THE DECAPOD REPTANTIA AND STOMATOPOD CRUSTACEANS OF

A TYPICAL HIGH ISLAND CORAL REEF COMPLEX IN FRENCH

POLYNESIA (TIAHURA, MOOREA ISLAND): ZONATION,

COMMUNITY COMPOSITION AND TROPHIC STRUCTURE

BY

MARIO MONTEFORTE

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Abstract :

In a typical High Island coral reef complex of French Polynesia (transect of Tiahura, Moorea Island, Society Archipelago), 73 species of decapod Reptantia and stomatopod crustaceans were collected. Over 9 stations localised along the transect, 3 different units of hard coral substrate of similar volume (about 17 litres each), were sampled at each station. The results are discussed from two aspects : the first shows that at least 50 carcinologic species occur within the cavitary biotopes ; 16 species (mainly Xanthid crabs), represent more than 90% of all collected individuals. Most of the dominant species are widely distributed along the transect (Chlorodiella barbata, Pilodius pugil, Liocarpilodes integerrimus, Galathea aculeata), and locally, some others are numerically important (Chlorodiella laevissima, Globopilumnus globosus, Daira perlata, Phymodius ungulatus, etc.). The second aspect concerns the repartition of species in the different biotopes in relation to their feeding habits. Based on the functional morphology of chelipeds, mouth-parts and gastric mill, and on gut content analysis, the species were placed into 5 MORPHO-LOGIC GROUPS : filter-suspension feeders, omnivores/herbivores, omnivores/carnivores, generalised omnivores and predators. The feeding habits and the distribution pattern of abundant species suggest that trophic and habitat partitioning may exist. The predominant species show either different nutritional modes, or inhabit different areas and/or biotopes. Distribution patterns of the morphologic groups in the different substrates are proposed, and schemes of interspecific relations are analysed.

INTRODUCTION.

In French Polynesia, studies concerning the carcino-logic fauna have essentially dealt with systematics and biogeography of the decapod Reptantia (Jacquinot & Lucas, 1853 ; Milne-Edwards, 1861-1904 ; Forest & Guinot, 1961, 1962 ; Seréne, 1972 ; Yaldwin, 1972 ; Griffin & Yaldwin, 1977). The few biological and ecological studies on these crustaceans are limited to commercial and edible species (Guinot, 1967 George, 1972, 1974), as well as to species associated to madreporian corals (Kropp & Birkeland,1981; Odinetz, 1983).

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The transect of Tiahura (Moorea Island), is a typical High Island coral reef complex (Salvat, et al., 1972). As such, many studies have been carried out there (Anonymous, 1977). However, the only ecological research on decapod crustaceans deals with species of the cryptofauna (Peyrot-Clausade, 1977b ; Monteforte, 1984a,b), the "petite faune" associated to algae (Naim, 1980a), and the crustaceans associated with pocilloporid corals (Odinetz, 1983).

In Tiahura, although crustaceans do not account for as large a number of species as molluscs and fishes, their relative abundance must not be underestimated : Odum & Odum (1955), and Hiatt & Strasburg (1960), pointed out that crustaceans represent a very important link in the energy transfer from producers and low-level consumers to higher consumers in coral reefs, and the larval input of these species to the water is also known to be very rich.

The importance of cavitary crustaceans in coral reefs has been studied by Garth (1974) and Peyrot-Clausade (1977a,b), but their trophic role within benthic communities is not well known. Feeding habits of crustaceans have been studied from morphologic and/or empirical observations (Orton, 1927 ; Nicol, 1932 ; Schafer, 1954 ; Ebling, et al., 1964 ; Muntz, et al., 1975 ; Warner, 1977 Zipser & Vermeij, 1978 ; Kunze & Anderson, 1979 ; Kropp, 1981 ; Rheinallt & Hughes, 1985 ; Rheinallt, 1986 ; Skilleter & Anderson, 1986). Works on trophic relations in nature are few and isolated ; most of them studied the crustaceans associated with sabellariid reefs (Rivosecchi, 1967 in Italy; Fausto-Filho & Furtado, 1970 in Brasil ; Gruet, 1970, 1971 in the North of France ; Gore, et al., 1978 in Florida). For French Polynesia, our work is the first approach to this subject. We have studied the distribution of crustacean species in the reef of Tiahura (Moorea Island) in relation to their different feeding habits. Species include those strictly inhabiting the hard substrates (living and dead corals), and other species either facultatively inhabiting these substrates or endogenous to sand substrates.

THE STUDY AREA.

The transect of Tiahura is located at the Northwest coast of Moorea Island (Fig. 1A). This area, "a typical High-Island coral reef complex" (Salvat, et al., 1972), is divided into three sections (Fig. 1B). From the beach towards the reef front (800 m long), these are :
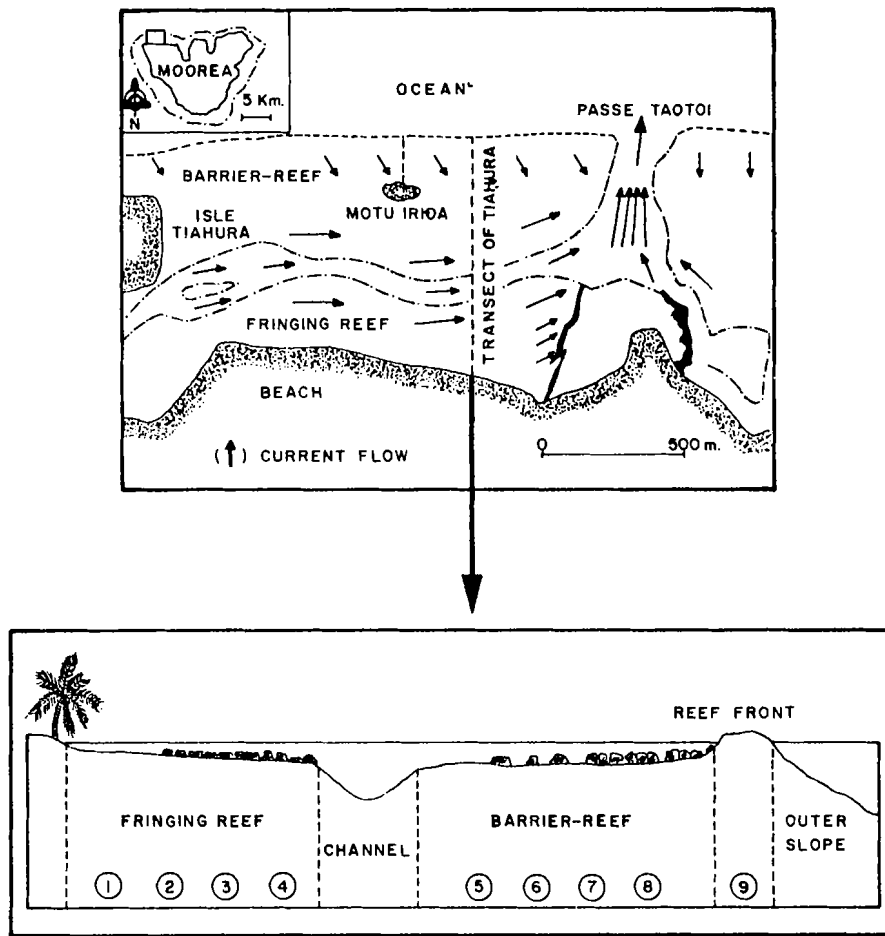
Fig. 1.- Localization of the study area.-

    1A : Position of the transect of Tiahura in Moorea Island and general aspect of the area.

    1B : Distribution of the sampling stations along the transect of Tiahura.

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- the fringing reef (250 m long and 0.20 m to 0.50 m average depth, and 2 m on the channel margin).
- the channel (50 m long, 10 to 13 m depth).
- the barrier-reef (500 m long, 1.5 to 2.50 m depth near the channel, and 0.50 m depth around the reef front).

A) The Fringing Reef.

Soft substrates (sand sediments) and debris are dominant in the fringing reef. Towards the channel, living coral colonies become abundant (Psammocora, Synarea), and they form huge coral heads at the margins of the channel (Fig. 2).

Hard substrates are mainly represented by Psammocora, Pavona cactus and Synarea, and dead coral colonies, which here cover a larger area than living corals. Dead coral provides an optimum environment for algal colonization : algae cover a large proportion of the fringing reef in Tiahura (Fig. 2).

B) The Channel.

The bottom of this channel is constituted almost totally of sand sediments (Fig. 2). This zone is under the constant influence of a strong current flowing parallel to the coast (Fig. 1A). The only benthic species inhabiting it are endogenous (Conus spp., polychaetes, Thallassinidae).

C) The Barrier-reef.

Scattered coral heads are situated on the outer margins of the channel. Towards the reef front, there is a gradual increase of coral colonies. Living coral colonies are more abundant than in the fringing reef, therefore algal colonisation is less here than in the former reef section (Fig. 2). Pavona cactus, Montipora, Porites and Acropora are well represented.

The reef front is constituted by a ridge of calcareous algae which, together with encrusting corals, provides a well developed cavitary biotope thoroughly colonized by the cryptofauna.

MATERIALS AND METHODS.

Nine stations were established along the transect of Tiahura (Fig. 1B). A total of 50 liters of hard substrate was sampled by SCUBA diving at each station, 1/3 of which was composed by dead corals and the other 2/3 of living
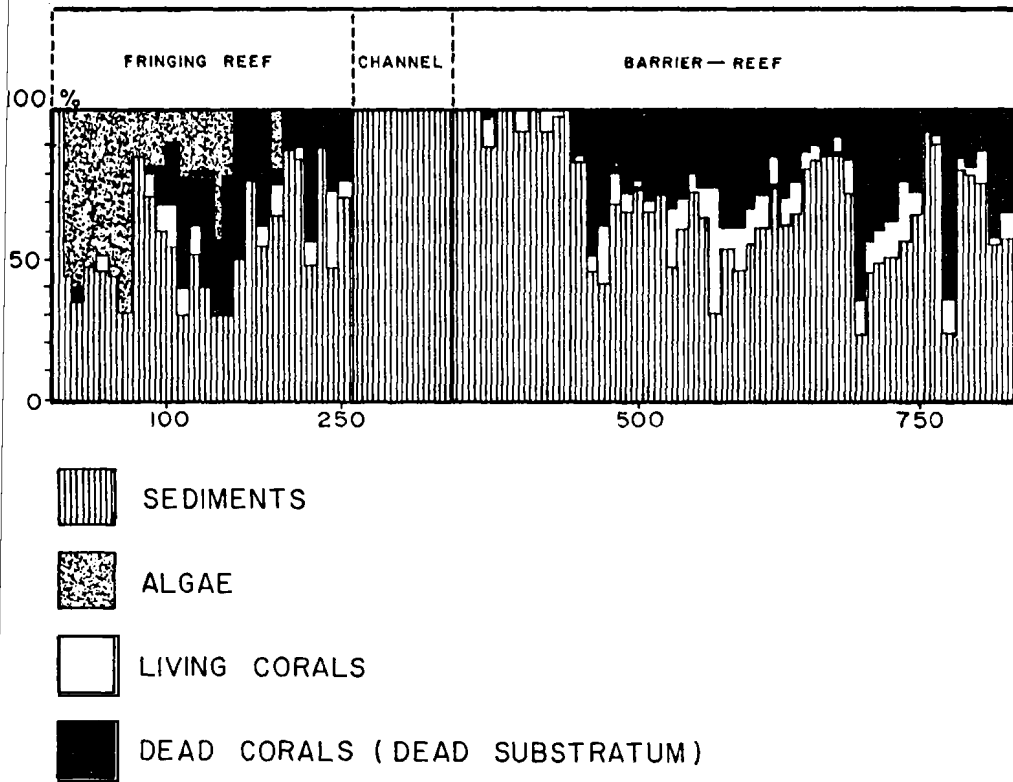
Fig. 2.- Distribution and relative covering area of the principal
types of biotopes in the transect of Tiahura.

corals.

The coral colony (dead or alive) to be sampled was selected by its size (all units sampled were similar in volume), its architecture (relatively regular geometric shapes and presence of a complex cavitary network), and its representativeness in the sampling station.

On the fringing reef, dead substrate and living coral colonies of Pavona cactus and Psammocora were sampled at each station. On the barrier-reef, dead substrate and living coral colonies of Pavona cactus, Montipora and Porites were taken.

The selected colony was covered in situ with a plastic bag (25x35 cm) in order to avoid the escape of the cavitary fauna. The colony was then detached from the substrate and the bag was closed immediately. The area around was surveyed, and some large and/or non-strictly cavitary species were captured by hand and also counted. However, the abundance of these species may have been underestimated, either because of difficulty in localizing the individuals (endogenous species), their facility to escape (swimming crabs), or their habit of forming aggregates (pagurid crabs : Ball, 1950 ; Ball & Haig, 1974 ; Hazlett, 1974).

Large-sized nocturnal species (very rare), those captured at the outer slope, and large semi terrestrial species (Coenobita perlatus and Cardisoma carnifex, both very abundant), were not included in the counts.

Determination of the feeding habits of the crustacean fauna in this study was based upon observation of the functional morphology of chelipeds, mouth-parts and gastric mill. Gut content analyses were also accomplished, but they were merely qualitative because of the small size of most of the individuals (< 20 mm width), and the deficient state of conservation of the collection after 3 months of storage and transport (Polynesia-Paris). Nevertheless, the information thus obtained was very useful for defining 5 MORPHOLOGIC GROUPS of species, related to their alimentary preferences.

RESULTS.

A) Specific Richness.

A total of 73 species of decapod Reptantia and stomatopod crustaceans was identified at the transect of Tiahura, xanthid crabs being largely dominant (Tab. 1). Compared with a total of 140 species collected during our

whole mission in French Polynesia (Moorea, Tahiti, Taka-
poto, Makatea and Mataiva), the observed specific rich-
ness of Tiahura was quite high : 52% of total collected
species, 18% of which were "endemic". This comparison
seems to confirm the representativeness of the transect
of Tiahura as a typical High Island coral reef complex
(Salvat, et al., 1972 ; Monteforte, 1984a,b).

Twenty-eight species were collected on the fringing
reef, 10 on the barrier-reef, 19 on the reef front (some
of them appeared also on the outer slope), and 16 species
were founded both on the fringing reef and the barrier-
reef. Several of these last were numerically dominant
along the transect.

B) Qualitative Distribution and Relative Abundance.

A total of 2500 individuals was captured in the
transect of Tiahura, hand captures included (Tab. 1).
Four species accounted for more than 75% of the total :
Chlorodiella barbata, Pilodius pugil, Galathea aculeata
and Liocarpilodes integerrimus. These, with 12 additional
species, accounted for about 95% of the total collected
individuals. The 16 speciescharacterize the carcinologic
fauna of Tiahura (Peyrot-Clausade, 1977b ; Monteforte,
1984a,b). The most numerically important of these species
are Chlorodiella laevissima (barrier-reef), Liomera bella
(wide distribution), Phymodius ungulatus (fringing reef),
Actaea cavipes (wide distribution), Chlorodiella cytherea
(wide distribution)(Fig. 3).

The 4 dominant species over the transect are widely
distributed, except on the reef front (Fig. 3). In fact,
the 12 species following in abundance are those that
primarily define the differences between the crustacean
communities of the fringing reef, the barrier-reef, and
the reef front. This last area presents a characteristic
arrangement of species, some of them appearing not very
far back towards the lagoon area of the transect, but
oftenly to 6 m depth on the outer slope.

C) The Feeding Habits.

Decapod crustaceans are primary and secondary consu-
mers : filter-suspension feeders, omnivores and preda-
tors. The limits of these divisions are not well defined
because of the various feeding habits (Gordon, 1964 ;
Warner, 1977). However, the functional morphology of
alimentary body structures has a close relationship with
the kind of food utilized by the species and feeding
behaviour (Dahl, 1952 ; Schafer, 1954 ; Bovbjerg, 1960 ;
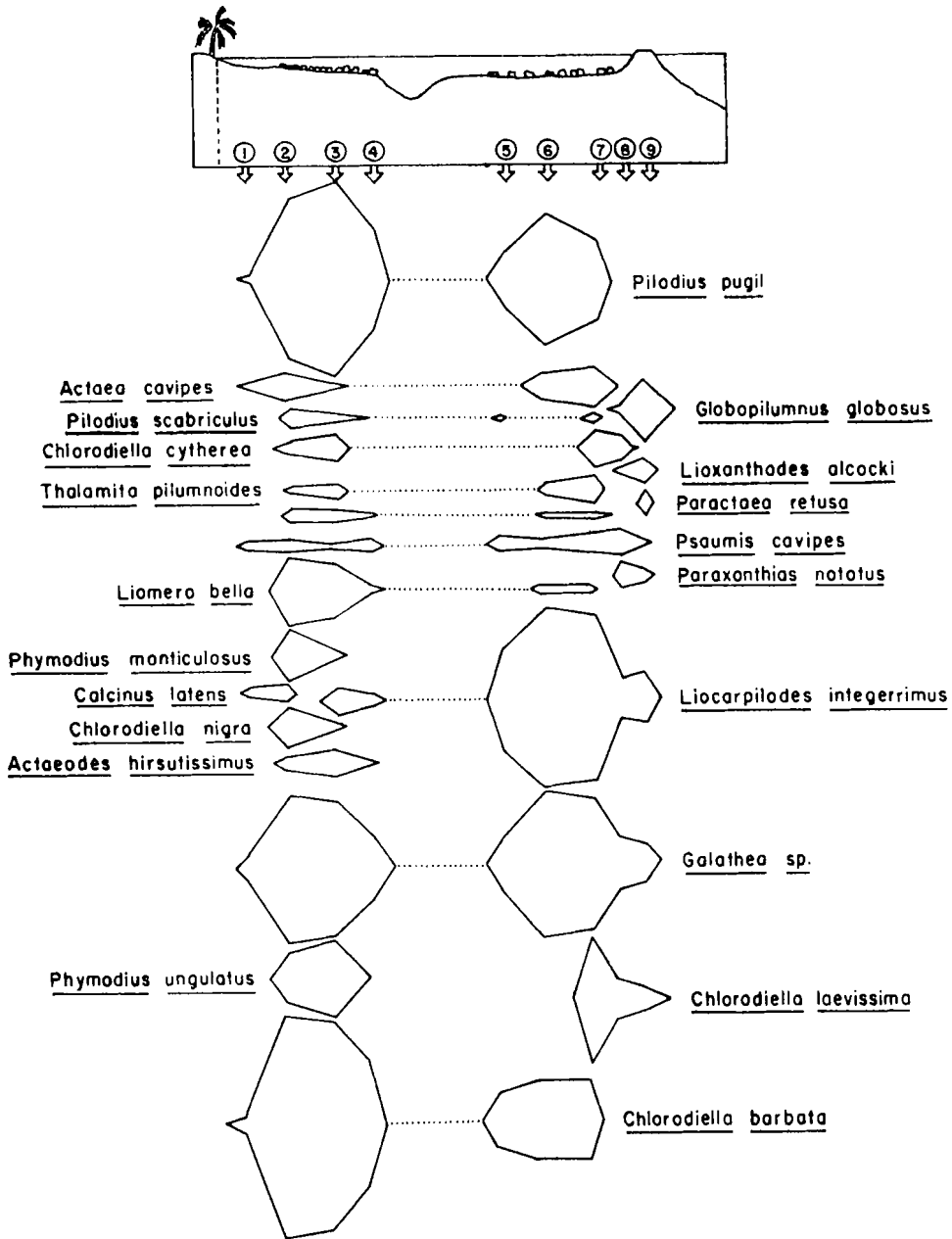Bakus, 1975 ; Caine, 1975 ; Warner, 1977). Observation of

Tab.   1.- List   of decapod Reptantia and stomatopod
       species: Numerical abundance of individuals
       collected in each station at the transect of
       Tiahura (Moorea).
       OSL : Outer Slope.
       TOT : Total transect.

SPECIES	1	2	3	4	5	6	7	8	9	OSL	TOT
STOMATOPODA											
Gonodactylus espinosus		7	6	4		3	3	2			25
Gonodactylus viridis		2	2	2	2	3	2	2			15
PAGURIDAE											
Aniculus aniculus										5	5
Calcinus gaimardi									1		1
Calcinus laevimanus	3	9									12
Calcinus latens	6	12									18
Calcinus sp.1		2									2
Calcinus sp.2		1	1								2
Calcinus sp.3				1							
Dardanus gemmatus			1						1		2
Dardanus lagopodes							1		1		2
Pagurixus sp.									1		1
Trizopagurus strigatus									1	1	2
GALATHEIDAE											
Galathea aculeata	13	79	53	24	22	77	54	18	13		353
PORCELLANIDAE											
Petrolisthes sp.1	1	1									2
Petrolisthes sp.2		2									2
Petrolisthes sp.3							2				2
Petrolishtes sp.4										3	3
Petrolisthes sp.5								1			1
Petrolisthes sp.6								1			1
Petrolisthes sp.7								1			1
Pachycheles sp.										2	2
HIPPIDAE											
Hippa sp.	2										2
CALAPPIDAE											
Calappa hepatica		2	3	2							8
PORTUNIDAE											
Carupa tenuipes										12	12
Portunus granulatus			3								3
Thalamita admete		3	3	1		1	2	4			14
Thalamita crenata		1	3	1	1	2	2	1			11
Thalamita pilumnoides		1	4			6	9				20
XANTHIDAE											
Actaea cavipes	1	8	2			9	14	1			35
Actaea sp.		1	2	1							4
Actaeodes hirsutissima		6	10	3							19
Atergatis floridus		6	11								17

Tab. 1 (cont.).

SPECIES	STATIONS 1	2	3	4	5	6	7	8	9	OSL	TOT
Atergatopsis cf. germaini								1			1
Chlorodiella barbata	4	232	196	54	20	28	30		1		564
Chlorodiella cytherea		5	8				13	8			34
Chlorodiella laevissima							61	14	12	5	92
Chlorodiella nigra		13	7								20
Daira perlata								10	6	5	18
Etisus anaglyptus									1	1	2
Etisus dentatus			3	1							4
Euxanthus exsculptus										1	1
Globopilumnus globosus								2	28	5	35
Lachnopodus bidentatus								1	3		4
Lachnopodus subacutus								1	2		3
Leptodius sanguineus	2	5									7
Liocarpilodes integerrimus			9	5	38	135	123	15	21		346
Liomera bella		24	20	7		2	2				55
Liomera rubra							1				1
Liomera rugata		1	1				1				3
Lioxanthodes alcocki								5	18		23
Lophozymus edwardsii									1	1	2
Lophozymus dodone			2								2
Lophozymus glaber							3				3
Lybia tesselata		1									1
Medaeus noelensis								3	3	2	8
Paractaea retusa									10		10
Paraxanthias notatus								15	6		21
Phymodius monticulosus		18	9								27
Phymodius nitidus									12	1	13
Phymodius ungulatus		20	28	1							49
Pilodius pugil	2	96	162	41	22	67	32				422
Pilodius scabriculus		9	3	2	2		5	2			23
Pilumnus sp.1							2				2
Psaumis cavipes	2	3	1	4	4	2	2	6	8	1	31
Pseudoliomera variolosa									2		2
Xanthias lamarcki		9	2		1	6	1	1			20
Xanthias latifrons										6	6
GRAPSIDAE											
Pachygrapsus minutus	3	5									8
Pachygrapsus plicatus	2										2

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Fig. 3.- Zonation and relative abundance of the principal
Decapod Reptantia collected in the transect of
Tiahura (only species collected in hard substrates).

these structures was a criterion for placement of a
particular specie into one or another of the 5 MORPHOLO-
GIC GROUPS defined in our study. Other criteria were : in
situ observations, gut content analysis, and other stu-
dies on morphologically similar species. The groups are:
filter-suspension or direct bottom-deposit feeders, omni-
vores/herbivores, omnivores/carnivores, generalized omni-
vores and predators.

C.1) Filter-suspension or Direct Bottom-deposit
     Feeders.

Species of this group belong essentially to the fami-
lies Galatheidae (Galathea aculeata) and Porcellanidae
(Petrolisthes spp.), which agrees with other principal
works (Nicol, 1932 ; Knudsen, 1964 ; Caine, 1975 ; Gore,
et al., 1978 ; Kropp, 1981).

These species show flat and slender chelipeds. The
fingers are long and acute with their internal margins
often finely dentate. On the ventral surface of the fixed
fingers there is a row of fine sharp-pointed spines which
sometimes serve actively when the animal obtains food by
rasping the substrate (Nicol, 1932 ; Caine, 1975).

The 3rd. pair of maxillipeds is very important. These
are extremely mobile structures bearing long and relati-
vely stiff setae at their distal margin which function as
a net to trap suspended particles or to sweep the bottom
directly (Fig. 4). These setae are cleaned by the 2nd.
and 1st. pair of maxillipeds which then bring the food to
the mouth (Nicol, 1932 ; Kropp, 1981).

At the interior of the endostome there is a pair of
well-calcified mandibles. In Galathea aculeata and Petro-
listhes spp. collected at Tiahura, teeth with finely
tuberculated surfaces were observed on these mandibles.
The structure of the gastric mill, although difficult to
appreciate, seems to show finely dentate masticatory
ossicles with soft setae at their margins. These features
are commonly found in species feeding upon small and
rather soft particles (Caine, 1975). In addition, these
individuals are very small (Galathea aculeata : 5 to 7 mm
total length, and Petrolisthes spp. <5 mm width), which
suggests that their food consists of such fine material
as plankton, phytobenthos, larval forms and detritus.
Unfortunately, identification of gut contents was not
possible, so the degree of alimentary selectivity for
these species is unknown to us.

Eight species of this morphologic group were found at
Tiahura, accounting for 17% of total individuals in the
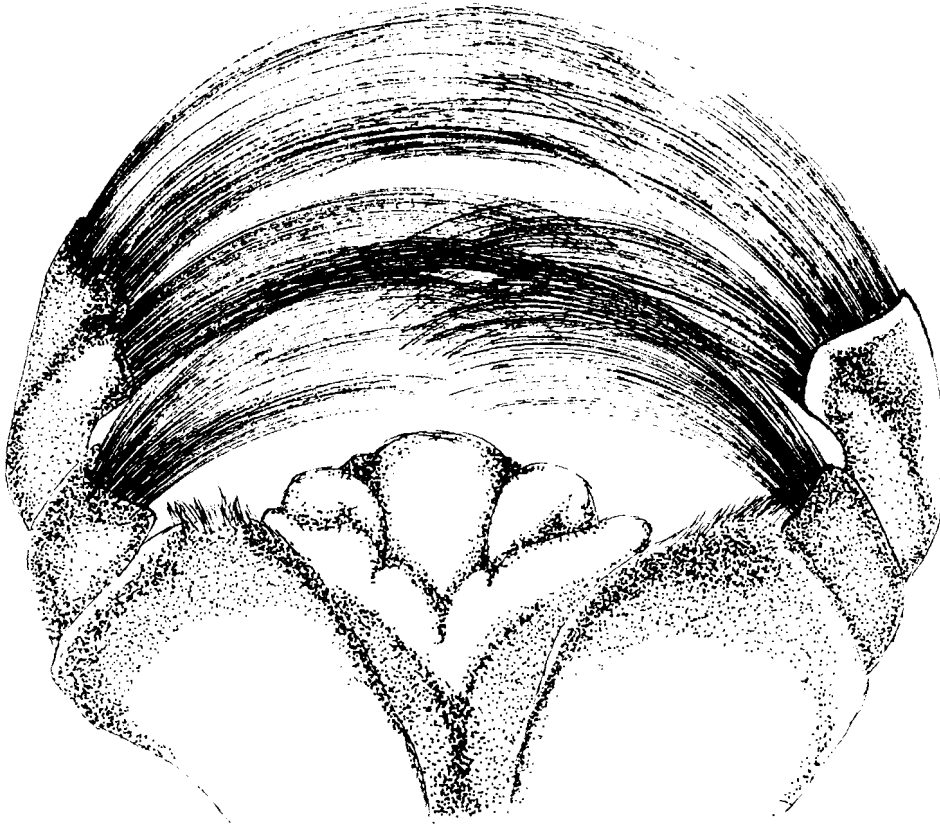
Fig. 4.- Group of filter-suspension or direct bottom-
         deposit feeders : 3rd. pair of maxillipeds of
         Petrolisthes sp. (ventral view).

transect (Tab. 2). One species was largely dominant, Galathea aculeata, which represents about 15% ; the other 2% was shared among 7 species of Petrolisthes.

On the fringing reef, filter-suspension feeders re-presented 13% of total individuals. On the barrier-reef, this group was comparatively more important : 25% of total individuals (Tab. 2).

C.2) Omnivorous Species.

These species are able to exploit a large biotope, their alimentary resources being very diversified : al-gae, small cavitary species as polychaetes, sponges, echinoderms, molluscs, other crustaceans, as well as disintegrated organic material and carrion.

The morphology of chelipeds is one of the principal bases utilized to classify the omnivorous species, al-though the morphology of the gastric mill, size of spe-cies and gut contents are also registered. Some main features of the chelipeds are relevant :

1) Chelipeds are more or less voluminous, straight or somewhat concave.
2) Internal margins of fingers :
   - with cutting edges.
   - with tuberculate surfaces (dentiform processes).
3) The claws, once closed :
   - leave a wide space between fingers (non-joined claws).
   - close almost perfectly (joined claws).
4) The fingertips are :
   - pointed or slightly blunt.
   - excavated as a well-defined hoof.

These characteristics are not present separately in a particular species, but oftenly occur in combination. There are species having similar chelipeds in size and form (homochelia), or species with different chelipeds (heterochelia). The morphology of dentary surfaces may also be similar in both chelipeds (homodontia), or diffe-rent (heterodontia) (Schafer, 1954).

From the distribution of these morphologic characte-ristics in a particular species, it was possible to deduce habitual food type very closely, and the methods utilized to obtain it. Upon the bases of these observa-tions, 3 MORPHOLOGIC GROUPS of omnivorous species were constituted : omnivores/herbivores, omnivores/carnivores, and generalized omnivores. We must recall that these divisions are not strict : a single species showing wide

distribution in the transect could present more generali-
sed or more restricted feeding habits depending on the
resources available, the biological cycle (of the species
itself or of the organisms composing its food resource),
or on the presence of a competitor (Gore, et al., 1978).

C.2.1) Omnivores/herbivores.

Species representing this group are Chlorodiella
barbata, C.nigra, C.cytherea, C.laevissima, Phymodius
ungulatus, P.monticulosus, Pilodius pugil, P.scabriculus
and Lioxanthodes alcocki.

The chelipeds of these species are rather straight
and not very massive. Fingers are slender and eventually
show 2 or 3 well-developed molariform teeth at their
inner margins, but the rest of the dentary surfaces are
smooth. The claws are non-joined. The fingertips are
excavated forming a hoof-like structure, generally well
defined (Fig. 5). This lastcharacteristic is commonly
found in crabs having preferentially herbivorous feeding
habits (Crane, 1947; Knudsen, 1960, 1964; Griffin, 1971 ;
Warner, 1977). It is in fact a structure very well adap-
ted to cut out laminar pieces from algae (Forest, pers.
comm., 1984 pers.obs.), or to spoon encrusting material
from the substrate (Skilleter & Anderson, 1986).

Homochelia is common in some species (Chlorodiella
spp., Phymodius spp.), but sometimes a slight heteroche-
lia is present (Pilodius spp., Lioxanthodes alcocki).
Homodontia is also common in this group.

The particular structure of the gastric mill (finely
tuberculate masticatory surfaces, blunt ossicles with
abundant setae), suggests that these species utilize food
particles not requiring extensive grinding. Moreover, in
the gut contents there were apparently no fragments of
mollusc shells, but algal material seemed to predominate.
The size of these species is small, rarely over 10 mm
width.

A total of 17 species of the transect of Tiahura were
included in this assemblage, or 24% of total species
richness. The relative abundance of this group was about
59% of total individuals in the transect ; it was the
dominant group, where Chlorodiella barbata and Pilodius
pugil accounted for more than 35%.

In the fringing reef, 11 species represented 74% of
total individuals in this sector. C.barbata and P.pugil
were the dominant species, but there was also an abundant
group of species such as Chlorodiella nigra, Phymodius

Fig. 5.- Group of omnivore/herbivore species : Right cheliped of Chlorodiella nigra (Xanthidae). Non-joined claw with hoofed fingertips.

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unqulatus, Phymodius nitidus, Pilodius scabriculus, etc.
(Fig. 3, Tab. 2).

For the reef flat of the barrier-reef, C.barbata and
P.pugil were still abundant, being gradually replaced
towards the reef front by Chlorodiella laevissima which
then became one of the dominant species. In total for the
barrier-reef, 17 species of this group accounted for 38%
of total individuals.

C.2.2) Omnivores/carnivores.

The chelipeds of species included in this group are
generally massive and straight, although they may be
slightly concave in some small-sized species (Liomera
spp., Psaumis cavipes, Xanthias lamarcki). The fingers
are short and quite strong, bearing tuberculate, cutting,
or tuberculate-cutting dentary surfaces, generally well-
developed. The fingertips are pointed or lightly rounded.
The claws are joined (Fig. 6). Homochelia and homodontia
are common (Xanthias lamarcki, Liomera spp., Actaeodes
hirsutissima, Psaumis cavipes, Daira perlata). Ill-marked
heterochelia also exists (Leptodius sanguineus), but when
differences exist, these are very evident (Pilumnus spp.,
Paraxanthias notatus, Globopilumnus globosus, Liocarpilo-
des integerrimus). This combination of structures, and
mainly the presence of protuberant teeth over the inter-
nal margins of fingers, characterize the crabs having a
preferentially carnivorous alimentary regime (Schafer,
1954 ; Knudsen, 1964 ; Vermeij, 1977a ; Warner, 1977 ;
Zipser & Vermeij, 1978).

Polychaetes and small molluscs surely constitute a
very important part of their diet, as shown by the gut
content analysis in which fragments of shells, opercules
and mandibules of polychaetes were often found. The stru-
cture of chelipeds and fingers is efficient for the
manipulation of hard and voluminous objects and for tea-
ring off soft tissues from shells (Warner, 1977 ; Skille-
ter & Anderson, 1986). The gastric mill is much more
massive than in that of herbivorous species, having the
masticatory ossicles edged with fine but sharp spines,
well-developed grinding surfaces, and few setae.

There were 28 species of this group in Tiahura, or
39% of total species richness. Their relative abundance
was estimated in 18% of total individuals.

In the fringing reef, 13 species composed 7% of total
individuals, where Liomera bella and Actaeodes hirsutis-
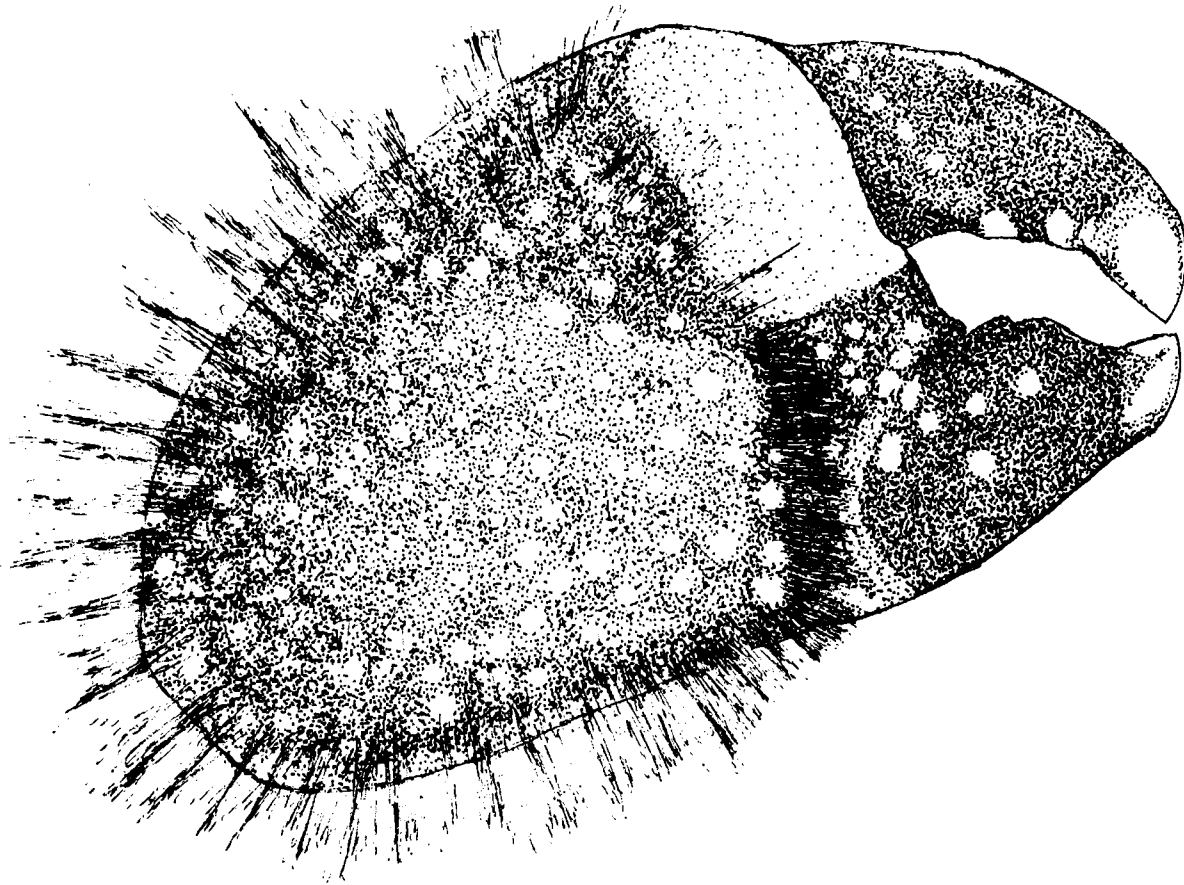sima accounted for 5%).

Fig. 6.- Group of carnivore/herbivore species : Right cheliped
of Globopilumnus globosus (Xanthidae), a facultative
malacophage crab.

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For the barrier-reef, 21 species were proportionally more important : 33% of total individuals in this sector. Liocarpilodes integerrimus were numerically dominant within this group (25% of total individual for the barrier-reef). However, this species was gradually replaced by a group of abundant omnivore/carnivore species towards the reef front (Globopilumnus globosus, Paraxanthias notatus, Daira perlata).

C.2.3) Generalized Omnivores.

Several authors consider as generalized omnivores the crabs of the family Grapsidae (Bacon, 1971 ; Griffin, 1971 ; Gore, et al., 1978), and those of the superfamily Paguridea (Orton,1927 ; Samuelson, 1970 ; Hazlett, 1974 ; Caine, 1975). However, some species may behave as predators (Vermeij, 1978), or even as corallivores (Glynn & Stewart, 1972 ; Glynn, 1973).

In the Grapsid species collected at Tiahura (Pachygrapsus minutus, P.plicatus, both being small-sized of some 5 mm width), the chelipeds are small and straight. The internal margins of fingers show cutting or finely serrated surfaces without prominent molariform tubercules. The fingertips are pointed. Heterochelia and heterodontia are weakly pronounced, the chelipeds being relatively similar. The claws are joined (space between fingers is narrow).

Concerning the pagurid crabs, their chelipeds have two functions : they are auxiliary in the alimentary activities, and play the role of an opercle for species inhabiting gastropod shells. Heterochelia and heterodontia are therefore strongly pronounced. However, although the structure of fingers is adapted to this living style, their internal margins do not bear protuberant tubercles, these surfaces being for cutting or finely serrated.

The food resources of generalized omnivore species are very diversified. They can actually use all kinds of detritus and organic debris, carrion, urban residues, etc., and although this morphologic group was represented at Tiahura by 11 species (15% of total species richness), numerically, they were very few (2% of total individuals in the transect). On the fringing reef this group comprises 3% of individuals. Pachygrapsus minutus (Grapsidae) and Calcinus latens (Paguridae) were practically the only numerically important species. In the barrier-reef this group was absent.

C.3) Predacious/carnivores.

Some omnivore/carnivore species may be able to behave as predacious, provided that they have a large adult size (over 30 mm width), massive subequal claws with sharp-pointed fingers, well developed molariform teeth on the internal margin of fingers, and the presence of a parti-culary prominent tooth situated in proximal position over the dactylus, generally on the major cheliped. These caracteristics distinguish the predacious malacophage crabs (Schafer, 1954 ; Crane, 1947 ; Reynolds & Rey-nolds, 1977 ; Vermeij, 1977 ; Warner, 1977).

Other well-known predacious species are the Portuni-dae (Schafer, 1954 ; Muntz, et al., 1965 ; Ropes, 1968 ; Hamilton, 1976 ; Warner, 1977 ; Rehinallt, 1985, 1986), the Calappidae (Shoup, 1968 ; Warner, 1977 ; Vermeij, 1978), and the stomatopods (Burrows, 1969 ; Caldwell & Dingle, 1975). These species are mainly specialized mala-cophages (Calappidae) and sometimes piscivores (portunids and stomatopods) (Figs. 7, 8).

Seven predacious species were considered in Tihaura (10% of total species). The omnivores/carnivores showing facultative predacious habits were not counted for this group.

Almost all of these species are widely distributed in the transect, except _Calappa hepatica_ (endogenous spe-cies, fringing reef), and _Carupa tenuipes_ (cavitary Por-tunidae of the reef front).

The total relative abundance of this group was esti-mated as 4%. For the fringing reef, 3% of total indivi-duals found in this sector belong to the present group ; for the barrier-reef they accounted for 5% of the indivi-duals of this sector. The most abundant species on both areas were _Gonodactylus viridis_ and _G.espinosus_, two cavitary stomatopods observed only in _Pavona cactus_ (High Islands) (Monteforte, 1984a).

Although the abundance of free-living species (_Thala-mita admete, T.crenata, Portunus granulatus_), and that of endogenous species (_Calappa hepatica_), may have been underestimated because of the various capture problems, it seems that predacious crabs play only an inferior role in the trophic network of a High Island reef complex. In this type of system, the higher trophic levels seem to be occupied mainly by carnivorous fishes which are much more efficient than crabs (Perès & Picard, 1969 ; Vivien & Peyrot-Clausade, 1974 ; Galzin, 1977b ; Harmelin-Vivien, 1981).

Fig. 7.- Group of predacious/carnivore species : Right cheliped
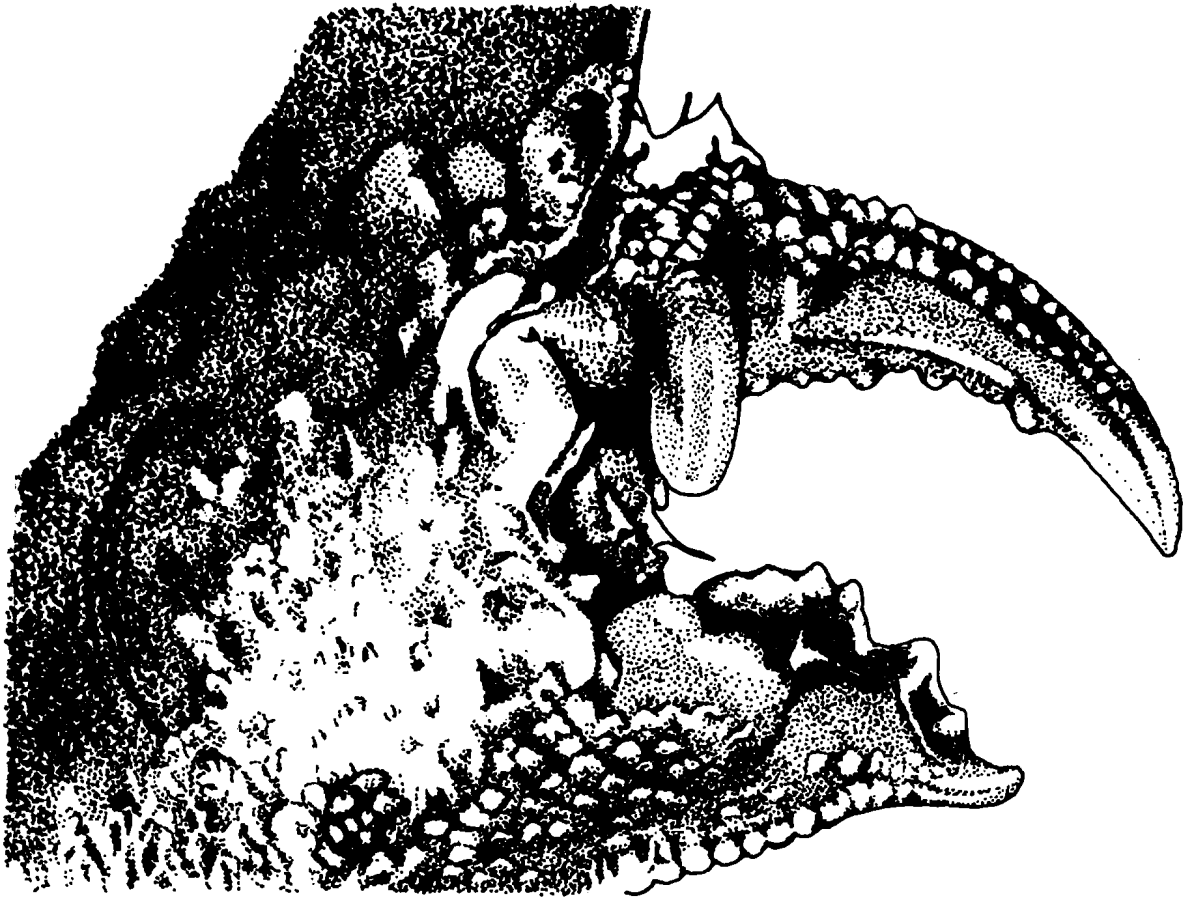of Thalamita admete (Portunidae). A fast-cutting chela
with the "malacophage tooth".

Fig. 8.- Group of predacious/carnivore species : Right (major) cheliped
of Calappa hepatica (Calappidae). A typical crushing chela of
a specialized malacophage crab.

Other alimentary habits important to mention are those represented by decapod crustaceans obligatorily associated with pocilloporid corals (Trapezia spp.) which are morphologically adapted to feed upon corallian mucus (Odinetz, 1983), by corallivorous pagurid crabs (Aniculus aniculus, Trizopagurus strigatus), and by pinnotherid crabs and the portunid Lissocarcinus orbicularis, respectively commensal with bivalves and holoturians.

D) Distribution of Morphologic Groups in the Substrates.

Living substrates seem to contain the majority (52%) of all collected individuals. However, each coral species is colonized differently. Pavona cactus and Psammocora are preferentially occupied (21% and 19% respectively, of total individuals), then Montipora (8%), and finally Porites (3%). Dead substrate is also highly colonized by cavitary crustaceans (44% of total individuals). The remaining 4% correspond to individuals captured by hand (Tab. 2, Fig. 9).

In pocilloporid corals, Odinetz (1983) found abundant populations of non-associated brachyuran and anomuran crustaceans. Comparing these data of abundance of non-associated crabs/volume of the coral colony with those of our study, Pocillopora and Psammocora seem to be similarly colonized by cavitary crustaceans. Nevertheless, Pavona cactus is the living coral colony that gathers the most abundant cavitary populations, which is a direct consequence of its architectural complexity.

D.1) The Fringing Reef.

The omnivore/herbivore species are dominant in all substrates (Tab. 2, Fig. 10). Within this group, Chlorodiella barbata (the dominant specie), shows affinities for dead substrates. On the contrary, Pilodius pugil (next in abundance), is more abundant in Psammocora.

Filter/suspension feeders (Galathea aculeata is the only numerically important one), show a light affinity for dead substrate (39% of total individuals of this group for the fringing reef) (Tab. 2, Fig. 10). The few exemples of Petrolisthes spp. were all collected in this substrate. Concerning the living colonies, Galathea aculeata showed noticeable preferences for Psammocora (34%), being less abundant in Pavona cactus (26%) (Fig. 10). It is possible that the swimming ability of this specie enables it to frequent the extracavitary biotopes so as to reduce the competition with corals and other benthic filter-feeders.
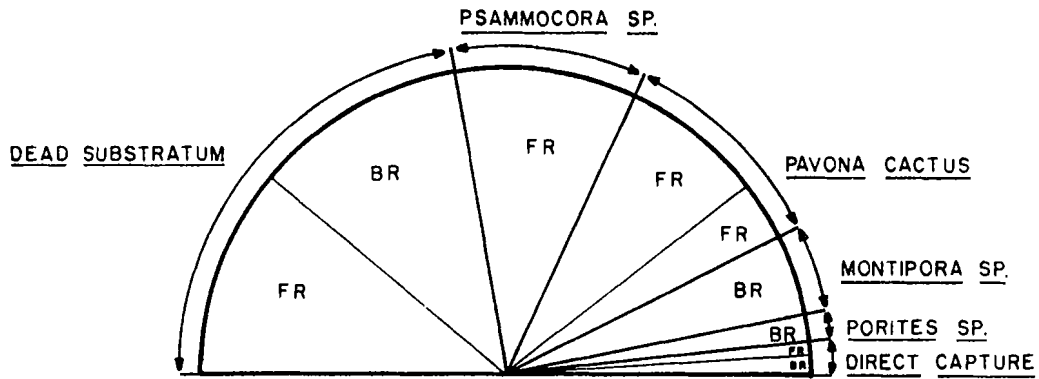
Fig. 9.- Relative abundance of individuals collected in
different substrates sampled in each sector of
the reef in Tiahura.

FR : Fringing reef.
BR : Barrier-reef.

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Tab. 2.- Relative abundance of morphologic groups in
different substrates sampled in each reef
sector of the transect of Tiahura (see Fig. 10
for reference).
FR : Fringing reef.
BR : Barrier-reef.
TT : Total transect.

MORPHOLOGIC GROUPS	SUBSTRATES	CAPTURES NUMERIC ABUNDANCE			RELATIVE ABUNDANCE OF INDIVIDUALS			RELATIVE ABUNDANCE OF MORPH. GROUPS		
		FR	BR	TT	FR	BR	TT	FR	BR	TT
FILTER-SUSPENSION	Dead subst.	71	132	203	4.9	12.5	8.1	39.2	50.6	45.9
	Psammocora	62		62	4.3		2.5	34.3		14.0
	P.cactus	48	42	90	3.3	4.0	3.6	26.5	16.1	20.4
	Montipora		65	65		6.2	2.6		24.9	14.7
	Porites		22	22		2.1	0.9		8.4	5.0
	TOTAL	181	261	442	12.5	24.8	17.6	40.9	59.0	100.-
OMNIVORES/HERBIV.	Dead subst.	388	212	600	26.7	20.1	23.9	36.0	53.7	40.7
	Psammocora	386		386	26.6		15.4	35.8		26.2
	P.cactus	303	57	360	20.9	5.4	14.3	28.1	14.4	24.4
	Montipora		105	105		10.0	4.2		26.6	7.1
	Porites		21	21		2.0	0.8		5.3	1.4
	TOTAL	1077	395	1472	74.2	37.5	58.8	73.2	26.8	100.-
OMNIVORES/CARNIV.	Dead subst.	31	224	255	2.1	21.3	10.2	29.0	64.7	56.3
	Psammocora	40		40	2.8		1.6	37.4		8.8
	P.cactus	36	51	87	2.5	4.8	3.5	33.6	14.7	19.2
	Montipora		40	40		3.8	1.6		11.5	8.8
	Porites		31	31		2.9	1.2		9.0	6.8
	TOTAL	107	346	453	7.4	32.8	18.1	23.6	76.4	100.-
GENER. OMNIVORES	Dead subst.	50		50	3.4		2.0	100.-		100.-
	Psammocora									
	P.cactus									
	Montipora									
	Porites									
	TOTAL	50		50	3.4		2.0	100.-		100.-
PREDACIOUS/CARNIV.	Dir. capt.	37	51	88	2.8	4.8	3.5			
	TOTAL	37	51	88	2.8	4.8	3.5	42.0	58.8	100.-
TOTAL FAUNA	Dead subst.	540	568	1108	37.2	53.9	44.2			
	Psammocora	488		488	33.6		19.5			
	P.cactus	387	150	537	26.6	14.2	21.4	(see Fig. 9)		
	Montipora		210	210		19.9	8.4			
	Porites		74	74		7.0	2.9			
	Dir. capt.	37	51	88	2.5	4.8	3.5			
	SUM. TOT.	1452	1053	2505	58.0	42.0	100.-			

The omnivore/carnivore species are weakly represented in the fringing reef. They seem to chose preferentially the living substrates (37% of total individuals of this group in the fringing reef for Psammocora, 33% for Pavona cactus, and 29% for dead substrate), but they account for a low proportion in comparison with the total individuals collected on each substrate (Tab. 2, Fig. 10).

The generalized omnivore species were exclusively collected in dead substrate at beach margins. They were weakly represented (Tab. 2, Fig. 10).

Among the predacious/carnivore species, Gonodactylus viridis and G.espinosus were only collected in Pavona cactus. Thalamita admete, T.crenata and Calappa hepatica were collected by hand. This group was weakly represented in the fringing reef.

D.2) The Barrier-reef.

The omnivore/herbivore species are numerically domi-nant on all the substrates of this sector, except in dead substrate, although it is preferentially colonized by them (54% of total individuals of this group in the barrier-reef). For living coral colonies, Montipora is prefered (27%), instead of Pavona cactus (14%) and Pori-tes (5%).

The abundant species are also particularly distribu-ted in the different substrates : in this case, Chloro-diella barbata and C.laevissima are abundant on dead substrate and Montipora, while Pilodius pugil colonize preferentially Pavona cactus.

Montipora is an encrusting coral. The colonies offer free surfaces for algal colonisation (specially in the outer barrier-reef ; Payri, 1982), to which the omnivore/herbivore species are then attracted, but apparently not for the coral species itself.

The relative abundance of omnivores/carnivores is more important in this sector than in the fringing reef. These species become slightly dominant in the dead sub-strates to which they show strong preferences (65% of total individuals of this group for the barrier-reef). Among living coral colonies, Pavona cactus was better colonized (15%), then Montipora (12%), and finally Pori-tes (9%). Liocarpilodes integerrimus is the dominant specie within this group in the inner barrier-reef, being gradually replaced towards the reef front by other omni-vores/carnivores (Globopilumnus globosus, Paraxanthias notatus, Daira perlata, etc.). This scheme could suggest

PSAMMOCORA SP.

DEAD
SUBSTRATUM

DEAD
SUBSTRATUM

PAVONA CACTUS

PAVONA
CACTUS

MONTIPORA SP.

PORITES SP.

D.C.

D.C.

FRINGING REEF

BARRIER—REEF

FILTER-SUSPENSION FEEDERS

OMNIVORE /HERBIVORE SPECIES

OMNIVORE /CARNIVORE SPECIES

GENERALISED OVMNIVORE SPECIES
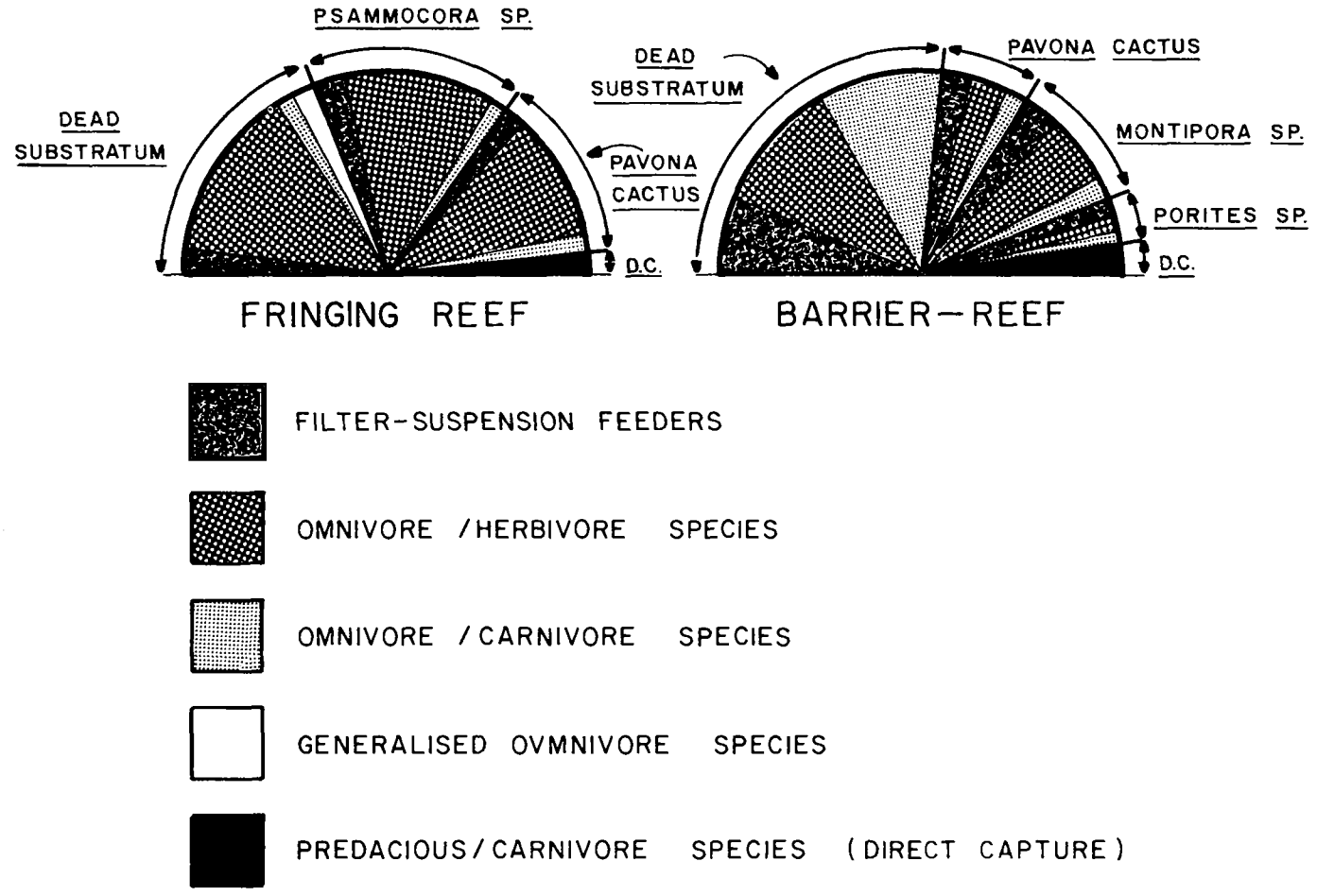
PREDACIOUS/CARNIVORE SPECIES (DIRECT CAPTURE)

Fig. 10.- Relative abundance of Morphologic Groups in
different substrates sampled in each reef
sector of the transect of Tiahura (see Tab. 2
for reference).

habitat partitioning among these species which show simi-
larities in their feeding behaviour.

In filter/suspension feeders, Galathea aculeata shows
also a strong tendency to colonize dead substrates (51%
of total individuals of this group for the barrier-reef).
Among living coral colonies, G.aculeata colonizes mainly
Montipora (25%), then Pavona cactus (16%), and finallly
Porites (8%).

The predacious/carnivores species are weakly repre-
sented in this sector, and most of them are not cavitary.
We noted once again Gonodactylus viridis and G.espinosus
only in Pavona cactus.

DISCUSSION.

The transect of Tiahura is a reef complex where the
most common biotopes of Polynesian High Islands are pre-
sent (Salvat, et al., 1972). Being a highly diversified
environment, the number and the type of species inhabi-
ting it is large and varied. The coexistence of a great
number of species within a given area produces interspe-
cific relations often very complex and specialized. Each
of the biotopes studied in this work shows an assemblage
of floristic and faunistic species, generally well-defi-
ned, whose composition depends on the interaction of
several factors : presence and distribution of substrates
available to colonisation (Connell, 1972 ; Gore, et al.,
1978), interspecific relations (Paine, 1974), complexity
of biotopes (Kohn & Nybakken, 1975), biotic and abiotic
environmental conditions (Abele, 1972 ; Connell, 1975),
and bioecologiccharacteristics of the species concerned.

The 73 species collected at Tiahura are adjusted to
this schema, and although the dominant species tend to a
wide distribution in the transect, the qualitative compo-
siton (and mainly the quantitaive composition) of popula-
tions is rather different from one area to another. These
differences are defined, first, by the spatial distribu-
tion of the 10-12 species following in abundance the 4
dominant species, and second, by the particular reparti-
tion of each species in the substrates.

In agreement with Abele (1972), Gore et al. (1978),
and others, the numerically dominant species within a
biotope are generally those that possess the best adapta-
tions (morphological or others) for favorable exploita-
tion of their resources. One of these adaptations which
seems to have a strong influence over the community
composition in the different biotopes is the alimentary
regime of species (Odum & Odum, 1955 ; Paine, 1966).

The type of food of crustaceans is closely related
with the morphology and the size of the species, both the
consumer and the prey (after different authors). On that
basis, we have proposed 5 MORPHOLOGIC GROUPS. In each
are included species having morphologic similarities
which may indicate the utilisation of the same kind of
food. These divisions are not strict : crabs are well-
known to show tendences to omnivorism, and the high
diversity of a high island coral reef system may favor a
non-specialized feeding behaviour, the choice of resour-
ces being quite large.

Nevertheless, some morphologic features observed in
the crustaceans in our work suggest that there actually
exists a certain degree of feeding selectivity. Besides,
the similar sizes of species (most of them do not measure
more than 20 mm width in their adult stage), suggest the
utilization of similar alimentary resources, and in con-
sequence, there would be a competition for these, for
they are certainly not unlimited. This condition confirms
the existence of alimentary specialisation, mainly in
abundant species, as mentioned by Gore, et al. (1978).

The effect of this specialisation is reflected in the
repartition of species in the transect and in the diffe-
rent substrates. Two factors inherent to the substrates
studied could determine these differences : the degree of
necrobiosis of the coral colony which permits a more or
less extensive colonisation by algae and their associated
fauna, and the complexity of the cavitary network which
offers adequate shelter to the cryptofauna. In these
terms, the dead substrate would be the best, it shows a
high algal colonisation, an abundant associated fauna,
and in most cases, a well-developed cavitary network. For
living corals, Pavona cactus and Psammocora present more
favorable factors for the colonisation by the carcinolo-
gic cryptofauna, which is not the case for Porites (the
colony is compact with few or no anfractuosities).

Moreover, it is necessary to take into account the
effect of the ecologic conditions proper to each reef
sector. Thus, the transect of Tiahura is spatially shared
by the omnivore/herbivore species that prefer the frin-
ging reef where dead substrate (and therefore algae), is
more abundant, and by the omnivore/carnivore species that
tend to aggregate in the barrier-reef, mainly in the
outer reef flat and the reef front areas, where polychae-
tes and molluscs, their principal food resource, are more
abundant (Peyrot-Clausade, 1976 ; Naim, 1980b ; Richard,
1982). The filter/suspension feeders search for low-
sedimentation areas with moderately strong currents (in-
ner barrier-reef), favorable to their filtering activi-

ties, while the generalized omnivores prefer the areas of organic deposition (shallow beach margins). Predacious/ carnivores species are not abundant in lagoon areas of the transect, although some facultative malacophages are localized in the reef front.

Within each of the morphologic groups, there are one or two numerically dominant species whose repartition over the transect of Tiahura, and in the different substrates suggests the influence of a trophic partitioning phenomenon(Schoener, 1974 ; Gore, et al., 1978). The four most abundant species in the transect (Chlorodiella barbata, Pilodius pugil, Liocarpilodes integerrimus and Galathea aculeata), utilize apparently different types of food, are distributed in a particular pattern in the substrates, and occupy more or less the same areas. The five or six following species also seem to show these three types of relationships. There would exist therefore, two main strategies to avoid or to reduce competition among these species : a trophic partitioning by restriction of their alimentary regime when two or more abundant species live in the same area (in this case each species will show different alimentary needs), and a habitat partitioning when two species living in the same area search for similar alimentary resources (here, one of the species would be less restrictive than the other in its alimentary regime, thus able to exploit a more extensive biotope, i.e. inhabit other types of substrate), or, if competition is inavoidable, a spatial exclusion takes place.

Interspecific relations are quite clear, in the present work, among the dominant species and among some of the abundant species, both in terms of spatial distribution and repartition on the substrates. However, the picture becomes more complex when more species interact. In this case, it is possible that interspecific relations would occur with assemblages of species. We may mention Liocarpilodes integerrimus (omnivore/carnivore : dominant species), with the group of less abundant omnivore/carnivore species in the barrier-reef and the reef front (Globopilumnus globosus, Paraxanthias notatus, Daira perlata, etc.) ; Chlorodiella barbata and Pilodius pugil (omnivores/herbivores : dominant species), with the group of omnivore/herbivore species in the fringing reef (Phymodius ungulatus, P.nitidus, Pilodius scabriculus, etc.)

Abele (1974) and Gore, et al. (1978), stated that marine decapod crustaceans utilize the substrate in three main ways : 1) as a permanent shelter, 2) as a feeding site, 3) as a direct food resource.

The data obtained in this study agree with these
findings, more than 90% of the species collected utilize
the cavitary substrate as shelter (except endogenous and
"free living" species). Then, the observations of gut
contents suggest that species utilize the substrate also
as a feeding site. But concerning the utilisation of
substrate as a direct alimentary resource, this could
only happen in living corals, and it is not always evi-
dent. Except for some of the well-known coralivores pagu-
rid crabs, we cannot demonstrate the existence of other
coralivore species (either strict or facultative), al-
though this posssibility is likely to occur, chelipeds
with sharp-pointed fingertips would be morphologically
adapted to crush the outer surface or the coralites and
then extract the soft tissues from the interior. Gore, et
al. (1978), observed a similar behaviour in Menippe nodi-
frons inhabiting the sabellariid reefs.

Predation activities among crustacean species appear
limited. Certain more or less large-sized species such as
Globopilumnus globosus, Xanthias lamarcki and Daira per-
lata, may probably attack smaller species inhabiting the
same area (Lioxanthodes alcocki, Paraxanthias notatus,
Liocarpilodes integerrimus, Chlorodiella laevissima,
etc.). Juveniles, and individuals undergoing molting
stages could also become prey. Besides, malacophage crabs
would consume numbers of pagurid crabs inhabiting gastro-
pod shells (Rossi & Parisi, 1973).

Finally, we may define the transect of Tiahura as a
topographically complex and irregular habitat, having a
relatively constant abiotic environment, which favors a
high specific diversity and numeric abundance. However,
it is not favorable to an ecologic specialisation of
species and to the presence of large predacious crabs.

The statement by Kohn (1968, 1971a) for Conus popula-
tions, and by Abele (1974) : "more structurally complex
habitats could support a higher number of species than
structurally simpler habitats", would have been confirmed
if we had compared the crustacean communities of High
Islands and atolls, a study that should be done in the
future.

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always present in my thoughts".
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