrot-Clausade, 1977) et leur consommation par deux familles de poissons, les Apogonidae et les Holocentridae. Ces deux grandeurs suivent les mêmes fluctuations, mais ne sont pas directement proportionnelles, comme l'indique le rapport consommation/biomasse.

of prey ingested by fishes and biomass of prey *in situ* (Harmelin-Vivien, 1979); but this biomass still influences the feeding of fishes. Vivien and Peyrot-Clausade (1974) and Harmelin-Vivien (1979) have shown that the weight of polychaetes ingested by Holocentridae and Apogonidae is maximum in biota where *in situ* biomass of polychaetes is the highest (Fig. 5). Consumption of prey by reef fishes fluctuates generally with the biomass of reef communities but is not directly proportional to it.

DISCUSSION AND CONCLUSION

Food webs of coral reef fishes

Coral reefs are the most complex marine ecosystem. Their trophic structure has been studied more particularly by Sargent and Austin (1954), Odum and Odum (1955), Hiatt and Strasburg (1960), Bakus (1969), Pérès and Picard (1969), Smith and Tyler (1972), Vivien (1973), Goldman and Talbot (1976). Lewis (1977) has made a good review of organic production on world coral reefs. The purpose of this paragraph is not to try to describe the food webs of a coral reef, but to discuss our actual knowledge on the role of reef fishes.

Primary and paraprimary production

Primary production on a coral reef is very high and diversified, but its various components are not equally utilized by reef fishes. Calcareous algae form the highest plant biomass of the reef. They aid coral cementation and are particularly well developed on outer reef flats but are browsed only incidentally by fishes. Randall (1961) and Bakus (1964; 1967; 1969) noticed the lack of large fleshy algae on reef flats except for the growth of coarse Phaeophyta like *Sargassum* and *Turbinaria* during summer. On Tuléar reefs large fleshy algae generally grow deeper on the lower coral flagstone. They form only 15 % of the total amount of algae browsed by reef fishes. The algal turf is composed of numerous short and filamentous algae, of blue-green algae and diatoms and grows on all rocks, rubble, dead corals, old shells, seagrasses, etc. This algal turf is the major food source for herbivorous fishes since it represents 85 % of the total weight of algae ingested. Wanders (1977) noticed its high turn over and its importance for herbivores. With exclusion experiments, Randall (1961), Bakus (1967), Earle (1972), Ogden (1976), Wanders (1977) and Ogden and Lobel (1978) proved that grazing by fishes and other large herbivores like sea urchins, is responsible for the low level of algal vegetation and Earle (1972) found that small invertebrates had no major grazing effect. They studied also the role of algae in fish feeding and the place of herbivorous fishes in reef communities.

Bacteria, detritus, organic flocs and dissolved organic matter play an important role in reef food webs which is not yet well defined or quantified (Lewis, 1977). Sorokin (1973; 1974) showed the importance of bacteria in the food webs of coral reefs by recycling dissolved or particulate organic matter. Since Marshall (1965; 1968) and Johannes (1967) numerous authors have studied composition, formation and transfer of particulate organic matter on the reef (Coles, Strathman, 1973;

Gerber, Marshall, 1974 *a*, *b*; Benson, Muscatine, 1974; Daumas, Thomassin, 1977; Benson *et al.*, 1978). Aggregates, the chemical composition of which varies with time (Daumas, Thomassin, 1977) are consumed by zooplankton (Gerber, Marshall, 1974 *a*, *b*) and plankton feeders like fishes (Johannes, 1967; Gerber, Marshall, 1974 *a*, *b*; Benson, Muscatine, 1974). A part of particulate organic matter would be trapped into reef cavities and soft bottoms and would be consumed by benthic organisms including fishes.

High trophic levels

Our actual knowledge of trophic relationships between primary and secondary producers and between predators of different trophic levels is still poor especially regarding relationships between invertebrates. A better knowledge is available about the trophic relationships of reef fishes (e. g. Hiatt, Strasburg, 1960; Talbot, 1960; Randall, Brock, 1960; Randall, 1967; Hobson, 1968; 1974; Jones, 1968; Vivien, 1973; 1975; Harmelin-Vivien, 1979).

The motile cryptofauna hidden in reef crevices reaches a very high biomass on Tuléar reef flats varying from 3 to 23 g/dm^3 (Peyrot-Clausade, 1977). Cryptofauna is used as an important food source by numerous reef fishes which live inside reef cavities or which possess morphological or behavioural adaptations to take organisms out of their cover. Part of the motile cryptofauna performs nycthemeral migrations; they emerge out of their shelters during the night and are then preyed upon by numerous nocturnal fishes. Studies carried out by Clausade (1970; 1971) and Peyrot-Clausade (1974; 1977) in Tuléar coral reefs and by Hutchings (1974) on the Great Barrier Reef pointed out the abundance and diversity of motile cryptic invertebrates, but data on their feeding behaviour are still lacking. In spite of a few studies on some invertebrate families like those on Molluscs by Kohn (1971; 1975) and Kohn and Nybakken (1975) rather few data are available on trophic relationships of reef invertebrates (review by Thomassin, 1976; 1978).

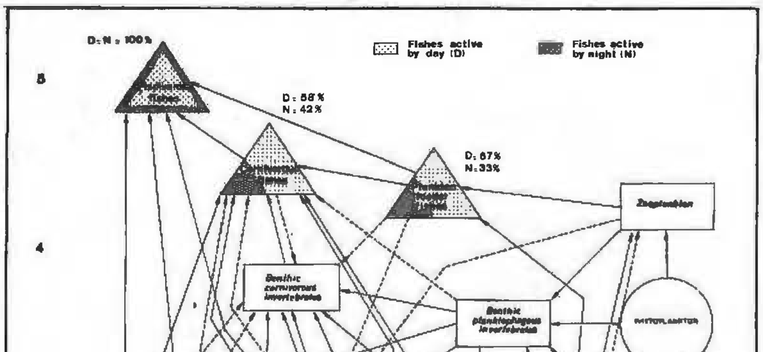

Figure 6

Schematic representation of trophic food webs of a coral reef pointing out the different actions of fishes according to their activity rhythms on the various trophic levels.

Schématisation des réseaux trophiques d'un récif corallien montrant l'aspect dynamique du rôle des poissons sur les différents niveaux trophiques en fonction de leur rythme d'activité.

From the results of fish feeding analysis, a schematic representation of trophic food webs was attempted for the coral reefs of Tuléar (Fig. 6). In spite of its simplification, Figure 6 shows the complexity of trophic relationships occurring between reef organisms. At least five trophic levels can be distinguished, but most of predators of high trophic levels belong to more than one trophic level as Bakus (1969) concluded in his study.

Dynamics of reef food webs

Studies on ecological distribution of fishes in various reef zones and analysis of their feeding behaviours and activity rhythms allow us to consider the dynamic processes of food webs in the coral reefs of Tuléar which are simplified on Figure 6. Trophic relationships between reef organisms vary in quality and in quantity with biota and time.

The distribution of the various kinds of feeding behaviour occurring in reef fishes (Tables 4 and 5) and the variations in their food consumption across the reef (Fig. 3) reveal that, for each trophic level, the relative proportions of the various components differ with reef zone. This confirms that different food resources are used by reef ichthyofauna in different habitats as Goldman and Talbot (1976) recorded for One Tree Island. Biomass pyramids are also modified with biota but quantitative data on invertebrate distribution are still too scarce to obtain a comprehensive idea about the variations of all energy transfers in the various reef zones. The only data on trophic relationships of benthic invertebrates in Tuléar concerns the mollusc fauna on the boulder tracts (Thomassin, Galenon, 1977). On boulder tracts molluscs comprise an average of 78 % of herbivorous species, 17 % of predators on motile invertebrates, 3 % of browsers of sessile invertebrates and 1 % of suspension feeders. Thus relative proportions of various feeding categories may be really different among benthic invertebrates and fishes in the same area, since 27 % of herbivorous species, 26 % of omnivorous and 47 % of carnivorous species were recorded in the fish fauna of boulder tracts.

Various kinds of prey are diversely used by fishes during the day or during the night (Table 7). During the day plants represent 27 % of the total amount of food ingested by fishes, sessile invertebrates 17 %, motile invertebrates 39 % and fishes 17 %. During the night motile invertebrates form 79 % of the food of nocturnal predators and fishes 21 %. Quantitatively the weight of food ingested by fishes at night represents only 37 % of the total weight of food consumed by reef fishes, the weight ingested by day making 63 % (Fig. 7). Fishes, with the addition of motile invertebrates, which together compose the main part of high trophic levels are consumed in equal quantities by day and by night. They represent 35 % by

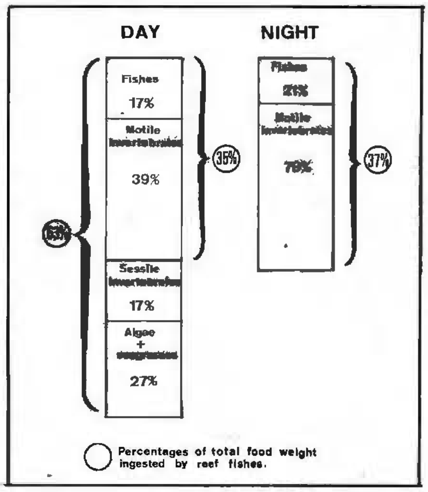

Figure 7

Consumption of the main trophic levels by reef fishes during the day and the night in Tuléar reefs. Low trophic levels are only consumed by day whereas high levels are used in same quantities by day and by night.

Consommation des principaux niveaux trophiques par les poissons le jour et la nuit dans les récifs de Tuléar. Les niveaux les plus bas ne sont consommés que le jour, tandis que les niveaux élevés sont utilisés en quantités équivalentes le jour et la nuit.

day and 37 % by night of the total weight of food of reef fishes. Higher trophic level consumption is therefore similar by day and night, but consumption of the lowest trophic levels stops during the night. The lowest trophic levels are exclusively consumed during the day, whereas the highest ones are used by reef fishes with similar efficiency by day as well as by night.

Contribution by fish to the gain and loss of energy by coral reefs

Oceanic waters surrounding coral reefs are well known for their low productivity. The high primary production of coral reefs, the transformation and recycling of detritus at the same place allow us to consider the reef as a self-sufficiency ecosystem. But a small part of its energy is removed from the surrounding oceanic waters. As suggested by Talbot (1965) and corroborated by Emery (1973) for Pomacentrid fishes, reef fish populations particularly plankton feeders on the outer slope take in part of their energy from oceanic plankton. Hobson and Chess (1978) demonstrated that diurnal plankton feeder fishes, preying upon holoplankton, are concentrated in areas subjected to constant water renewal. In Tuléar coral reefs, the highest densities of planktophagous fishes were effectively observed on the outer reef slopes (Table 5).

Loss of energy occurs in two different ways by reef fishes; by predation of adult reef fishes by large transient pelagic fishes, marine mammals or birds, and by loss of a large amount of eggs and larvae swept along off the reef by currents. Most of reef fish species possess pelagic larvae, even those laying benthic eggs. Some of these larvae stay on or return to the reef to replace adult fishes or to settle new areas, some are consumed on the reef and some enter the pelagic food chain (Sale, 1978). Analysis of stomach contents of pelagic fishes (Tester, Nakamura, 1958; Nakamura, 1965; Fourmanoir, 1969; 1971; Grandperrin, 1975) prove that larvae, post-larvae and juveniles of reef fishes may occupy a large place in the feeding of pelagic species. Grandperrin (1975) in his study on the trophic relationships of tunas found 58 % of reef species in the food of the Albacore (*Thunnus alalunga*) and 73 % in the diet of the Yellowfin tuna (*Thunnus albacares*). Thus low energy transfers nevertheless occur between coral reefs and surrounding waters.

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