



SECRETARIAT OF THE PACIFIC COMMUNITY
REEF FISHERIES OBSERVATORY

**ECOLOGY AND BIOLOGY OF NEW CALEDONIA'S
MAIN SEA CUCUMBER SPECIES
2006**

Sections from Chantal Conand's seminal thesis:
"Aspidochirote holothurians of the lagoon of New Caledonia: biology, ecology and exploitation",
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Institut de recherche pour le développement (IRD, ex-ORSTOM)



"Les holothuries Aspidochirotes du lagon de Nouvelle-Calédonie: biologie, écologie et exploitation"
Thesis, Université de Bretagne Occidentale (July 1988),
published by ORSTOM, Études et Thèses (1989), 393 p.

CONAND C. 2006. Ecology and biology of New Caledonia's main sea cucumber species. Sections of Chantal Conand's thesis: *Les holothuries Aspidochirotés du lagon de Nouvelle-Calédonie : écologie, biologie et exploitation*, originally published by ORSTOM (1989), translated and published by the Secretariat of the Pacific Community's Reef Fisheries Observatory, and Information and Translation Sections. Noumea: SPC, New Caledonia. 98 p.

GENERAL PRESENTATION

SPC's Reef Fisheries Observatory, and Information and Translation Sections have translated two chapters of Chantal Conand's seminal thesis on the ecology and biology of sea cucumbers (CONAND C., 1989 - Les holothuries Aspidochirotés du lagon de Nouvelle-Calédonie: biologie, écologie et exploitation. Études et Thèses, ORSTOM, Paris: 393 p). Although this thesis was published in 1989, many results were never made available to the wider audience of non-French speakers. Since the initial publication of this work, interest on holothurian resources and their management has only increased, and SPC hopes this translation will be of use to fishers, researchers and managers alike.

Chantal Conand is now Professor Emeritus at La Reunion University. Her PhD was undertaken at the ORSTOM (now IRD) Center in New Caledonia, and the Laboratoire Océanographie Biologique of the University of Bretagne Occidentale. She is still involved in sea cucumber research, as the scientific editor of the Beche-de-mer Bulletin published by SPC and several programmes of regional and international interest.

The full thesis content section is shown below, with the translated parts of chapters, which are presented on the following pages, highlighted in blue. The references section is reproduced in full from the original version of Chantal Conand's thesis.

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Additional notes from the author, Chantal Conand:

Taxonomy used in the thesis

Scientific names of a few species have changed since this thesis was published:

- *Holothuria nobilis* is now restricted to the Indian Ocean and in the Pacific the species is *H. whitmaei* (Uthicke et al. 2004)
- *Stichopus variegatus* is now *S. herrmanni* (Massin 1999)

The species studied in the thesis are presented with photographs in Chapter I, not translated here.

Additional figures and tables

A few relevant figures and tables, from parts of the thesis that have not been translated, are presented in [Appendix 1](#) on page 97 of this document.

Language used in some tables and figures

Some tables and figures presented in this document have not been translated. Please note that decimals are separated by a coma in French, not a full stop: (e.g.: 0,16 m in French is equivalent to 0.16 m in English).

CHAPTER II: ECOLOGY OF THE ASPIDOCHIROTE HOLOTHURIANS

4 AUTOECOLOGY

4.1 ANALYTICAL METHOD

The technical constraints of sampling were such as to restrict data collection to qualitative information concerning physical factors (substrate, depth, water movement) and biotic factors. As this was a first-time large-scale study on the various biotopes of the reef complexes, simple methods were used. They do, however, make it possible to address the distribution and ecological requirements of the main species on the basis of their occurrence and numerical abundance.

- Geographical distribution: for each of the seven regions, a first table (A) shows the number of stations at which the species occurs and the percentage calculated from the total number of stations used in this region (see Table 9).
- Distribution by biotope: for both reef and lagoon biotopes, a second table (B) shows the number of stations where the species occurs and the percentage calculated from the total number of stations used in this region (see Table 10).
- Quantitative distribution, according to bathymetry and distance offshore, in miles: a first graph (C) illustrates variations in abundance in terms of these factors; the densities plotted on the x-axis are logarithmic values in order to make them less scattered.
- Distribution in relation to substrate: this is presented in a triangular diagram (D). These figures (Shepard, 1954) are based on the particle-size distribution of the sediments and express the respective percentages of gravel, sand and pelites (Fig. 16A). These diagrams are used in benthic ecology (Glémarec and Monniot, 1966; Glémarec, 1969; Guille, 1971; Thomassin, 1978). They have been adapted to represent three categories, covering the nine types of substrate defined above (Fig. 16B). Hence (D) = hard substrates + gravel, i.e. the fractions (1) + (2) + (3) + (4), (S) = sand, i.e. (5) + (6) and (P) = pelites, i.e. (7) + (8) + (9).

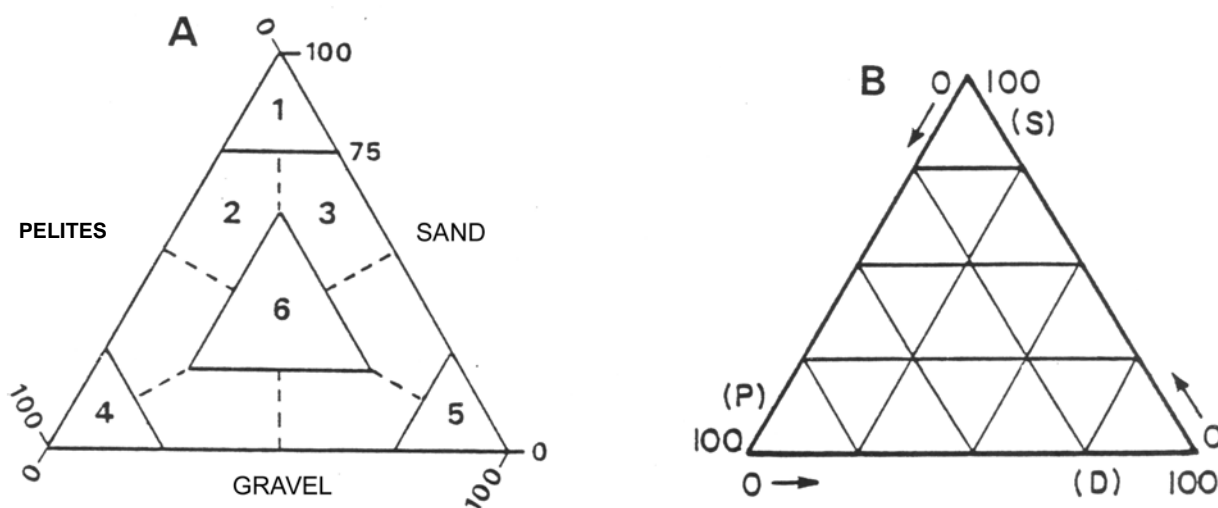


Figure 16: Triangular diagram. A: by Shepard (after Glémarec and Monniot, 1966); B: adapted for this study, (D): hard substrate and gravel, (S): sand, (P): muddy sand and mud.

From the coverage rates of each category, the stations where a species occurs are plotted on diagram (D).

The tables (A) and (B) and the graphs (C) and (D) are included in the text as a summary figure for commercial or frequently occurring species; for other species, the relevant tables and graphs are to be found in Annex 2.

4.2 GENERAL RESULTS ON DISTRIBUTION, DENSITY AND BIOMASS

4.2.1 Frequency

General results can be presented from the data as a whole. On the basis of frequency of occurrence, it is possible to define several groups of species (Fig. 17):

- very frequent: 2 species, recorded at over 80 stations, i.e. 40% of all stations where holothurians occurred;
- frequent: 9 species, recorded at over 35 stations, i.e. 17%;
- infrequent: 13 species, recorded at over 10 stations, i.e. 5%;
- scarce: 24 species, recorded at 1 to 10 stations, i.e. under 5%.

Figure 18 presents the species in order of frequency of occurrence and classifies them by commercial grade.

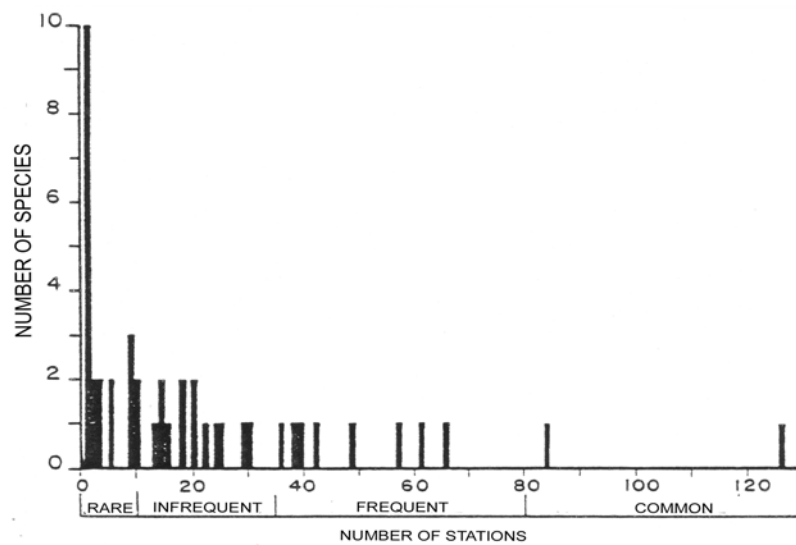


Figure 17: Species occurrence frequency.

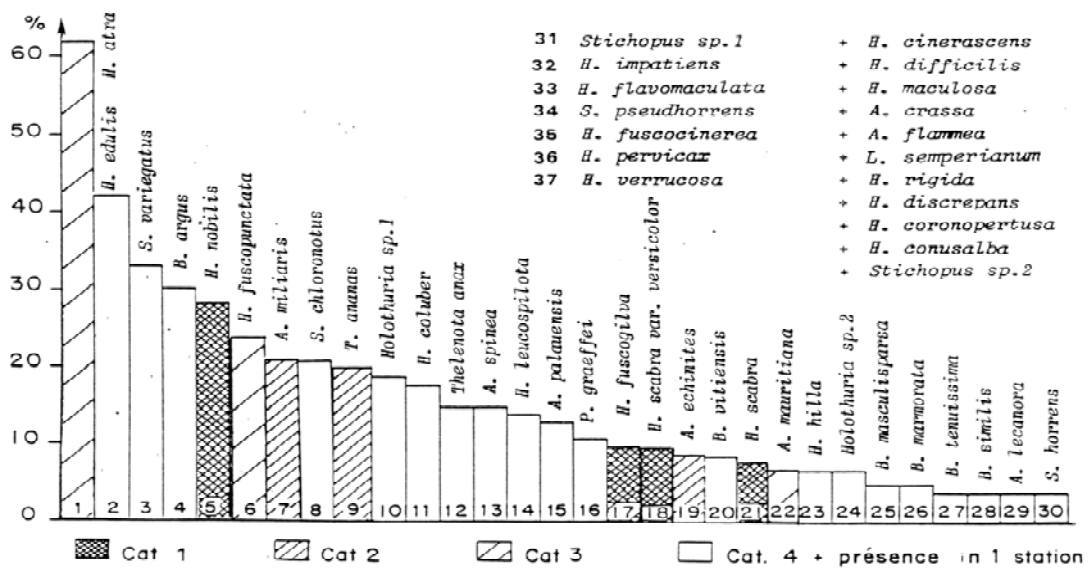


Figure 18: Species arranged by frequency of occurrence and commercial value.

Species belonging to the top grade are infrequent, with the exception of *H. nobilis*, which is frequent; of second-grade species, *A. miliaris* and *T. ananas* are frequent. But the very frequent species, *H. atra* and *H. edulis*, have little or no commercial value.

4.2.2 Abundance

In order to provide an overall picture of the respective abundance of each species, their mean density and biomass have been calculated for the stations at which each was recorded from the corresponding line in the general two-dimensional tables.

The density, d , values given, except for scarce species, (Table 11) make it possible to classify species by decreasing numerical density.

Table 11: Density and biomass (fresh weight) of the main species. d : mean density of the species; d_t : density of all species; b : mean biomass; b_t : total biomass.

Species	Density				Biomass			
	\bar{d} (n/100m ²)	rank	% d_t	rank	\bar{b} (g/100m ²)	rank	% b_t	rank
<i>H. nobilis</i>	0,13	26	0,4	21	237	25	2,1	17
<i>H. fuscogilva</i>	0,11	28	0,1	26	283	23	0,9	24
<i>H. scabra</i>	6,83	3	5,5	7	2416	2	6,0	4
<i>H. s. var. versicolor</i>	0,82	13	0,9	13	977	6	3,2	11
<i>A. miliaris</i>	5,12	5	10,1	2	2082	3	12,6	2
<i>A. echinites</i>	8,47	2	7,7	3	1814	4	5,1	7
<i>T. ananas</i>	0,18	24	0,4	21	489	17	3,0	13
<i>H. atra</i>	5,45	4	34,9	1	756	10	14,8	1
<i>A. mauritiana</i>	8,66	1	6,6	6	2505	1	5,8	5
<i>H. fuscopunctata</i>	0,31	21	0,8	14	475	18	3,6	9
<i>H. edulis</i>	1,13	11	4,8	8	243	24	3,2	11
<i>S. variegatus</i>	0,49	18	0,8	14	510	16	5,2	6
<i>B. argus</i>	0,21	22	0,7	17	360	20	3,4	10
<i>S. chloronotus</i>	2,86	8	6,1	5	323	21	2,1	17
<i>Holothuria sp. 1</i>	0,42	19	0,8	14	314	22	1,9	19
<i>H. coluber</i>	1,55	10	2,8	9	530	15	3,0	13
<i>T. anax</i>	0,14	25	0,2	24	609	12	2,9	15
<i>A. spinea</i>	1,08	12	1,6	10	841	7	3,9	8
<i>H. leucospilota</i>	5,05	6	7,4	4	1672	5	7,5	3
<i>A. palauensis</i>	0,10	29	0,1	26	175	27	0,7	26
<i>P. graeffei</i>	0,50	17	0,6	18	376	19	1,3	20
<i>B. vitiensis</i>	0,70	15	0,6	18	828	8	2,3	16
<i>H. hilla</i>	0,60	16	0,5	20	40	29	0,1	28
<i>Holothuria sp. 2</i>	1,89	9	1,3	12	548	14	1,2	21
<i>B. maculisparsa</i>	0,20	23	0,2	24	569	13	1,1	22
<i>B. aff. marmorata</i>	0,37	20	0,1	26	680	11	0,9	24
<i>B. tenuissima</i>	0,12	27	-	-	80	28	0,1	28
<i>B. similis</i>	3,00	7	1,4	11	790	9	1,1	22
<i>A. lecanora</i>	0,05	30	-	-	31	30	-	-
<i>S. horrens</i>	0,81	14	0,4	21	190	26	0,3	27

The species with the highest mean densities, between 5 and 10 specimens per 100 sq. m., are *A. mauritiana*, *A. echinites*, *H. scabra*, *H. atra*, *A. miliaris* and *H. leucospilota*. These are all reef flat species. Regarding the scarce species, it should be mentioned that *H. cinerascens* and *H. difficilis*, although recorded at only one station, occur there in a high density of 8.5 and 3.8 specimens per 100 m² respectively.

From the general table contents, **mean dominance** was calculated for each species; it is expressed in terms of the percentage its total density represents in relation to overall species density (Table 11). Ranking of the resulting values shows the place of each species on the scale of the total sample taken from the lagoon. The species that emerge as numerically dominant are *H. atra* (35%), *A. miliaris*, *A. echinites*, *H. leucospilota*, *S. chloronotus* and *A. mauritiana*.

Values for the mean **weight density** of species, b, were calculated in the same way as the numerical densities, except for scarce species (Table 11). The ranking shows that they only exceed 1 kg per 100 m² with *A. mauritiana*, *H. scabra*, *A. miliaris*, *A. echinites* and *H. leucospilota*. Despite its high densities, *H. atra* only comes in 10th place.

Mean **weight dominance** is also presented in terms of the percentage of total biomass in relation to the total biomass of all species. The resulting ranking is important from the commercial exploitation point of view. *H. atra* represents almost 15% of the total, followed by *A. miliaris*, *H. leucospilota*, *H. scabra*, *A. mauritiana* and *S. variegatus*. *A. miliaris* and *H. scabra* therefore emerge as the most valuable species.

Lastly, Fig. 19 summarises observations on **mean densities and biomasses** for species whose respective values exceed 10 specimens and 10 kg per hectare. A number of groupings of species is apparent, depending on their mean weight. One group clearly emerges with high values for the two parameters, formed of *A. mauritiana*, *H. scabra*, *A. echinites* and *A. miliaris*, with *H. leucospilota*. Medium-value species roughly range from *Holothuria sp.* to *H. atra*. Above these, high mean weight species are more dispersed, from *A. palauensis* to *A. spinea*, while below, the lighter species include *S. horrens*, *H. edulis* and *S. chloronotus*.

The **frequency distributions** of species densities (Figures 20A and 21A) and biomasses (Figures 20B and 21B) are given in a more detailed way. For more clarity, the commercial species have been separated from other frequent species. The mean density for each species is plotted as a symbol. The symbols for the biotopes defined in Fig. 12 are used for the mean densities, as calculated in the biotopes in which the species is frequent.

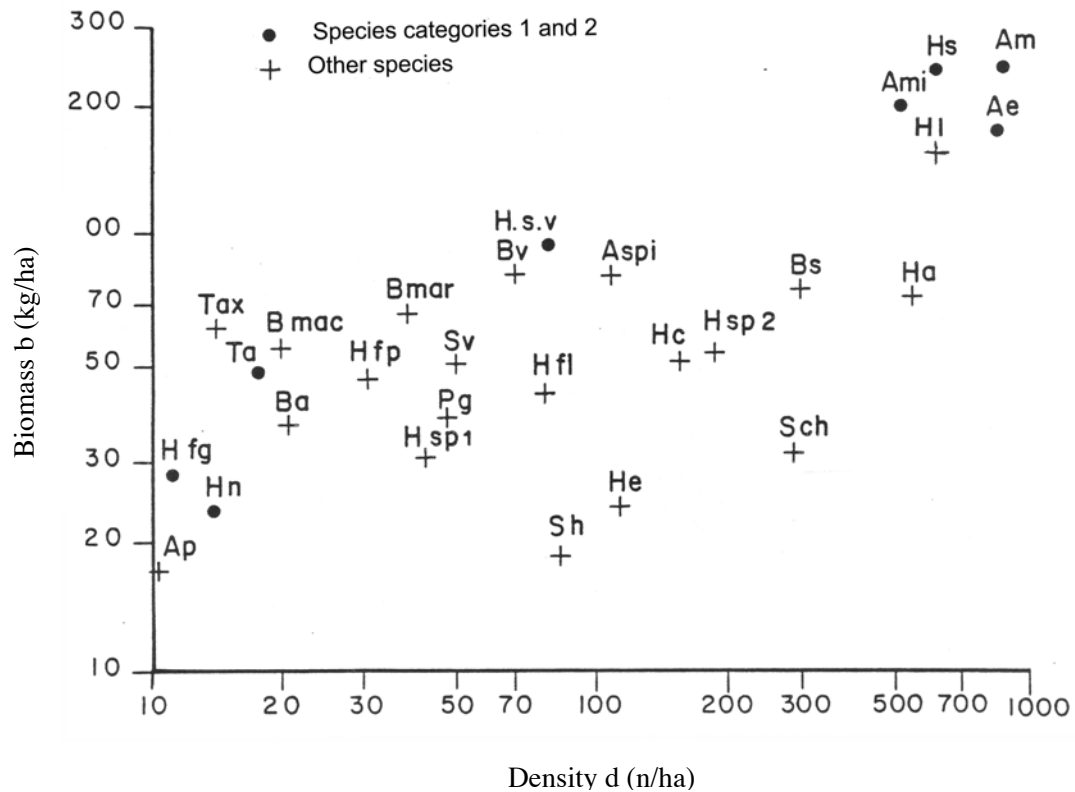


Figure 19: Relationship between density and mean biomass per hectare for the main species.

It clearly emerges that both densities and biomasses are highly variable, ranging from a few to several thousand specimens per hectare. In every case, the variance is higher than the arithmetical mean density, meaning that distribution is contagious, which is the most common scenario (Elliot, 1971). Two types of distribution can however be visually distinguished on these two figures.

- The densities are relatively homogeneous, after logarithmic conversion of the values, in the populations of species *H. nobilis*, *H. fuscogilva*, *T. ananas*, *T. anax* and *B. argus*; in this group, the values infrequently exceed 100 specimens per hectare.
- The values are more scattered for the other species, with, in some cases, maximum figures of several thousand specimens per hectare.

The biomass distributions are also highly variable, from under one kg to several tonnes per hectare in the aggregations.

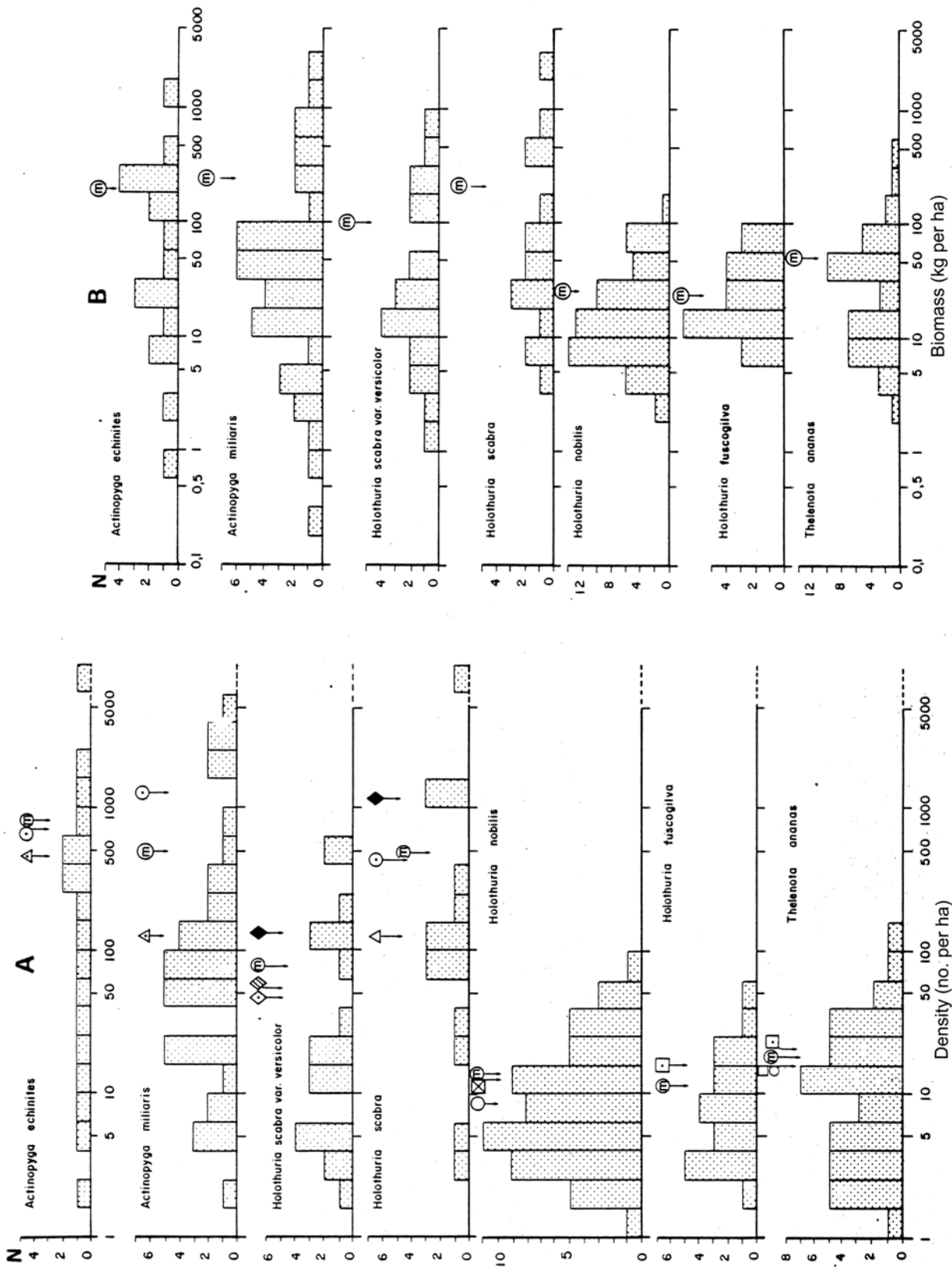


Figure 20: Density (A) and biomass (B) frequency distributions of the commercial species. N: number of observations; m: arithmetical mean; symbols (see Fig. 12): means in main biotopes.

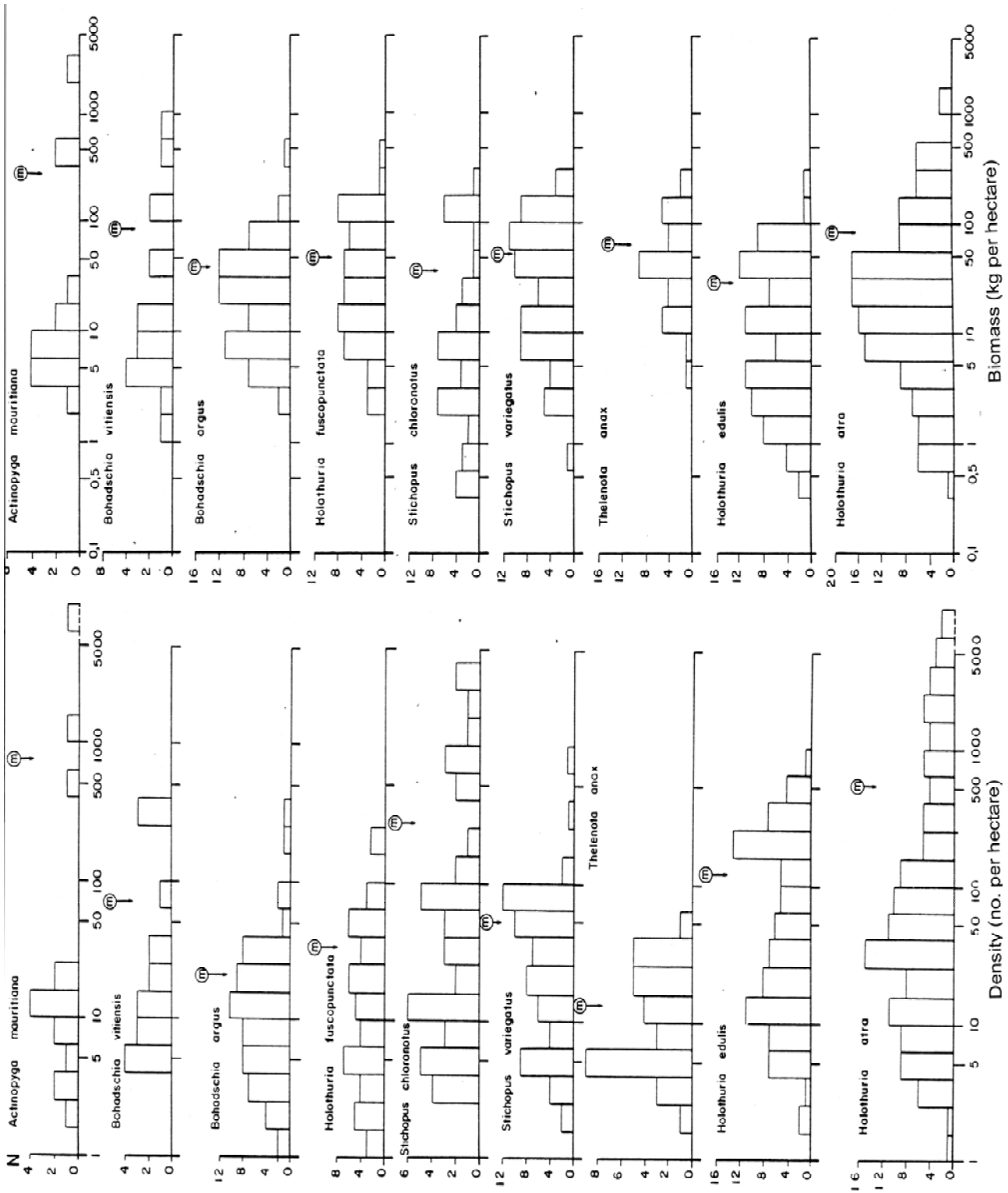


Figure 21: Density (A) and biomass (B) frequency distributions for other species.
 N: number of observations; m: arithmetical mean.

4.3 ECOLOGY OF MAIN SPECIES

4.3.1 Commercial species, grades 1 and 2

Holothuria (Microthele) nobilis

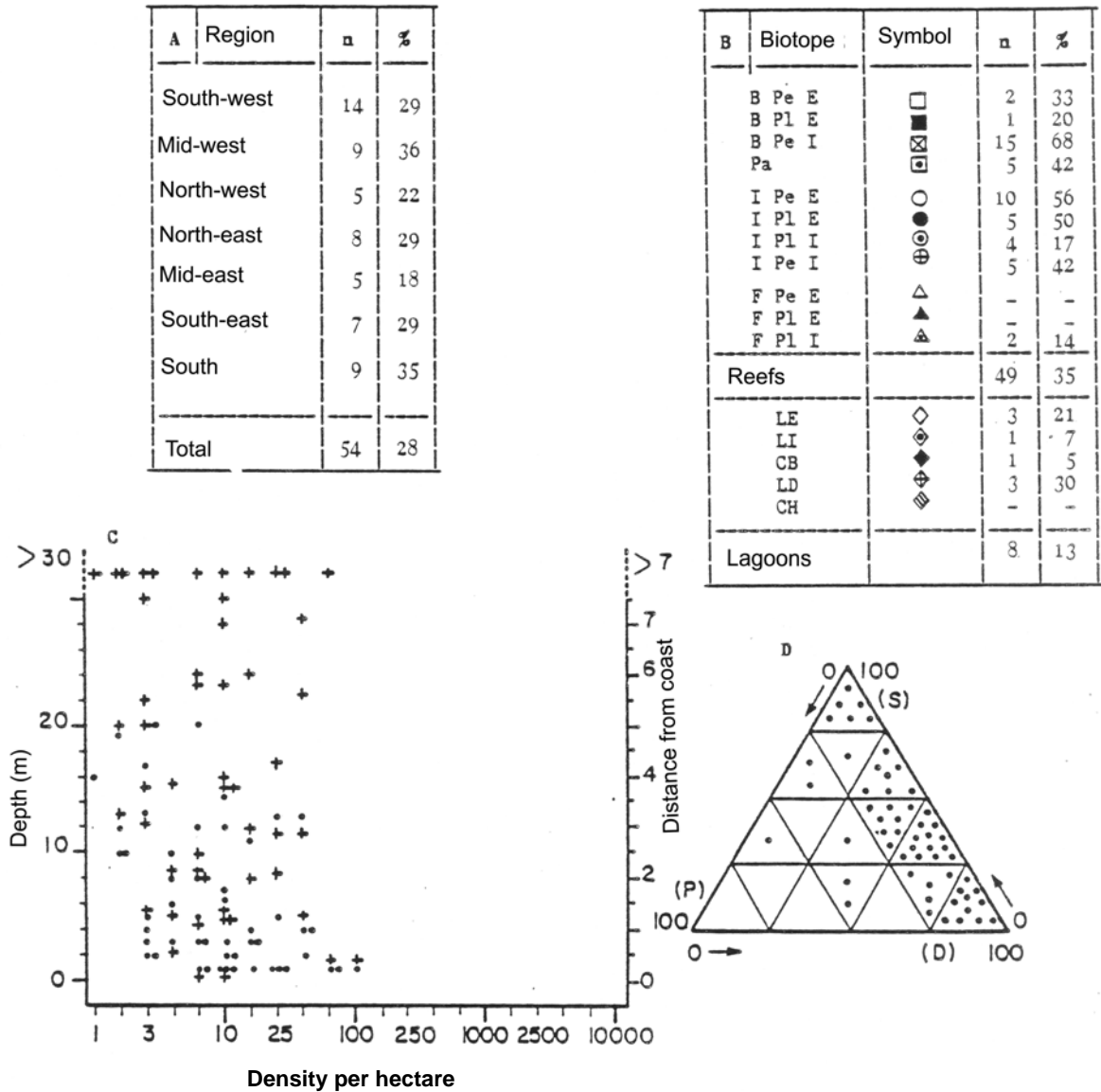


Figure 22: Distribution and abundance of *H. nobilis*.

- *Holothuria nobilis* is a frequent species all round New Caledonia. It is scarce in coastal zones under terrigenous influences and particularly frequent on barrier reef and islet reef slopes and also quite frequent on the associated reef flats.
- Its bathymetric distribution is usually between 0 and 20m. Population densities never exceed 100 specimens per hectare.
- Its requirements as regards the substrate appear on the triangular diagram. The distribution of stations shows that it is highly 'pelophobe' and seems to prefer hard substrates with sand in some abundance.

Holothuria (Microthele) fuscogilva

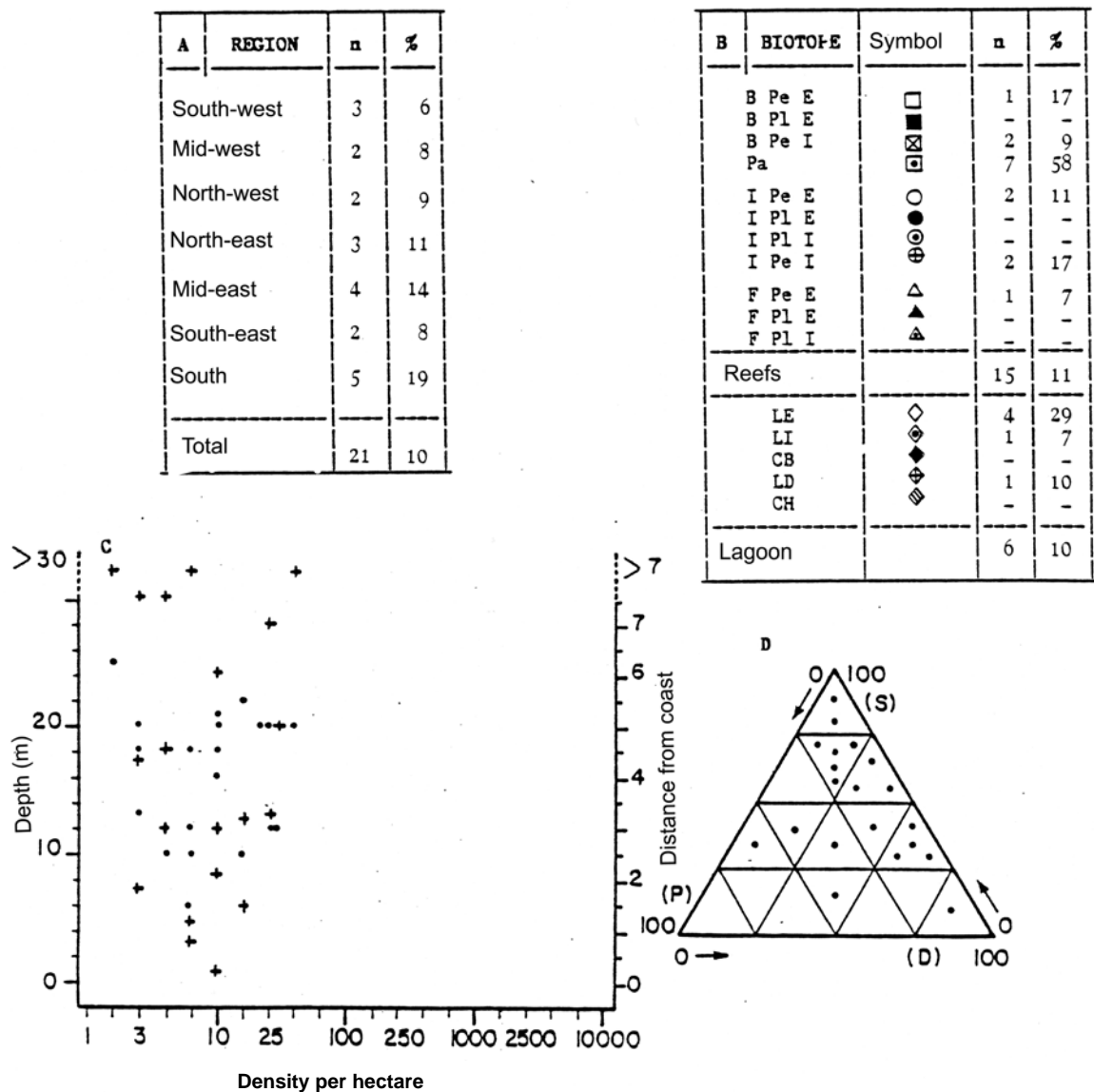


Figure 23: Distribution and abundance of *H. fuscogilva*.

- *Holothuria fuscogilva* is an infrequent species, but one that is found in all locations round New Caledonia.
- It is especially frequent in barrier reef passages and quite frequent in the external lagoon.
- Its bathymetric distribution is deeper than that of *H. nobilis*; indeed, it is not often observed above 10 m, but can be found at depths of up to 40m.
- Population densities are quite low, not exceeding forty specimens per hectare. It is a tolerant psammophilous (sand-loving) species.

Holothuria (Metriatyla) scabra

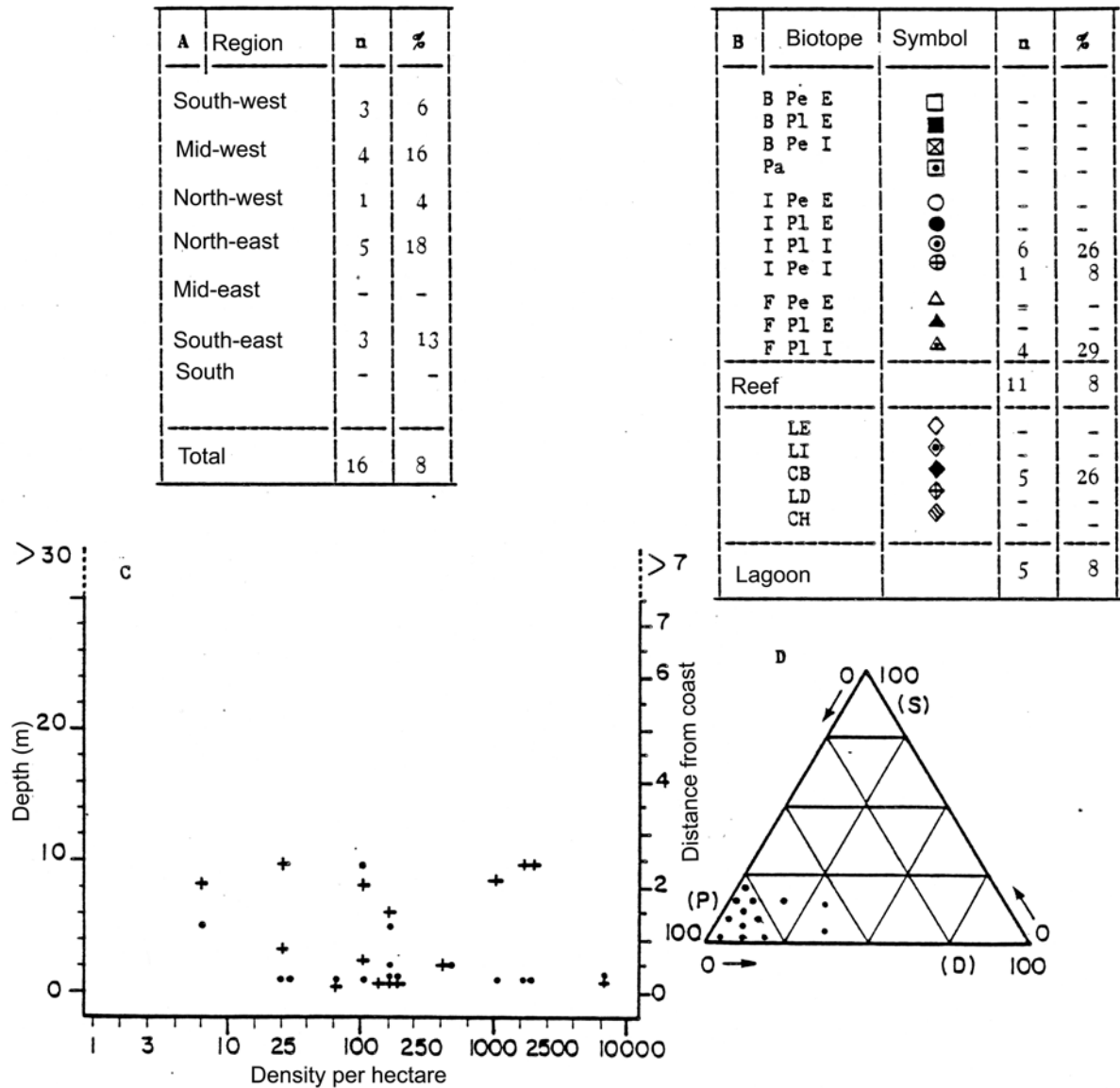


Figure 24: Distribution and abundance of *H. scabra*

- *Holothuria scabra* is an infrequent species, but is widely distributed around New Caledonia.
- It is absent from the barrier reefs and coral areas, as it occurs only on inner reef flats and bays with a strong terrigenous influence. It has not been observed more than 2.5 miles offshore.
- Its bathymetric distribution is shallow and it is not often found in depths over 5 m.
- Population densities can be high, up to several thousand specimens per hectare.
- This species likes muddy sand and sandy mud bottoms.

Holothuria (Metriatyla) scabra var. *versicolor*

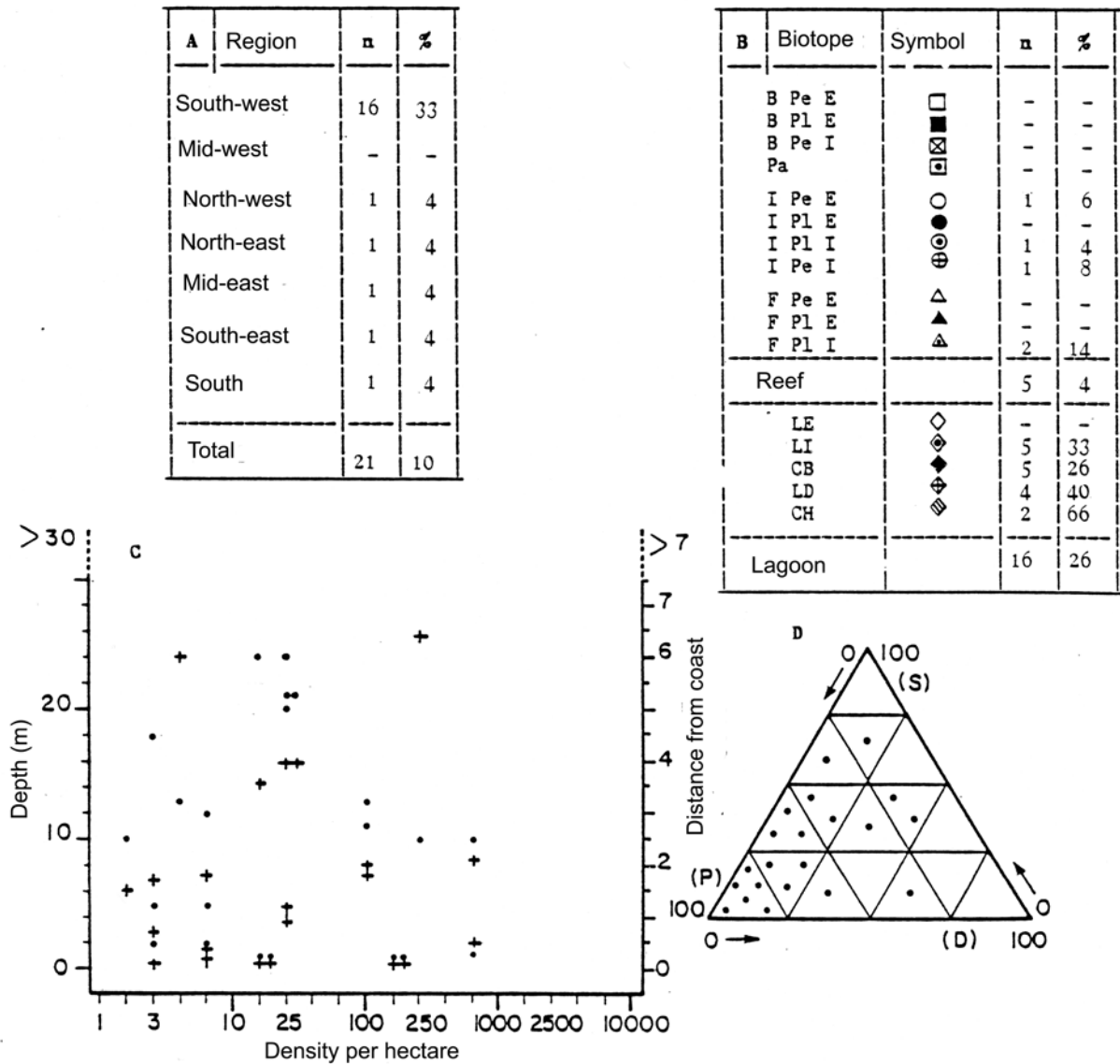


Figure 25: Distribution and abundance of *H. scabra* var. *versicolor*.

- *Holothuria scabra* var. *versicolor* is also fairly infrequent; it is distributed all around New Caledonia, but is more common in the south-western lagoon.
- It has a very marked terrigenous affinity, but is usually found at deeper stations, up to 25m; it is less a shoreline-dweller than *H. scabra*, sometimes occurring at up to 6 miles offshore. It is frequent in lagoon areas with slab floors.
- Populations do not exceed a density of a few hundred specimens per hectare.
- Its substrate requirements are also less strict, although it is most frequently found in muddy sands or sandy mud.

Actinopyga miliaris

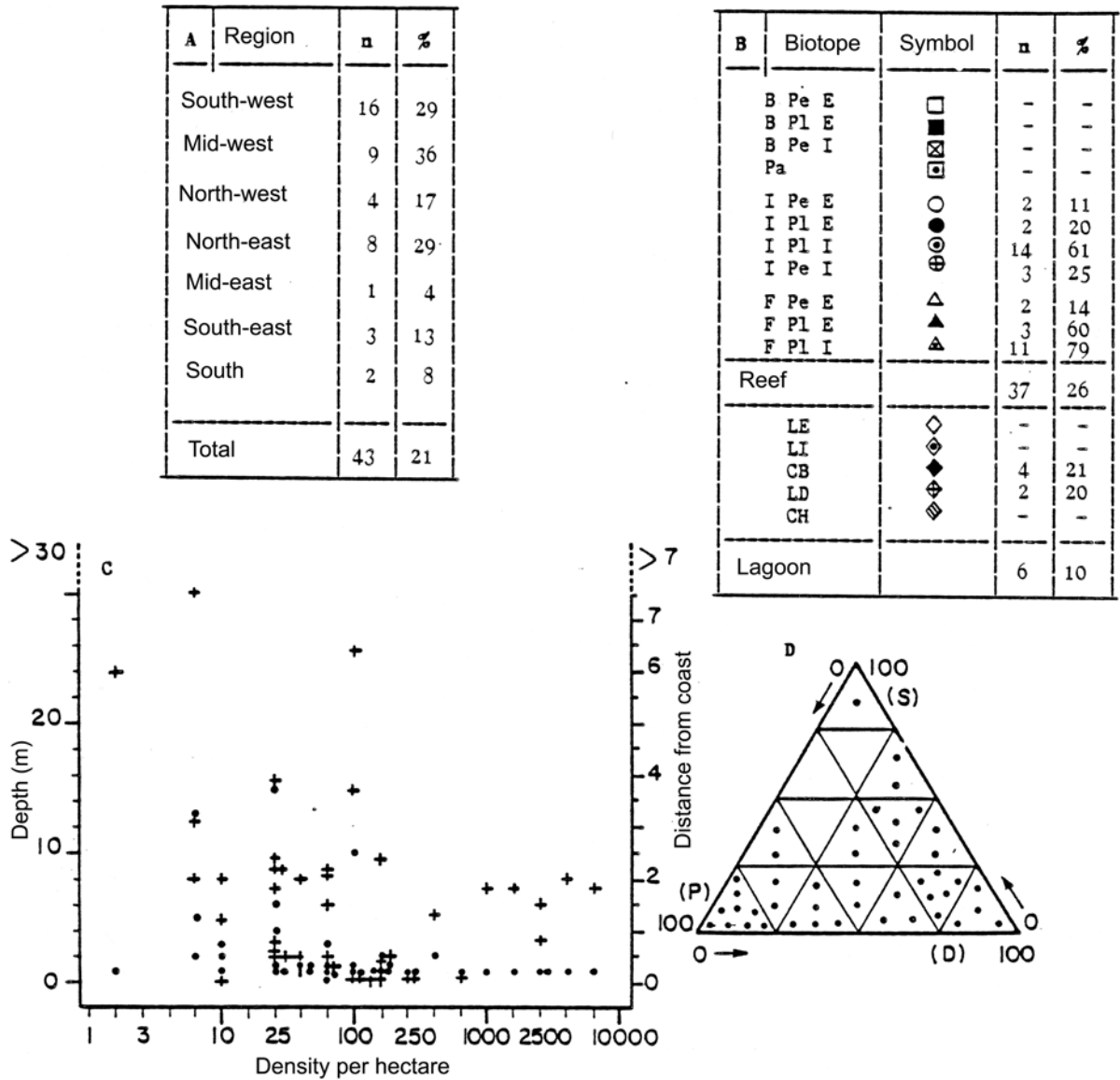


Figure 26: Distribution and abundance of *A. miliaris*.

- *Actinopyga miliaris* is a common species in New Caledonia, particularly on the west coast and in the north. It is very frequent on the inner flats of islet and fringing reefs.
- Completely absent from the barrier reefs, it prefers terrigenous influences. The highest population densities are found on reef flats covered with dense seagrass beds, less than 2 miles offshore.
- This species is infrequently found at depths below 10 m. These populations can reach high densities, up to several thousand specimens per hectare.
- The triangular diagram shows the heterogeneous nature of the substrates on which it occurs. Its absence from clean fine sand bottoms is worth noting. Mixed substrates like muddy sands strewn with coral blocks and rubble are highly suitable. It has frequently been observed in thick seagrass beds, feeding off the leaves' felt-like epiphytic covering.

Actinopyga echinites

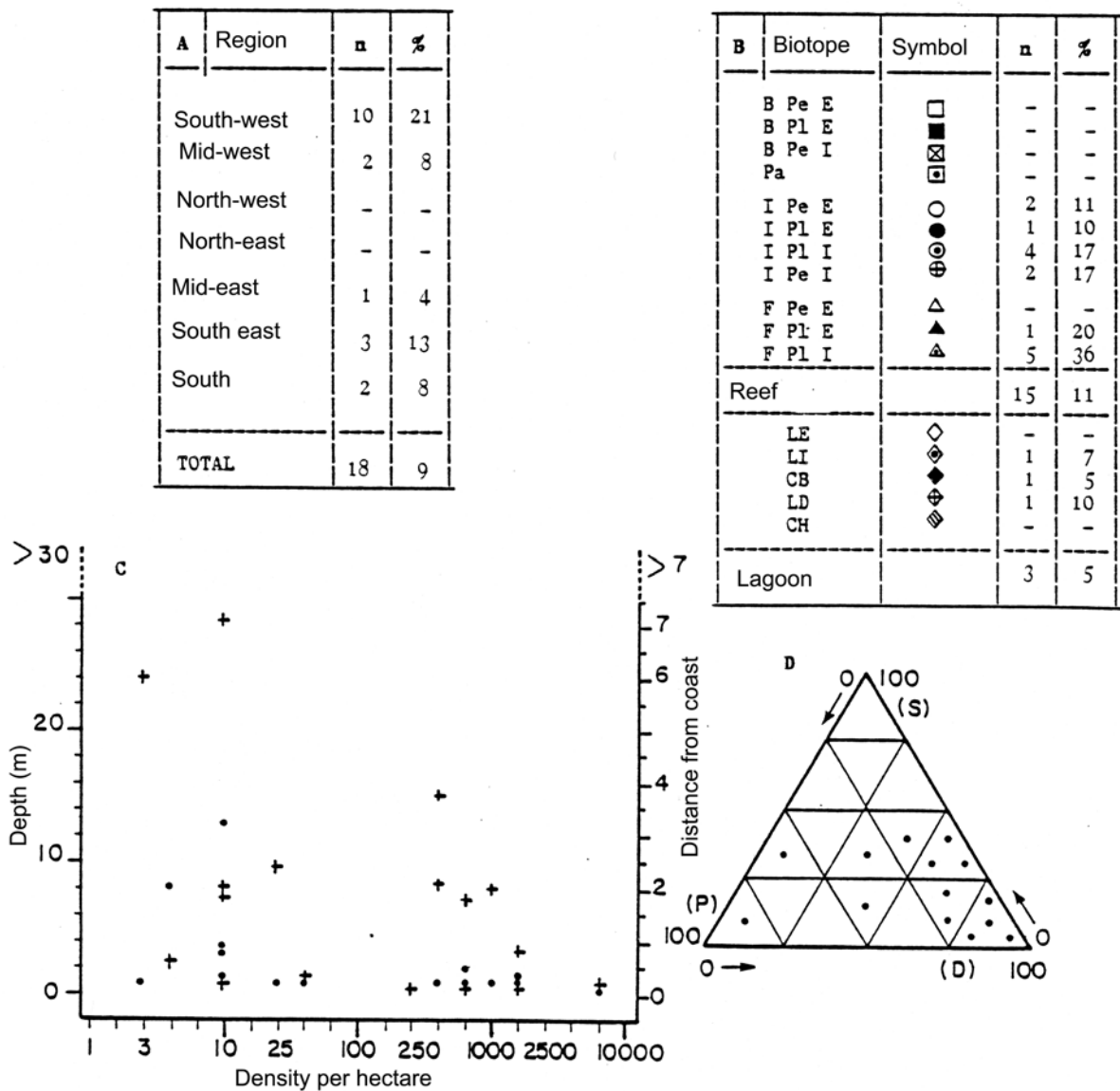


Figure 27: Distribution and abundance of *A. echinites*.

- *Actinopyga echinites* is more common in the south of the island, on both west and east coasts.
- This species has a preference for the reef environment, but does not occur on barrier reefs. It is to be found on islet and fringing reefs, in areas under terrigenous influence.
- Its depth distribution is comparable to that of *A. mauritiana*, infrequently exceeding 10 m.
- It mostly inhabits outer reef flats, where there is an abundant supply of brown algae and on inner reef flats in seagrass beds and coral rubble.
- It can occur in high population densities.

Thekenota ananas

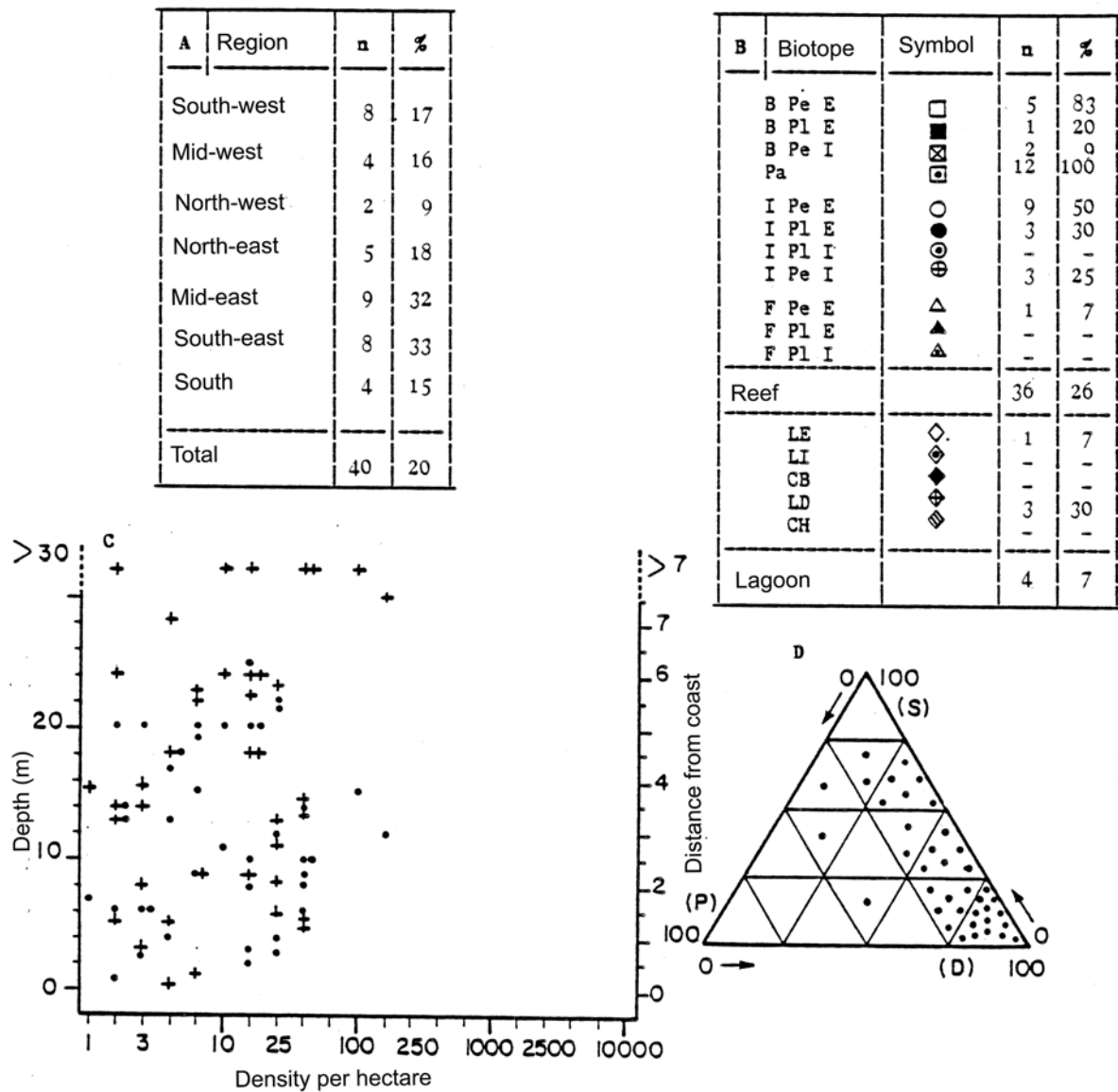


Figure 28: Distribution and abundance of *T. ananas*

- *Thekenota ananas* is a common species, occurring all around New Caledonia.
- It is a reef-dwelling species, more common in coral areas outside terrigenous influence. Observed at all passage stations investigated, it likes areas with vigorous water movement.
- Its bathymetric distribution ranges from flats covered with only shallow water at low tide to depths of over 25 m.
- Populations are not very dense, infrequently exceeding some one hundred specimens per hectare.
- This species likes hard bottoms covered in a layer of coral sand of varying depth.

4.3.2 Low commercial value species, Grade 3.

Holothuria (Halodeima) atra

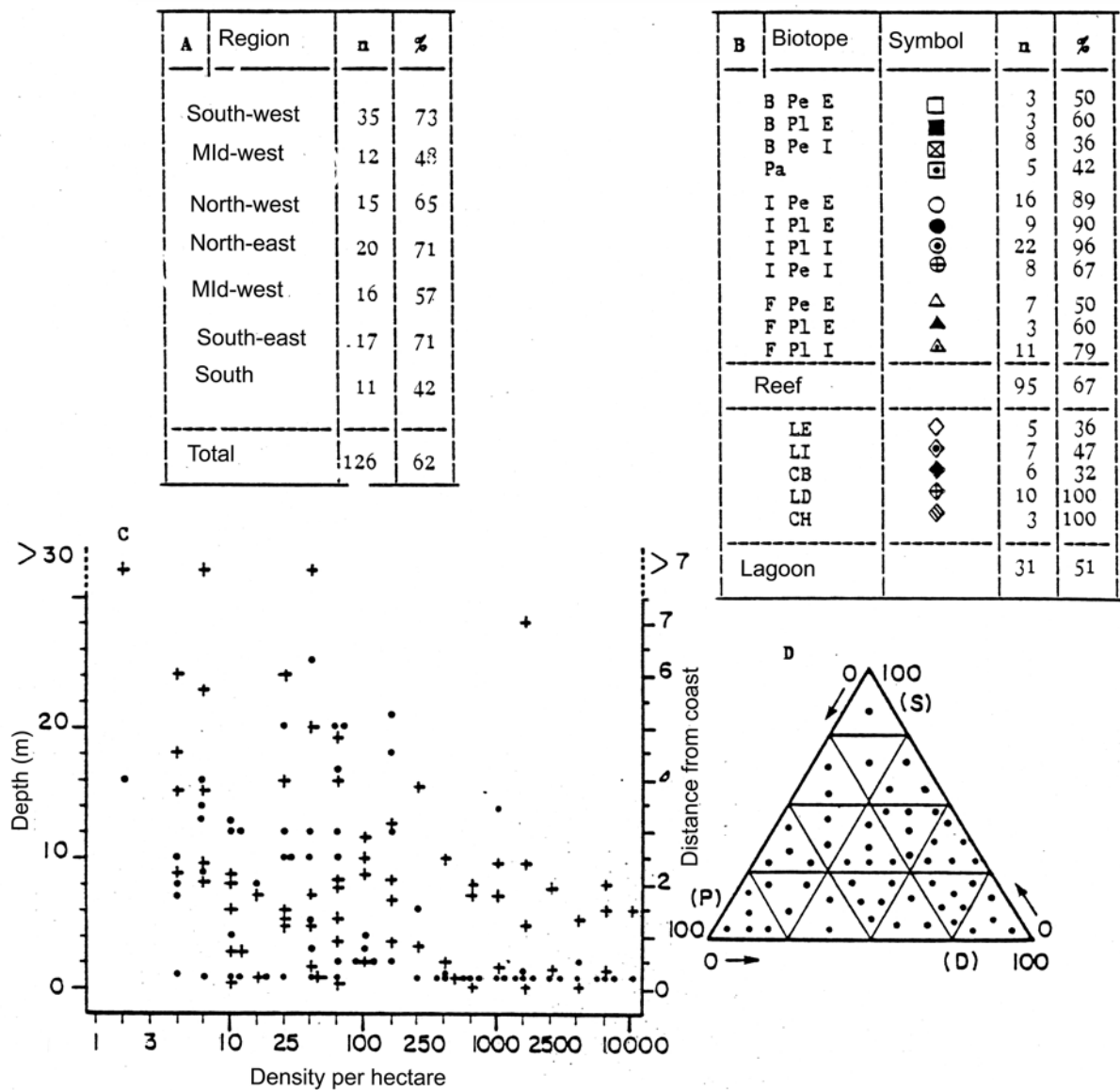


Figure 29: Distribution and abundance of *H. atra*.

- *Holothuria atra* is the most common species in all geographical areas of the New Caledonian lagoon.
- It is also frequent both in reef biotopes and in those under terrigenous influence.
- It is not usually found at depths of over 25m. Its populations can be very dense, but when they are, they tend to inhabit shallow reef flats, often not far from shore.
- Some reef flat populations reach very high densities.
- This species is almost ubiquitous in shallow waters.

Actinopyga mauritiana

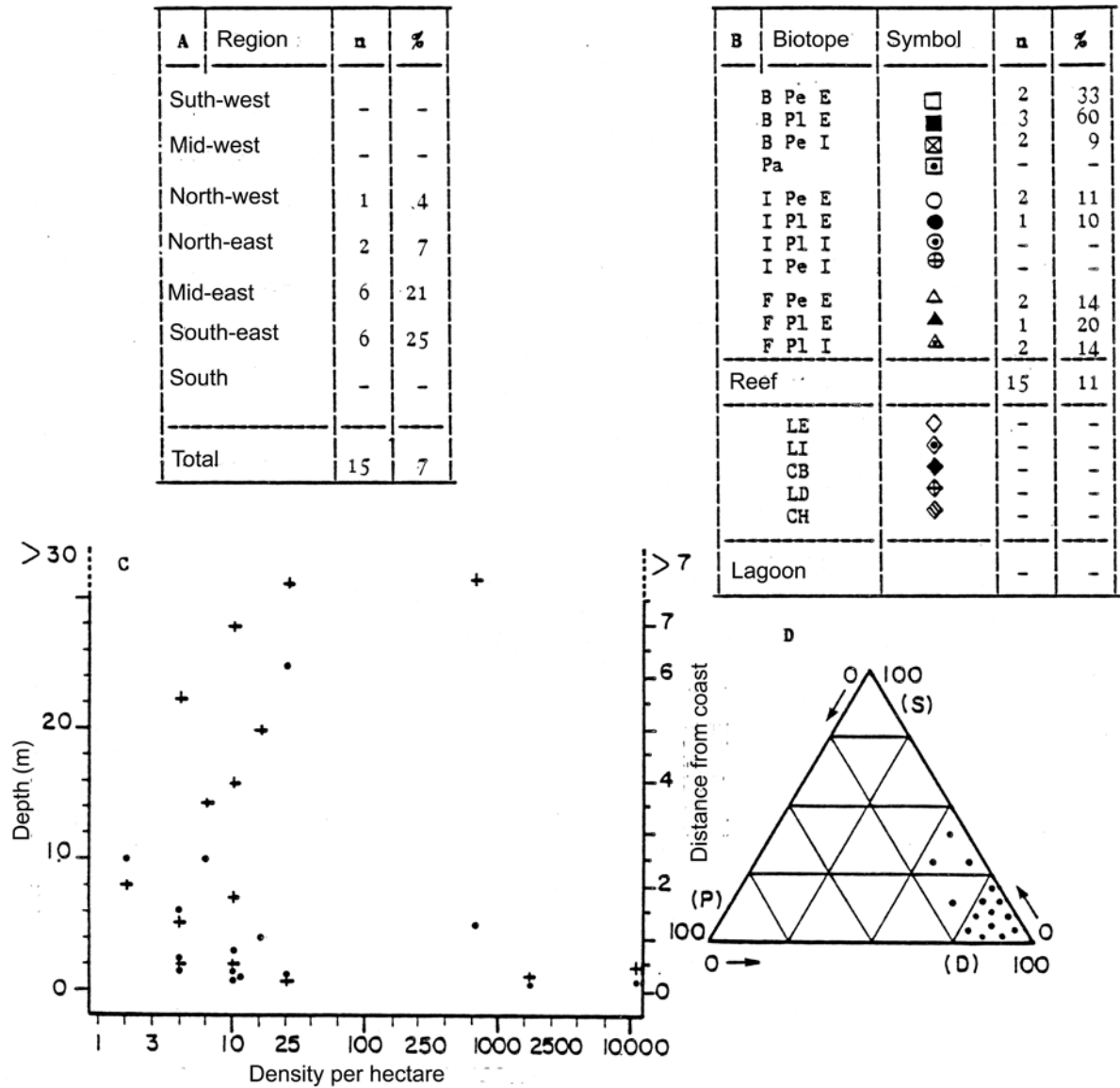


Figure 30: Distribution and abundance of *A. mauritiana*.

- *Actinopyga mauritiana* is more frequent on the east than on the west coast.
- This is an exclusively reef-dwelling species, which is common on the barrier reef. It lives on outer reef slopes and reef flats with vigorous water movement at depths usually not over 10 m.
- It can reach very high population densities on a localized basis.
- Its distribution is strictly limited to hard substrates, with a partial coral sand covering.

Holothuria (Microthele) fuscopunctata

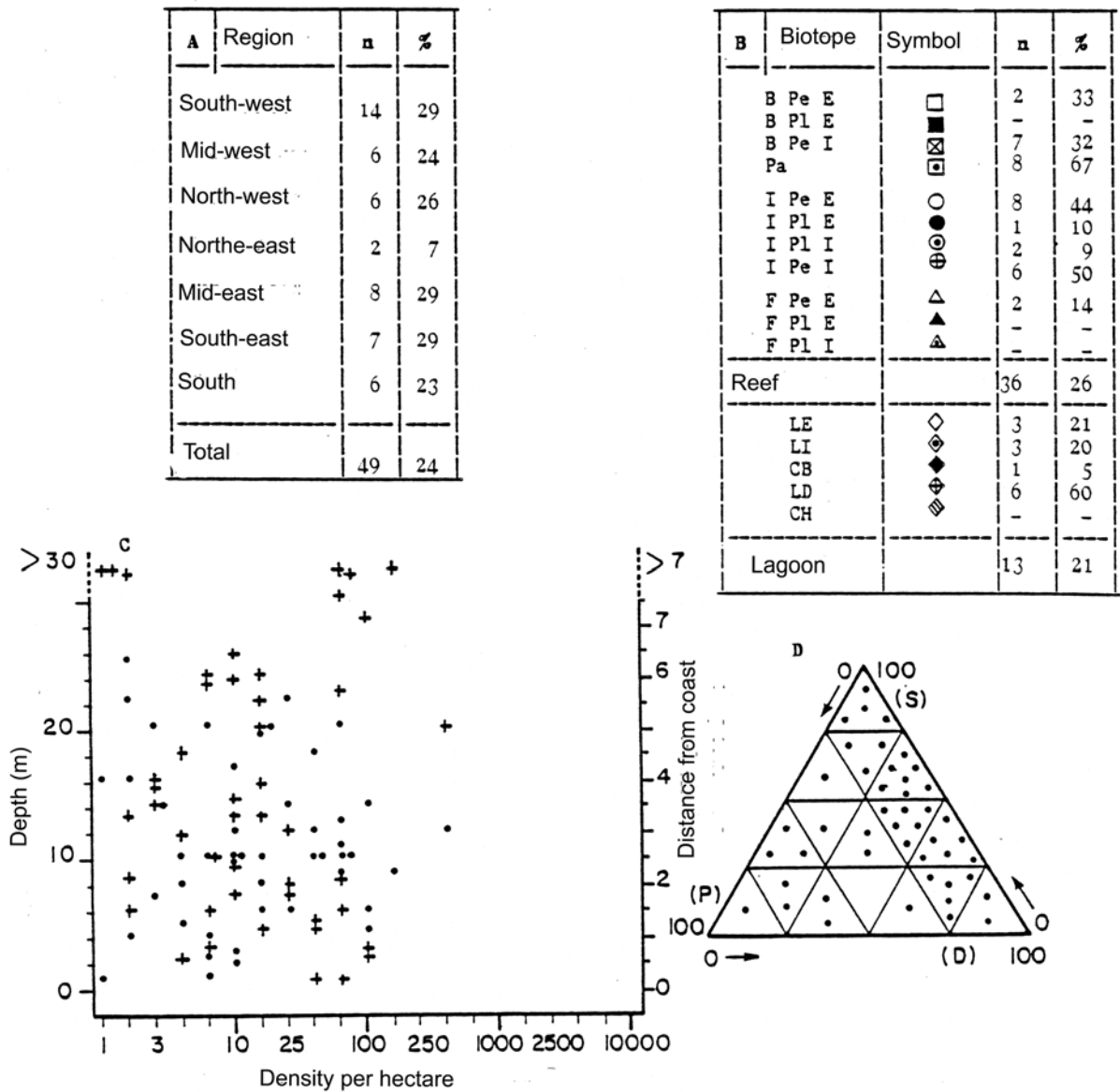


Figure 31: Distribution and abundance of *H. fuscopunctata*.

- *Holothuria fuscopunctata* is a frequent species, found throughout the New Caledonian lagoon.
- It is scarce on outer or inner reef flats or in bays; it is more common on outer or inner reef slopes and at the bottom of outer slopes.
- Its bathymetric distribution extends to depths of 25 m, but the densest populations, over 60 specimens per hectare, are found between 5 and 12 m.
- Although it is fairly tolerant as regards substrate, it is more frequent in areas where the sand has a low pelite content.

4.3.3 Other very frequent and frequent species.

Holothuria (Halodeima) edulis

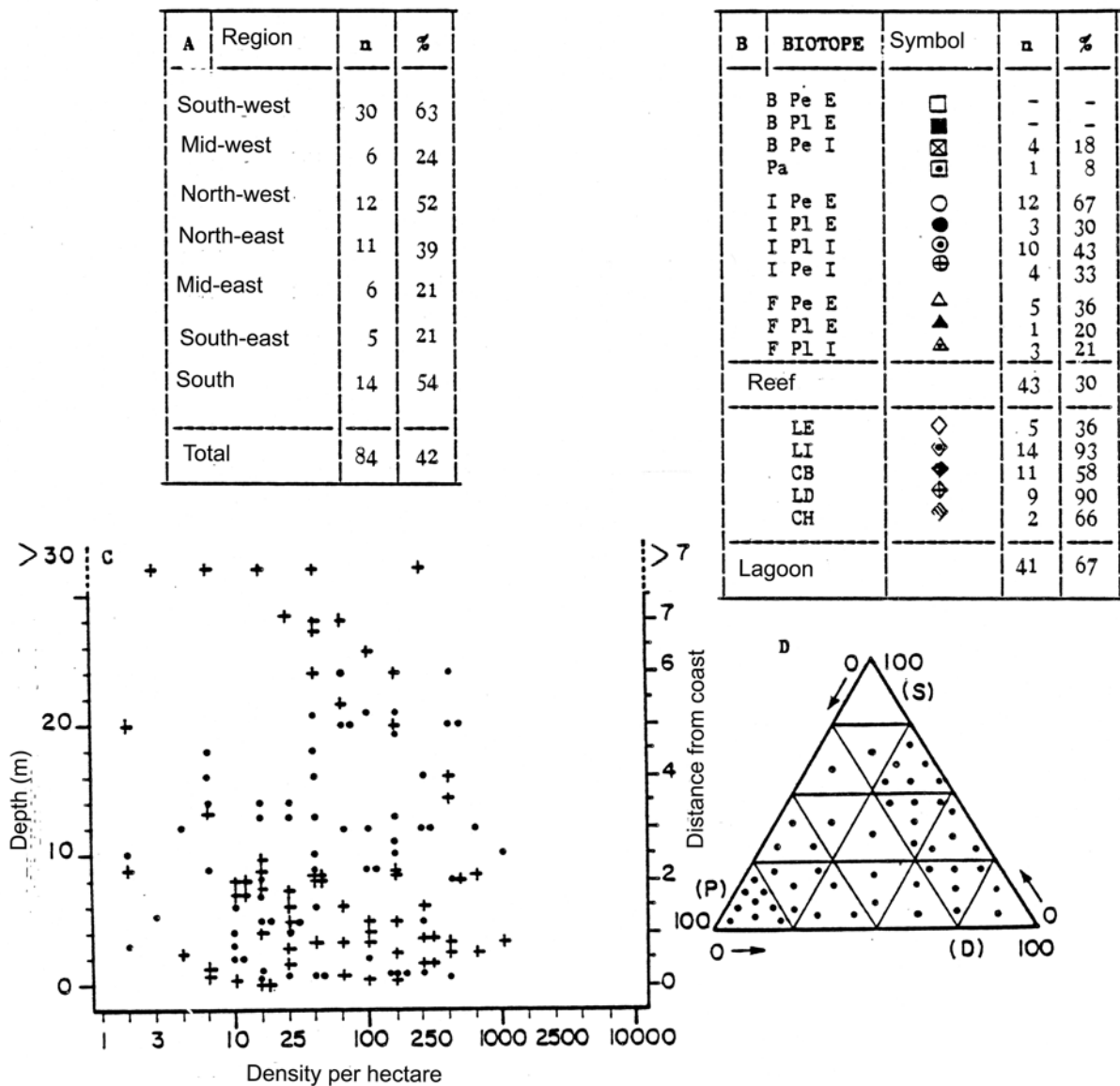


Figure 32: Distribution and abundance of *H. edulis*.

- *Holothuria edulis* is a very frequent species all around New Caledonia, but particularly in the south-western and southern areas.
- It is scarce on the barrier reef, where it was totally absent from outer reef flats and slopes in our harvests. A different form of colour, ecology and ethology has been observed on the outer slopes (Féral and Charbonnier, 1986).
- Its membership of the group of species under terrigenous influence is proved by its frequent occurrence in coastal lagoon waters.
- Its bathymetric distribution is a little deeper than *H. atra*.
- The densest populations do not exceed 1000 specimens per hectare and are located at depths of some 10 m.
- Apart from pure sand, it is tolerant as regards substrate, with an affinity for pelite-rich sediments.

Stichopus variegatus

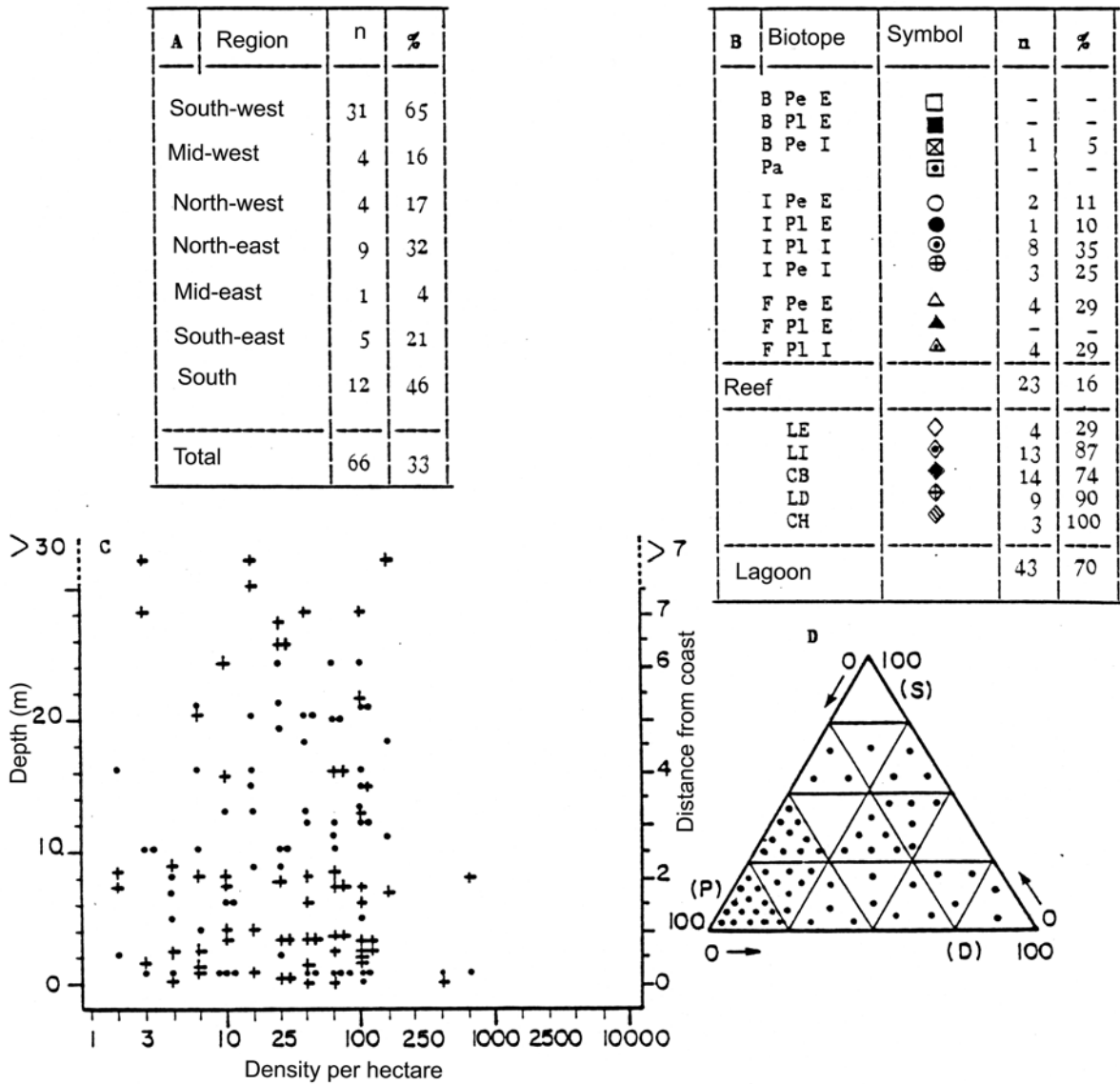


Figure 33: Distribution and abundance of *S. variegatus*.

- *Stichopus variegatus* is a frequent species all around New Caledonia, especially in the south and south-west.
- It is a coastal-dweller with a very strong affinity for terrigenous influences, occupying seagrass beds and rubble bottoms on inner reef flats of islets and fringing reefs, inner lagoons and bays.
- Its bathymetric distribution is quite broad, from 0 to 25 m.
- Its maximum population densities reach several hundred specimens per hectare.
- It favours soft substrates, from muddy sand to mud.

Bohadschia argus

A	Region	n	%
	South-west	13	27
	Mid-west	6	24
	North-west	6	26
	North-east	5	18
	Mid-east	11	39
	South-east	11	46
	South	9	35
Total		61	30

B	Biotope	Symbol	n	%
	B Pe E	□	2	33
	B Pl E	■	1	20
	B Pe I	⊠	12	55
	Pa	◻	6	50
	I Pe E	○	13	72
	I Pl E	●	2	20
	I Pl I	⊕	1	4
	I Pe I	⊗	9	75
	F Pe E	▲	3	21
	F Pl E	△	2	-
	F Pl I	▴	2	14
Reef			51	36
	LE	◇	6	43
	LI	◆	-	-
	CB	◊	3	16
	LD	⊙	1	10
	CH	⊗	-	-
Lagoon			10	16

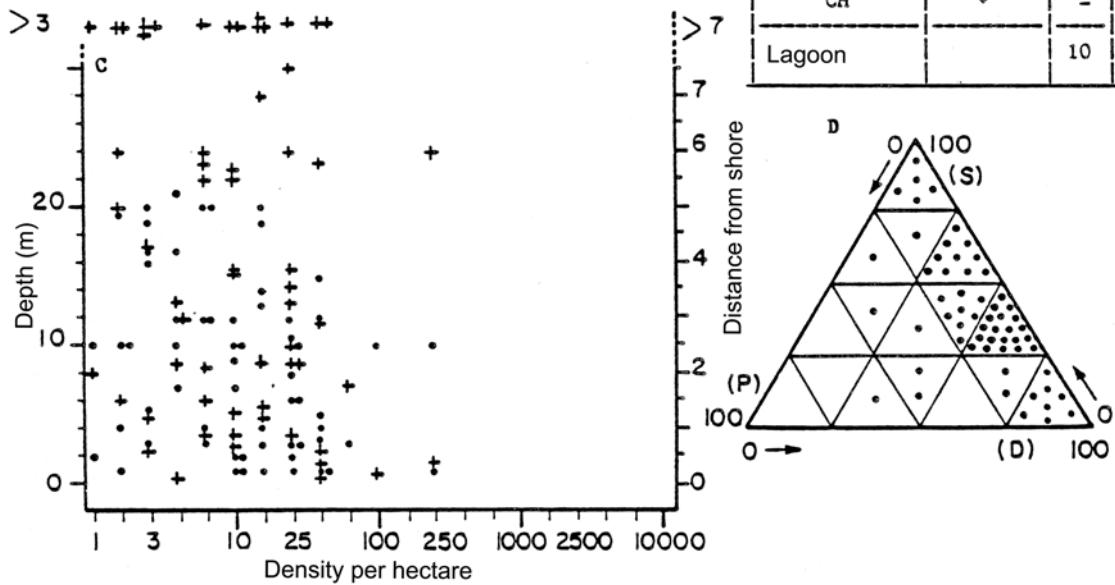


Figure 34: Distribution and abundance of *B. argus*.

- *Bohadschia argus* is a common species in all parts of New Caledonia.
- It is a typical reef-dwelling species, which also occurs in the outer lagoon. It is very frequent on barrier reefs and windward islet slopes.
- Its bathymetric distribution ranges from submerged reef flats to depths of 22 m.
- Population densities infrequently exceed some one hundred specimens per hectare.
- It inhabits hard substrates, covered in coarse sand, in areas with marked water movement.

Stichopus chloronotus

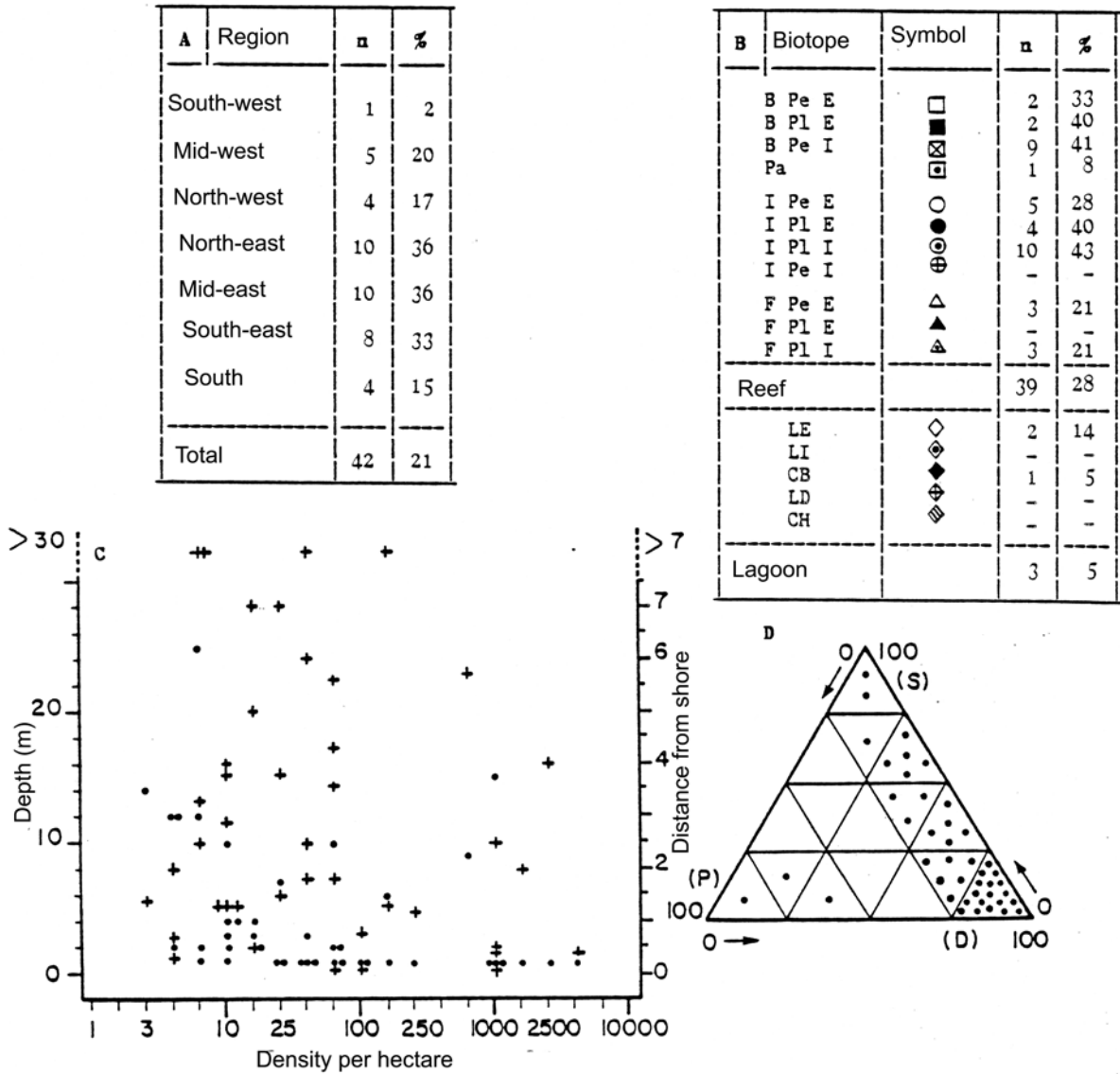


Figure 35: Distribution and abundance of *S. chloronotus*.

- *Stichopus chloronotus* is a common species all around New Caledonia.
- It is a reef-dweller, occurring on both upper reef drop-offs and reef flats.
- It most frequently occurs in the upper layers, not often being found at depths exceeding 12 m.
- Population densities can reach several thousand specimens per hectare.
- This species likes hard substrates, covered in coarse or fine sand.
- Population densities can reach several thousand specimens per hectare.

Holothuria sp. 1

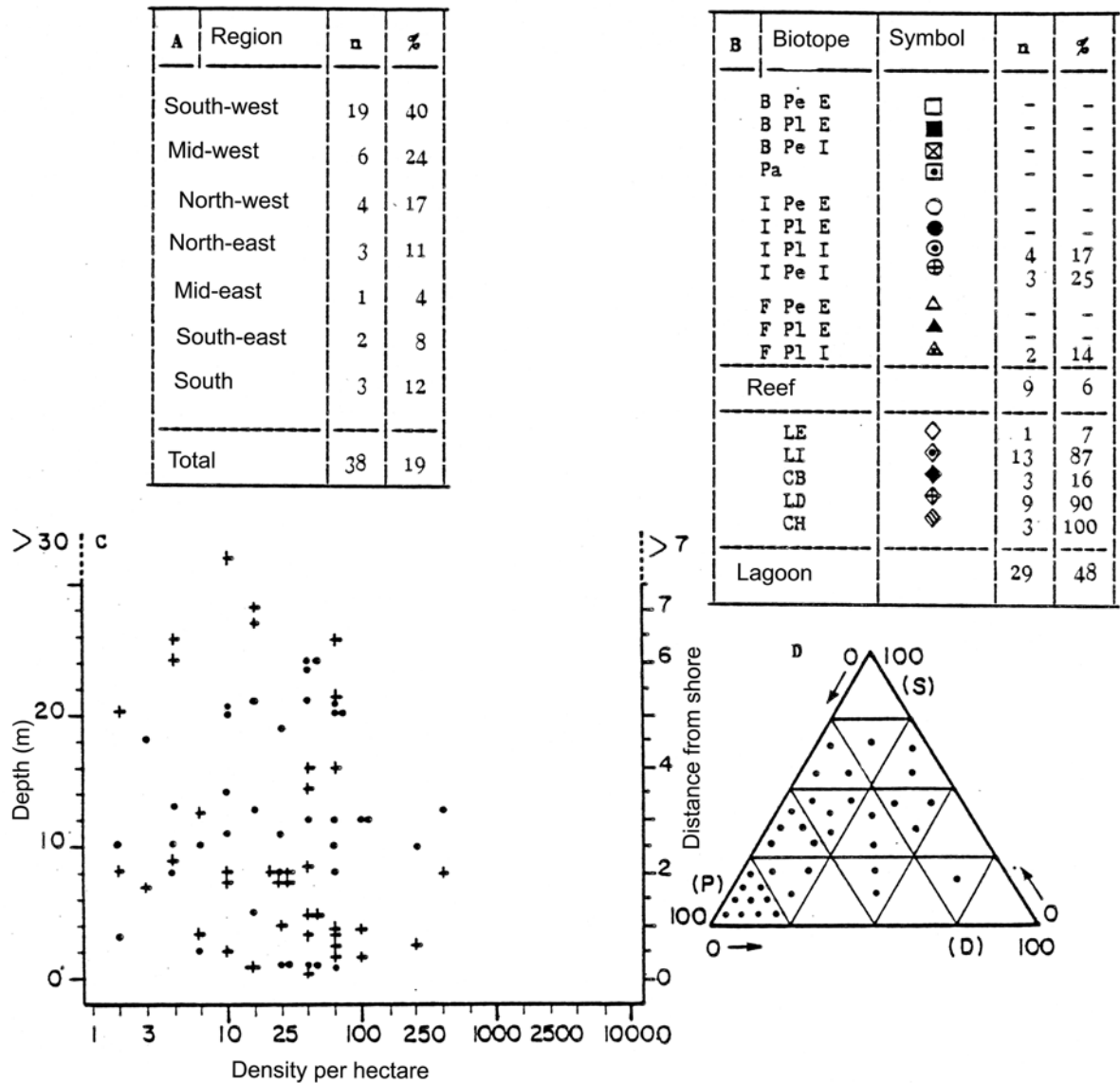


Figure 36: Distribution and abundance of *Holothuria sp. 1*.

- *Holothuria sp. 1* occurs all around New Caledonia and is particularly common on the west coast.
- It is a lagoon species undergoing terrigenous influence.
- Its bathymetric distribution shows that it is more common at depths of 10 to 20 m, but it also occurs on inner reef flats.
- Population densities do not often exceed some one hundred specimens per hectare.
- It is absent from hard substrates and prefers muddy sand or mud bottoms. It lives partly covered by the surface layer where its presence is revealed by a hump, but it is possible that its densities were under-estimated.

Holothuria (Acanthotrapeza) coluber

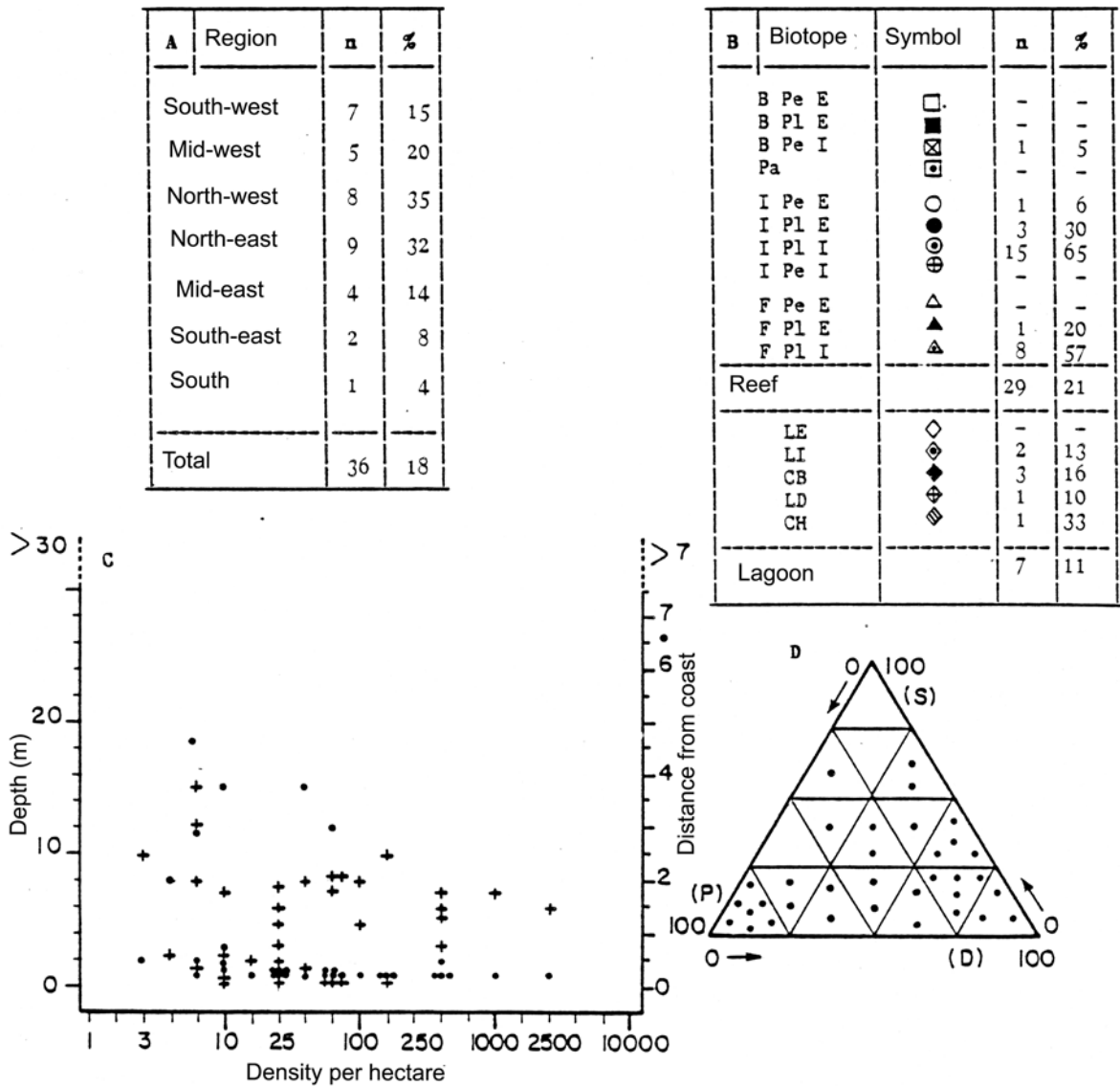


Figure 37: Distribution and abundance of *H. coluber*.

- *Holothuria coluber* is the last frequent species. It is present all around New Caledonia, but is more frequent in the north, on both coasts.
- It inhabits areas under terrigenous influence and in particular reef flats strewn with blocks and rubble.
- From the bathymetric point of view, it is generally to be found in areas left dry during exceptionally low tides, but has sometimes been recorded at depths exceeding 15 m.
- Population densities, on average 155 specimens per hectare, infrequently exceed a thousand specimens.
- Absent from pure sand bottoms, it is found on mixed substrates where the pelite fraction is large.

4.3.4 Infrequent species (see Annex 2)

Thelenota anax is an infrequent species, but is found all around New Caledonia.

Its affinity for the reef habitat is partly concealed in the table because of its frequency in the outer lagoon. This is a species that inhabits reef slopes not subject to terrigenous influence and passages. It is therefore found in areas with strong water movement. Never observed above a depth of 8 m, it can be found at depths of up to 28m.

Population density is 14 specimens per hectare on average and up to a maximum of 45. Its substrate requirements are not very strict. The fine fraction is however formed of organogenic pelites.

Actinopyga spinea is an uncommon species, except in the south-western area. It is a typically lagoon-dwelling species occurring very frequently in the inner lagoons.

Its bathymetric distribution ranges from 5 to 30 m. Population density, with a mean of 108 specimens per hectare, can reach a thousand.

This species inhabits soft substrates, especially where the pelite content is high; it may burrow under the top layer.

Holothuria leucospilota is an uncommon species, especially on the east coast.

It is completely absent from the barrier reefs and coral slopes, while occurring frequently on reef flats and in coastal lagoons of areas close to the shore.

Its bathymetric distribution, usually located in the intertidal zone, can reach depths of 12 m.

Population densities can locally be high, exceeding several thousand specimens per hectare, with a mean of 505.

It is absent from pure sand bottoms and is found on mixed substrates, with blocks, rubble and muddy sand.

Actinopyga palauensis is an uncommon species, but occurs throughout the New Caledonian lagoon.

It has a marked affinity for reef areas, occurring in passages and on the outer slopes of barrier reefs and islets.

It is observed in areas with strong water movement from 0 to 22 m.

Population density, with a mean of 10 specimens per hectare, does not exceed 100.

This species lives on hard substrates, especially coral slabs, with a more or less complete covering of coarse or fine sand.

Pearsonothuria graeffei is an uncommon species. It occurs only on the east coast, mainly in the south-east and centre-east regions.

This is a reef-dwelling species, inhabiting the slopes, which are usually quite steep in these zones. This is the part of the lagoon with the freshwater input, where green algae populations, in particular *Halimeda incrassata* and *H. opuntia*, are well developed.

Its range extends from submerged reef flats to depths of up to some 20 m, in areas located less than 5 miles offshore.

Population density, 50 specimens per hectare on average, infrequently exceeds 100.

This species lives on hard sand-covered substrates, where there is also a terrigenous pelite fraction.

Bohadschia vitiensis is an uncommon species, more frequently found on the west coast.

It prefers lagoon habitats and inner reef flats undergoing a terrigenous influence.

It is found at depths of 0 to 25 m, less than 7 miles offshore.

Mean density is 70 specimens per hectare and total density can reach several hundred.

It lives partly or completely buried under soft sand/mud or muddy substrates.

Holothuria hilla is an uncommon species, nevertheless found all around New Caledonia.

It is mostly absent from the barrier reefs and is found on block and rubble bottoms on islet reef flats and fringing reefs, as well as in coastal zones.

Its bathymetric distribution ranges from 0 to 20 m, but the dense populations occur on the reef flats. Mean density, 60 specimens per hectare, could be underestimated, because of the sometimes cryptic habitat.

Absent from clean sand bottoms, it seems to be more frequent in mixed habitats.

Holothuria sp. 2 is an uncommon species, most frequently found in southern parts of New Caledonia. It lives only in lagoon areas.

It has been observed at depths of up to 24 m, sometimes in dense populations, reaching some one thousand specimens per hectare, with a mean density of 190, which can be underestimated because of its burrowing habit.

It inhabits sandy mud bottoms.

Bohadschia maculisparsa is an uncommon species, occurring in the southern and south-western parts of New Caledonia.

It has been harvested at depths of between 5 and 20 m. Its mean density is 37 specimens per hectare, rising to a maximum of some one hundred.

It is a lagoon species, living partly buried in sand-and-rubble bottoms, sometimes in current-prone zones.

Bohadschia aff. *marmorata* is an uncommon species, found all around New Caledonia except in the north.

It is a lagoon species, occasionally found also on reef slopes.

It has been harvested at depths of between 10 and 30 m.

Mean density is quite low, at 20 specimens per hectare.

It likes soft substrates.

Bohadschia tenuissima is a species that would appear to be more common in the south-western part of New Caledonia.

It is a lagoon species, occurring at depths of between 5 and 20 m, in muddy sand and sandy bottoms with shell debris. Its mean density is 11 specimens per hectare.

Bohadschia similis is an uncommon species, most frequently occurring in the northern reaches of the New Caledonian lagoon.

It inhabits inner reef flats subject to terrigenous influence.

Its populations can reach high densities, with an observed mean of 300 specimens per hectare.

It lives partly buried in muddy sand or sandy mud.

Actinopyga lecanora is an uncommon species in these observations, possibly because of its nocturnal behaviour.

It is a reef-dwelling species, often concealed in crevices in the coral or rubble.

Its bathymetric distribution reaches depths of up to 20 m. It has a low mean density, 5 specimens per hectare.

It lives on hard substrates and rubble containing coarse sand.

4.3.5 Scarce species

The limited observations carried out yield information on the ecology of these species. Their geographical distribution and distribution by biotope are given in Annex 2. The following species occur at more than one station.

Stichopus horrens is a scarce species in the context of this study, but its cryptic habitat in blocks and crevices and its nocturnal behaviour mean that it has probably been underestimated.

Its mean density is 80 specimens per hectare.

It inhabits hard substrates and areas with large-sized rubble.

Stichopus sp. 1 is a typical lagoon-dwelling species. It was harvested at seven stations at depths ranging from 10 to 30 m. and distances offshore of 1 to 7 miles. Its substrates always include a pelite fraction exceeding 50%, often as high as 75%, and it is never found on a hard substrate. Its mean density is 29 specimens per hectare, with a maximum density of 120.

Holothuria impatiens was harvested at 6 stations on islet inner reef flats and fringing reefs. It is therefore a shallow-water species, found in areas under terrigenous influence. The substrates of slab coral or coral blocks and rubble are often covered in a layer of muddy sand. Density is low, 17 specimens per hectare on average, with a maximum of 42.

Holothuria flavomaculata was harvested at 6 stations on the east coast and in the south. It lives at depths of between 2 and 20 m, on inner reef flats or the ends of bays. In these habitats, a mud fraction is always present and the brownish-red colour of the sediment is due to the high metallic oxide content. Population density is 76 specimens per hectare on average, with a maximum of 190. The highest densities are observed in muddy bays with platform reefs.

Stichopus pseudhorrens was only harvested at 4 stations in the south-western and southern regions. It has an affinity for reef habitats, living reef slopes, in passages and in the outer lagoon, in areas under terrigenous influence where there is strong water movement. It is a fairly deep-dwelling species, observed at depths of 10 to 30 m, on slabs or amidst coral debris containing clean coral sand, but also possibly containing organogenic pelites. Density is always very low, on average 3 specimens per hectare.

Holothuria fuscocinerea was only harvested at 3 reef slope or reef flat stations, at depths of between 1 and 20 m. It was observed among coral blocks and rubble.

Holothuria pervicax was only harvested at three outer or inner reef flat stations on the same type of substrate as *H. fuscocinerea*.

Holothuria verrucosa was only harvested at 2 inner reef flat stations. These three species have a cryptic habitat, in blocks and rubble. Their frequency and abundance could therefore have been underestimated.

Lastly, ten species were only found at a single lagoon station during this study.

Holothuria cinerascens was harvested on the outer reef flat of a very broad fringing reef at Unia, near Yaté. In this area, the submerged barrier reef does not break the swell and this reef offers hydrodynamic conditions comparable to those of a barrier. The substrate is formed of a coral slab, containing crevices filled with coarse sand. The animals are buried in this sand, apart from their front section. The density of this population, spread along a narrow strip several meters wide, parallel with the outer slope, is high, reaching some 1 000 specimens per hectare.

Holothuria difficilis was harvested on the outer reef flat of Kundy Islet, in the centre-west region. It was also observed on the inner reef flat of the Ricaudy fringing reef near Nouméa and in an Ouvéa Island lagoon seagrass bed in the Loyalty Islands. It must therefore be much more common than our research has shown. At the study station, the animals were under blocks of dead coral, whereas on Ouvéa they were on leaves of *Cymodocea* feeding off the epiphytic felt. The density is high, 400 specimens per hectare.

Holothuria maculosa was harvested from one south-western lagoon station in Bourail Bay at a depth of 25 m on coral sand. The five specimens amounted to a density of 25 per hectare. This location is quite surprising because the species had been found on a reef flat at Amédée Islet, south-western lagoon (Féral and Charbonnier, 1986).

Actinopyga crassa. A single specimen was harvested in Uitoé Passage, south-western New Caledonia, at a depth of 8 m. The substrate was a slab, covered in coarse coral sand, experiencing strong tidal current activity.

Actinopyga flammea. A single specimen was harvested, on the outer reef slope at Améré Islet at a depth of 20 m. The substrate is strewn with coral blocks. The tidal currents are very strong at this station.

Labidodemas semperianum. A single animal was harvested on Laurent Reef, centre-east region, at a depth of 4 m, but this species has been observed near Yaté, on the fringing reef. At the harvest station, a leeward islet slope, small coral sand pockets are surrounded by coral.

Holothuria rigida. A single animal was harvested, on the fringing reef at Unia, south-east region, on the reef flat coral slab.

Holothuria discrepans. A single specimen was harvested, on the inner reef flat of a fringing reef on Yaba Island, in the north-western region. It was found amidst large pieces of *Acropora* rubble.

Holothuria coronopertusa. A single animal was harvested, in Uitoé Passage, south-western region, at a depth of 20 m. The substrate is a slab covered in coral sand, experiencing strong tidal current activity.

Holothuria conusalba. The holotype had been found during sampling on Ricaudy Reef, south-western region, and a specimen was harvested during the HOLOT programme on the reef flat of Ouane Islet, north-western region. The substrate is a slab sustaining living coral, in microatolls and sandy hollows with various algae populations.

Stichopus sp. 2. A single specimen was harvested in the south-western lagoon at a depth of some 20 m. A fairly thick covering of coral sand sustaining a population of green algae covered the slab.

Some final observations concern *Holothuria* sp. 3, which was only harvested during bottom trawling on soft mud (F. Conand, personal communication). On this substrate, the quadrat technique by diving is unsuitable because of the reduced visibility and the self-burying lifestyle of the species. It was harvested in Saint Vincent Bay, center-west region, at depths of 5 to 11 m. Catches from three trawls, each lasting one hour, were 10, 2 and 36 specimens respectively. In La Foa Bay, center-west, at depths of between 10 and 19 m, 37 animals were harvested and three were harvested in Canala Bay, center-east, at depths of between 13 and 20 m. In these trawls, apart from a single specimen of *H. scabra* in Saint Vincent Bay, *Holothuria* sp. 3 was the only species found. In contrast, other trawls yielded *S. variegatus*, 1 specimen, and *A. miliaris*, 3 specimens, in Chasseloup Bay, north-west, and *H. scabra*, 120 specimens, in Harcourt Bay, north-east, plus 67 specimens, in La Foa Bay, centre-west.

4.4 DISCUSSION OF RESULTS

These results, obtained by a conventional analysis of autoecology, relate to a fairly extensive geographical area and a varied range of biotopes and should therefore be useful for a comparison with other published works on the tropical Pacific.

4.4.1 A synopsis of results obtained in New Caledonia

The autoecological approach is necessary, especially in the case of small artisanal operations. Typically, these fisheries are not multi-specific, because different species are exploited depending on country and period. The observations presented herein therefore provide useful information on distributions and abundances.

4.4.1.1 Species distribution

With regard to distributions, the analysis has revealed the affinities of each species as regards environmental factors.

Geomorphological factors

The first gradient in the reef complexes of New Caledonia is perpendicular to the shoreline. It corresponds to the terrigenous and reef-related influences, which are mostly antagonistic and roughly related to distance offshore. In fact, the submarine valleys of rivers and channels permit the extension of terrigenous influences to areas quite a distance offshore.

- Species with an affinity for the reef, mostly found on the slopes, passages and outer reef flats of barrier and lagoon reefs and in the outer lagoon, are therefore found in clear water, oxygenated by the strong water movement in this zone and on a substrate under marine organogenic influence. These are in particular: *A. mauritiana*, *A. palauensis*, *B. argus*, *H. fuscogilva*, *H. nobilis*, *H. cinerascens*, *H. coronopertusa*, *S. chloronotus*, *T. ananas*, *T. anax*, *S. pseudohorrens*.
- In contrast, the species with a terrigenous affinity, most frequently occurring on inner reef flats of the inner lagoon and bays, live in sheltered areas, where the water is often more turbid and where the substrates undergo a continental influence. These are: *A. miliaris*, *A. spinea*, *B. tenuissima*, *T. suppress*, *B. vitiensis*, *H. coluber*, *H. edulis*, *H. leucospilota*, *H. scabra* and *H. scabra* var. *versicolor*, *Holothuria* sp.1, sp. 2, sp. 3 and *S. variegatus*.
- The other species are more tolerant of intermediate conditions of this gradient or are ubiquitous like *H. atra*.

Edaphic factors

Substrate requirements can be deduced from the triangular diagrams. Depending on the location of the stations where the species were harvested, several zones can be demarcated. By adapting the terminology proposed by Glémarec (1969) for temperate benthic populations and Thomassin (1978) for tropical populations, it is possible to define the following particle-size affinities, represented on Fig. 38.

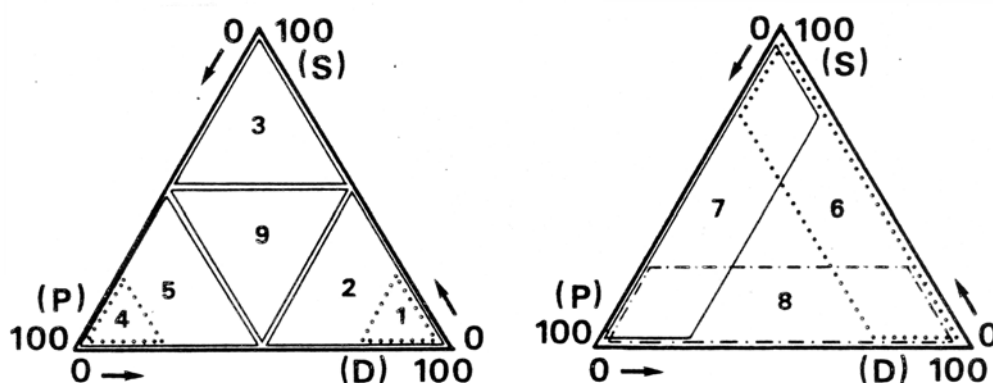


Figure 38: Particle-size affinities for aspidochirote holothurians of the lagoon.

1. Epifauna or cryptofauna of slabs: *A. mauritiana*, *H. cinerascens*.
2. Gravel-dwelling species: *P. graeffei*, *A. flammea*, *L. semperianum*, *H. impatiens*, *H. pervicax*, *H. discrepans*, *H. verrucosa*, and *H. fuscocinera*.
3. Tolerant psammophilous species: *H. fuscogilva*, *S. pseudohorrens*, *B. marmorata*. It should be mentioned that there are no strictly psammophilous species, because there are no holothurians in the submarine sand dunes, for example.
4. Mud-loving species: *H. scabra*, *B. similis*, *Holothuria* sp. 3.
5. Tolerant mud-loving species: *H. scabra versicolor*, *A. spinea*, *Holothuria* sp. 2, *S. variegatus*, *B. tenuissima*.
6. Gravel-dwelling and psammophilous species: *H. nobilis*, *T. anax*, *B. argus*, *H. fuscopunctata*, *S. chloronotus*, *A. Palauensis* and *A. lecanora*.
7. Psamilliphous and mud-dwelling species: *Holothuria* sp. 1, *B. vitiensis*, *A. miliaris*, *Stichopus* sp. 1.
8. Gravel-dwelling and mud-dwelling species: *A. echinites*, *H. coluber*, *H. leucospilota*, *H. hilla*, *S. horrens*, *H. flavomaculata*.
9. Species thriving on varied substrates: *H. edulis*, *B. aff. marmorata*.
10. Ubiquitous species: *H. atra*.

Depth

Lastly, depth, which is never very great in the lagoon, can be used to distinguish between coastal zones and reef flats, which are sometimes above water from permanently submerged areas. Exposure to the air in fact causes extremely difficult conditions for organisms in tropical areas because of the high temperatures that can be reached when exceptional low tides occur in the middle of the day in the hot season. During these seasons in New Caledonia the highest tidal amplitudes occur during the night and the lowest diurnal tides occur between May and September. This attenuates the effects of temperature rises and evapotranspiration. As with the geomorphological gradient, it is possible to distinguish three species categories.

- Species usually found in zones prone to drying out: *A. echinites*, *A. mauritiana*, *A. miliaris*, *B. similis*, *H. cinerascens*, *H. coluber*, *H. leucospilota*, and *S. chloronotus*.
- Species of lagoons and slopes are usually submerged. In order of increasing depth, a general trend enables them to be classified as follows: *P. graeffei*, *T. anax*, *A. palauensis*, *H. flavomaculata*, then *H. fuscogilva*, *H. fuscopunctata*, *S. pseudohorrens*, *B. marmorata*, *B. maculosparsa*, *Stichopus* sp. 1, *Holothuria* sp. 2, sp. 3, *T. anax* and *A. spinea*.
- The other species are more tolerant, but can also escape the stress of drying out either by their burrowing habit or because of their cryptic habitat in reef flat cavities or in seagrass beds where a wet environment is maintained.

These categories may be less precise than those that could be defined on the basis of particle-size studies nevertheless permit a classification of species' affinities with all types of lagoon substrates.

4.4.1.2 Species abundance

The main results obtained on species abundance are summarized in Fig. 39. The relative abundance of the main species is plotted on the basis of data from Table 11 relating to densities and biomasses from the total harvest of all species.

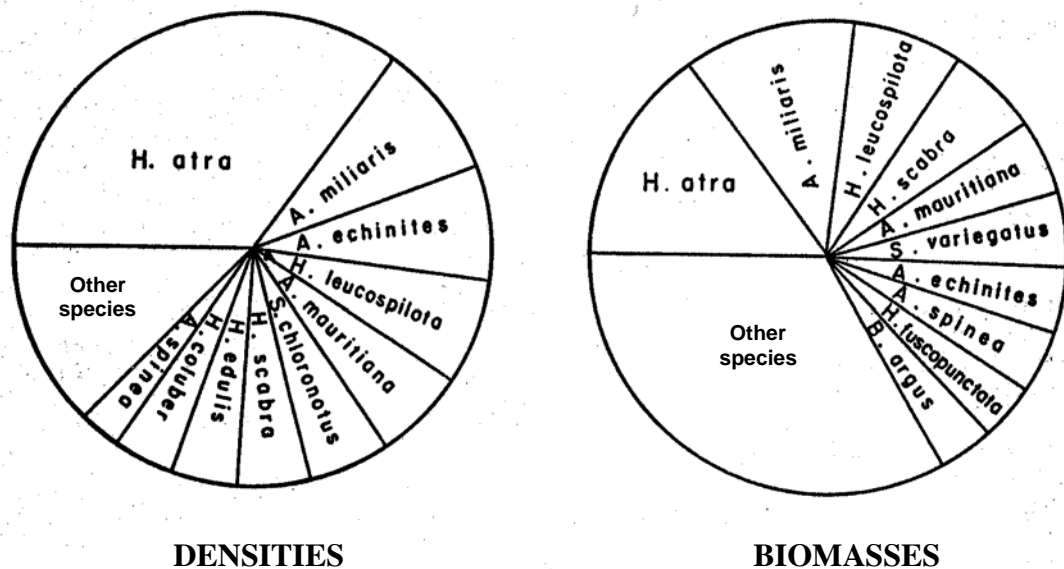


Figure 39: Relative abundance of the main species.

In order to be able to include holothurians in the lagoon energy balance calculations, a tentative assessment of their weight densities, both mean and maximum, was performed for the main species. As neither direct measurement of the calorific content of the tegument nor indirect measurement from biochemical constituents has yet been carried out, it seemed possible to use certain results from Lawrence (1980) for an initial approximation. The data he presents in fact show that the energy equivalent of the fresh tegument differs little between species, being situated at some 0.50 kcal per gram, equivalent to 2092 J. The results obtained on the dry tegument of deep-dwelling species by Sibuet and Lawrence (1981) and Walker *et al.* (1987) confirm this consistency, both on individuals of different sizes and between different species. For example, the mean value of 0.50 kcal per gram of fresh tegument was used to calculate the calorific contents of species for which the ratio of tegument to total weight had already been worked out (see Table 6). The results presented in Table 12 show that the maximum values are usually higher than the means by one point on the scale. They are sometimes considered as reflecting the maximum capacities of a system, but as they are very much affected by the influence of sampling, we prefer to use the mean values rather than these. It emerges that medium-sized species such as *A. echinites*, *A. mauritiana*, *A. miliaris* and *H. scabra* have a density, in energy terms, which is much higher than that of some of the large species.

Table 12: Mean and maximum weight densities, in fresh weight and calories, of the main species in New Caledonia.

b: mean biomass in g; *B max*: maximum biomass in g; *c*: mean biomass in kcal; *C max*: maximum biomass in kcal; *T/P*: ratio of tegument weight to total weight.

(1), (2), (3): tegument calorific values, calculated from Lawrence (1980), i.e. (1) = 0.54, (2) = 0.52, (3) = 0.40 kcal/g.

Species	Biomass b	g/100 m ² B max	T/P	Biomass c	kcal/100 m ² C max
<i>A. echinites</i>	1 814	12 670	0,47	426	2 977
<i>A. mauritiana</i>	2 505	25 556	0,51	639 (1)	7 038 (1)
<i>A. militaris</i>	2 082	23 983	0,58	604	6 955
<i>A. palauensis</i>	175	705	0,45	39	139
<i>B. similis</i>	790	5 106	0,59	233	1 506
<i>H. atra</i>	756	11 994	0,35	137 (2)	2 183 (2)
<i>H. scabra</i>	2 416	18 720	0,56	676	5 242
<i>H. s. versicolor</i>	977	6 864	0,50	244	1 716
<i>H. fuscogilva</i>	283	625	0,57	81	178
<i>H. fuscopunctata</i>	475	1 657	0,47	112	389
<i>H. nobilis</i>	237	1 298	0,51	60	331
<i>S. chloronotus</i>	323	1 734	0,60	77 (3)	428 (3)
<i>S. variegatus</i>	510	1 983	0,69	176	684
<i>T. ananas</i>	489	4 963	0,73	178	1 811

This first broad approach does not however take into account the relative surface areas of the various biotopes. A better understanding of the geomorphology of the lagoon would make it possible to weight these values and to provide a more realistic picture.

4.4.2 Comparison with other results obtained in the tropical Pacific.

A comparison with other results obtained in the region will be attempted, despite the difficulties involved, in order to present a synopsis of available knowledge (see 1.1).

With regard to species distribution, the results obtained in New Caledonia are generally consistent with previous descriptions. Of those dealing with a number of species, which are often presented in the order of the taxonomy, in particular by Yamanouchi (1939), Rowe and Doty (1977), Levin (1979), Sloan *et al.*, (1979), Harriot (1980), Féral and Charbonnier (1986) and Massin and Doumen (1986), species' affinities are comparable, which would tend to prove that their distribution is linked to that of the reef and lagoon biotopes. An exception is *H. fuscogilva*, whose distribution in Fiji is different from that observed in New Caledonia, because, on the reefs of Suva and Levuka, it is abundant on shallow *Syringodium isoetifolium* seagrass beds (Gentle, 1979).

With regard to the **numerical abundance** of species, this is presented, based on recent data from the literature, without reproducing what is already available in Bakus (1973). In Table 13, only the species

studied by more than one author are included, with density values being expressed in terms of a surface area unit of 100 m². In recent years, our understanding has been extended to more regions and the results given are very variable. The disparity between methods and objectives leads to differences for the same species of several orders-of-magnitude. The size of the quadrats used definitely influences these values, especially the maximum density ones.

It is a striking fact that abundant and exploited species like *A. miliaris* and *H. scabra* are as yet little known, apart from the work by Shelley (1981) and reports by the fisheries services. Species *H. atra* has, however, been quite extensively researched. Its high densities are often reported, in particular on atolls where its densities can reach several dozen specimens per m² (Salvat, 1975, Webb *et al.*, 1977).

Table 13: Mean and maximum densities of aspidochirote holothurians in the Indo-Pacific region in number of specimens per 100 m²

Reference Species	LEVIN (1) 1979 Indo-Pacific	HARRIOT (2) 1980 G.B. Reef	GROSENBAUGH (3) 1981 Yap, Lagoon	ROBERT-BRYCE (4) 1982 G.B. Reef	HARRIOT (5) 1985 G.B. Reef	HAMMOND et al. (6) 1986 G.B. Reef	MASSIN-DOUMEN (7) 1986 P.N.G.	CONAND (8) 1987 New Caledonia	ROME-DOITY (9) 1977 Guam	LAWRENCE (10) 1980 J. Marshall
<i>A. echinites</i>	>1		1 023	15			2,7	8,5	75	
<i>A. mauritiana</i>	>1					0,05 - - 0,02	0,1	8,7	150	1200
<i>B. argus</i>	>1					0,3 0,4 0,2	0,3	0,2		
<i>H. atra</i>	>1	84 43 17 18	10	< 5		0,9 12,6 1,3	54,0	5,5	130	5200
<i>H. edulis</i>	<1	1 10 9 10	23	30		- - 1,0		1,1		
<i>H. leucospilota</i>	>1	8 16 15 3	10	< 5		0,1 0,05 0,05	46,8	5,1	160	2400
<i>H. nobilis</i>	<1			< 5	0,1 0,1	0,1 - 0,2	0,1	0,1		
<i>H. difficilis</i>	>1			< 5		- - 0,02		3,8		32400
<i>H. cinerascens</i>	>1			175				10,3	360	
<i>H. hilla</i>	>1		3					0,6	50	
<i>H. impatiens</i>	<1	2 32 19 5		15		1,2 2,2 0,8		0,2		5200
<i>S. chloronotus</i>	>1	- 1 1 15				- 0,1 -		2,9		1500
<i>T. ananas</i>	<1				0,5 1,0	6,8 9,3 2,0		0,2		

- (1) 1: 'broad' distribution, eurytype in various biotopes; 2: 'narrow' distribution, stenotope
- (2) Heron Island. 1: inner reef flat; 2: median reef flat; 3: outer reef flat; 4: lagoon
- (3) Mean values calculated from two 30 sq. m. transects in a seagrass bed.
- (4) Beacon Island, Western Australia.
- (5) Surveys of 9 reefs. The values have been multiplied 3 to correct the under-estimation. 1: outer slope; 2: inner slope.
- (6) Brewer and Rib reefs, in the median section of the central region, 30n transects, each 400 sq. m. in area. 1: outer reef flat; 2: inner reef flat; 3: leeward slope.
- (7) Laing Island, eastern reef flat, mean of 9 quadrats, each 1600 sq. m. in area.
- (8) 1: mean density for all stations where the species occurs; 2: maximum density.
- (9) Hoover Beach reef flat, maximum density, 20 sq. m. quadrats.
- (10) Maximum density, 0.33 sq. m. quadrats.

5 TAXOCENOSES

5.1 ANALYTICAL METHODS

5.1.1 Holothurian abundance on various types of reef formation

The analysis was conducted on the basis of the crude values from the two-dimensional tables, which are quantitative data, by grouping the stations (sum of columns) rather than the species, for the 16 main biotopes. The results are considered from the angle of both classifications, through the four kinds of formation, i.e. along the 'coast-offshore' gradient and according to the functional morphology in five groupings.

The results, densities and biomasses in each classification, are compared by two successive tests. A variance analysis, using one classification criterion, the 'F' test, makes it possible to test the equality of the means calculated for each grouping and each type of formation (Sokal and Rohlf, 1981). If the null hypothesis of equality is rejected, the means can be compared two-by-two using a 't' test.

5.1.2 Determination of fauna composition by inertia analysis and automatic classification.

Inertia analysis or factor analysis involves analyzing the structure of a data matrix and appraising the resemblances or differences between variables or observations. It is frequently used in benthic ecology to describe and interpret the structure of ecosystems (Chardy and Glémarec, 1974; Guille and Ponge, 1975; Chardy *et al.*, 1976) or some parts of them, for example taxocenoses (Domain, 1972; Intès, 1980).

While its theoretical foundations are long-established, its use only developed with the progress of computer science, making it possible to process large data sets rapidly. It is particularly useful in little known fields where cross-checking with previous data is not possible, but allows 'the mathematical translation of ecological intuition' (Laurec, 1979). It would therefore seem suitable for research on holothurians of the New Caledonian lagoon (Conand and Chardy, 1985). The various methods are described in general works by Lebart and Fenelon (1971), Lebart *et al.* (1977) and Legendre and Legendre (1979). The possible options, contributions and limits of each are also discussed in works by Frontier (1974), Blanc *et al.* (1976), Chardy *et al.* (1976), Dessier and Laurec (1979) and especially Laurec (1979).

The objective of this study is to report on the structure, as defined by a taxonomic group, and therefore to estimate the fauna affinities between stations or biotopes.

The data are always based on the two-dimensional tables (Imax, Jmax). The possible ways of processing are legion and result from choices at various levels.

- Data coding: depending on the nature of the characteristic used, it is possible to distinguish between qualitative and quantitative analysis. Qualitative analysis uses binary or logical variables with presences being coded 1 and absences 0. It seeks to demonstrate which species are indicative of the environment, whereas quantitative analysis attempts to take a more functional approach to the system. The joint use of these approaches should yield an understanding of these aspects.
- Measurement of similarity and dissimilarity: Euclidean distances are used because they offer the possibility of addressing the issue of the duality between variables and observation. Generally speaking, the distance between stations i_1 and i_2 is:

$$d^2_{i_1, i_2} = \sum_{j=1}^{j \max} (x_{i_1, j} - x_{i_2, j})^2$$

and the distance between species j_1 and j_2 is:

$$d^2_{j_1, j_2} = \sum_{i=1}^{i \max} (x_{j_1, i} - x_{j_2, i})^2$$

The techniques used here are variants of the ‘General Analysis’ defined by Lebat and Fénelon (1971). The following coefficients have been chosen from the conclusions and recommendations formulated by Chardy *et al.* (1976) and Laurec (1976).

- For the **qualitative analysis**, a coefficient that does not take double absences into consideration, the Ochiai similarity coefficient, is used. As this study covers an extensive geographical area, there are numerous double absences and they have little ecological significance (Blanc *et al.*, 1976).

$$s_{i_1, i_2} = \sum_{j=1}^j \max \frac{x_{i_1, j}}{\sqrt{TI_{i_1}}} \cdot \frac{x_{i_2, j}}{\sqrt{TI_{i_2}}}$$

où $TI_{i_1} = \sum_{j=1}^j \max x_{i_1, j}$ et $s = 1 - d$

- For the **quantitative analysis**, the coefficient of correlation between variables was chosen for an analysis of the main components. Density and biomass values were converted into log values (x + 1). They were also reduced to attenuate their heterogenous nature:

$$d^2_{i_1, i_2} = \sum_{j=1}^j \max \left(\frac{x_{(i_1, j)}}{S_i} - \frac{x_{(i_2, j)}}{S_j} \right)^2$$

where S_j is the standard deviation from line j .

The other options concern the mass assigned to the points, which is equal for all, and the position of the origin, which is situated at the barycentre of the cluster of observation points (stations). The calculations were performed on the DPS 7 computer of the Ifremer Brest Centre, using the COM 4c Programme, which offers the various options.

Each analysis yields **factor axes** that explain a percentage of variance. Each pair of axes in fact corresponds to a sub-space and its extent is expressed in terms of percentage of inertia. The extent of the various elements (observations or variables) is assessed by their contribution in relation to these axes.

In the principal component analysis (PCA), the R mode analysis, in which the variables are centred, should be distinguished from the Q mode analysis, in which the centering is performed on the observations. In the first case, as the lines are centred, the origin is located in the barycentre of the cluster of observation points and the analysis leads to an optimum representation of the observations rather than the variables. Similarly, in the Q mode analysis the variable configurations are optimum.

The pairs of factor axes define the factor planes, on which the observation points and variables are plotted and from which the visual analysis is performed. These (dual) configurations make possible the simultaneous interpretation of the links between observations and variables, not in terms of proximity but of relative position in relation to the axes.

Also, it is possible to introduce zero mass elements into the analysis. These **supplementary variables**, which are not involved in the determination of axes, throw light on the structures. Three categories of element have therefore been introduced:

- Abiotic parameters, including physical and edaphic factors;
- Biotic parameters, relating to the accompanying flora and fauna;
- Synthetic parameters, calculated from raw data, number of species, holothurian biomass and density.

Lastly, the visual interpretation on the graphs of an excessive number of points, such as the 216 observations, is difficult. It is however possible to plot the element class **barycentres**, which has been done by grouping stations by biotope. In addition to their simplifying role, the respective contribution of these barycentres also has value for the interpretation of the observations-variables relationship.

5.1.2.2 Automatic classification

While factor analyses produce optimum representations of variables and observations, automatic classification methods make it possible to divide these elements into classes, in such a way as to make each one as consistent and different from the others as possible. The combination of techniques yields useful information (Laurec, 1979).

Ascending ranking (Benzecri, 1973) was performed using Euclidian distances. The dendrograms were prepared using the Jambu (1981) method with the species and biotope projection coordinates in the sub-space defined by the first three axes of the quantitative analysis on the biomasses.

5.2 RICHNESS OF THE VARIOUS BIOTOPES

5.2.1 General results

Examination of the two-dimensional tables (species x stations) makes it possible to make some preliminary comments, in order to provide an overall picture of the richness of the various environments.

Over the 216 stations studied, specific richness varies from 0 to 13 species, with a mean of 5 species per station (Table 14).

Table 14: Specific richness of the various biotopes.

BIOTOPE	Number of species per station													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
B Pe E	1		1	1	2		2							
B Pl E	1	3		1		1								
B Pe I	1	1	7	6	4	2	1		1					
Pa		1	2		1		2	5	1					
I Pe E			2	1	1	4	2	3		5				
I Pl E				1	5	1	2		1					
I Pl I			2	2	1	4	8	3	1	1		1		
I Pe I			1	2	1		3	5						
F Pe E		3	3	4	2	1	1							
F Pl E		1	2		2									
F Pl I			2		3	1	3		3	1			1	
LE	2	1	2	4	1	2	1	2				1		
LI	4			1	3	4	1	1	3	1		1		
CB	4	3	4	1	2	2	1	4					1	1
LD						2			2	4	2	1		
CH						1	1							
Divers	1													
TOTAL	14	13	28	24	28	23	30	23	12	12	2	4	2	1

Stations without holothurians only represent 6% of the total sample. They are divided into two groups. The first comprises the barrier reef and the deep outer lagoon; these are environments where the number of species present is generally low. The second covers coastal areas, the inner lagoon and bay areas, which are not always easy to demarcate; in these environments, the number of species can be high and the absence of holothurians appears surprising at first. Two theories can be formed:

- their absence is a fact in some coastal environments, because of fresh water inflows, as they are a limiting factor for this stenohaline group;
- their absence is apparent and comes from a bias in the sampling, which is not suitable for coastal stations with a muddy substrate; this would appear to be confirmed by the harvest of *Holothuria sp.*, only 3 per trawl.

The biotopes with the highest specific richness are:

- the slab-bottomed lagoon, probably because of the microhabitats it offers;
- the inner reef flats of fringing and islet reefs, which are also heterogenous environments, even at a reduced spatial scale;
- the inner lagoon and windward slope of lagoon reefs.

The **density** and **biomass** are highly variable. The mean values, which only have a relative significance in view of the sampling, are 9.75 specimens per 100 m² and 3.19 kg per 100 sq. m., with maximum values being respectively 154 specimens and 27.47 kg per 100 sq. m. Overall holothurian abundance, per biotope, is estimated by the mean gross density and biomass values, arranged in ascending order; their position was calculated from the sum of positions for each of these two parameters (Table 15).

It emerges that the gradation is substantially the same for both densities and biomasses. Values rise from the barrier reef towards the fringing reef and also from the outer slope to the inner reef flat. These two gradients, 'coast-offshore' which is very clear on a lagoon-wide scale, and 'slope-inner reef flat', which corresponds to the functional structure of each reef, complicate the analysis task. Their respective extent will be studied.

The values presented remain estimations and cannot be considered as absolute measurements on a lagoon-wide scale. Their mean variation for both density and biomass extends over three orders of magnitude.

Table 15: Mean holothurian density and biomass for the various biotopes.

BIOTOPE	DENSITY n/100 m ²	BIOMASS Weight in (g)/100 m ²
Barrier, external slope	0,62	810
Fringing, slope	0,88	852
Outer slope	0,93	2 078
Islet leeward slope	1,21	1 547
Islet, windward slope	1,55	1 496
Barrier, flat, inner slope	2,21	1 172
Pass	1,01	2 121
Barrier, outer flat	1,78	1 624
Lagoon channel	3,38	2 161
Outer flat, islet	8,06	2 562
Bay	8,80	3 097
Lagoon pavement	8,14	4 591
Inner lagoon	8,85	3 657
Fringing, inner flat	25,91	5 701
Islet, inner flat	35,30	8 155
Fringing, outer flat	54,80	11 266

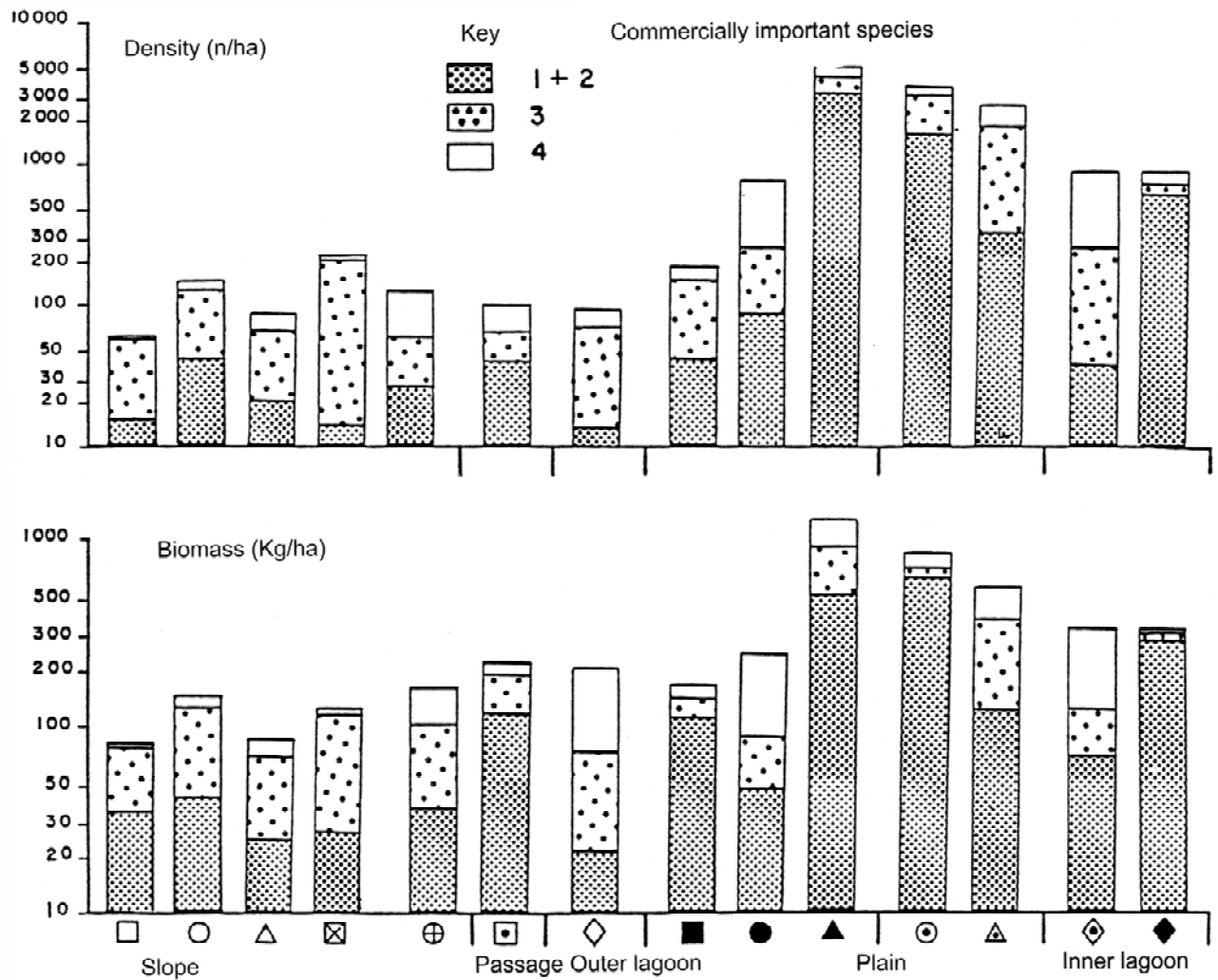


Figure 40: Holothurian biomass and density, per commercial grade, in the main biotopes assembled in groupings. For biotope symbol key, please refer to Fig. 12.

The general distribution of holothurian abundance is illustrated in Fig. 40, in which values are presented after logarithmic conversion in order to attenuate their dispersal. This representation also shows biotope richness in terms of the commercial grades of the various species. For those in grades 1 and 2, high and average value, the fringing reef flats, inner islet reef flats and bays are ten times richer than the other environments. The slopes are poor environments not reaching 50 kg per ha.

5.2.2 Results in relation to reef classifications.

In order to show the influence of the ‘coast-offshore’ and ‘slope-inner reef flat’ gradients, for these two classifications the biomass distributions are presented after logarithmic conversion (figures 41A and B).

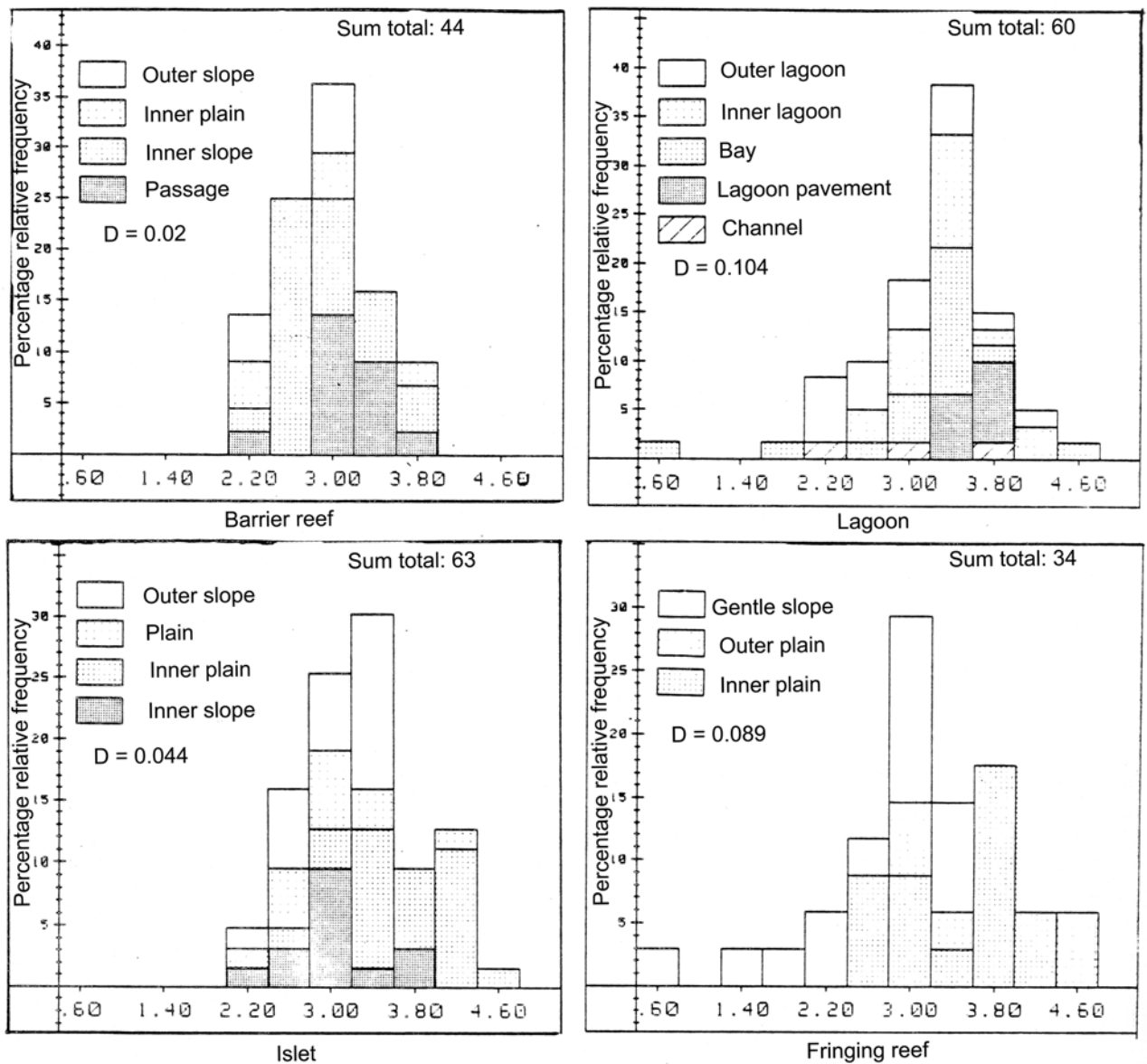


Figure 41A: Biomass frequency distributions by reef type. Log-converted data; D: value calculated by the Kolmogorov-Smirnov test.

Firstly, their consistency with the normal law was verified using Kolmogorov-Smirnov Test (Sokal and Rohlf, 1981). As the D values were lower than the table values, the normality hypothesis was not rejected at the $\alpha = 0.05$ probability threshold.

Lastly, the results of the 'F' tests, between the mean densities (and also the biomasses) of the various types of structure and also of the various groupings (Table 16) make it possible to reject the null hypothesis of the equality of means at the threshold $\alpha = 0.05$.

Lastly, the 't' tests, between the means taken two by two, make possible comparisons (Table 17). They reveal the following inequalities:

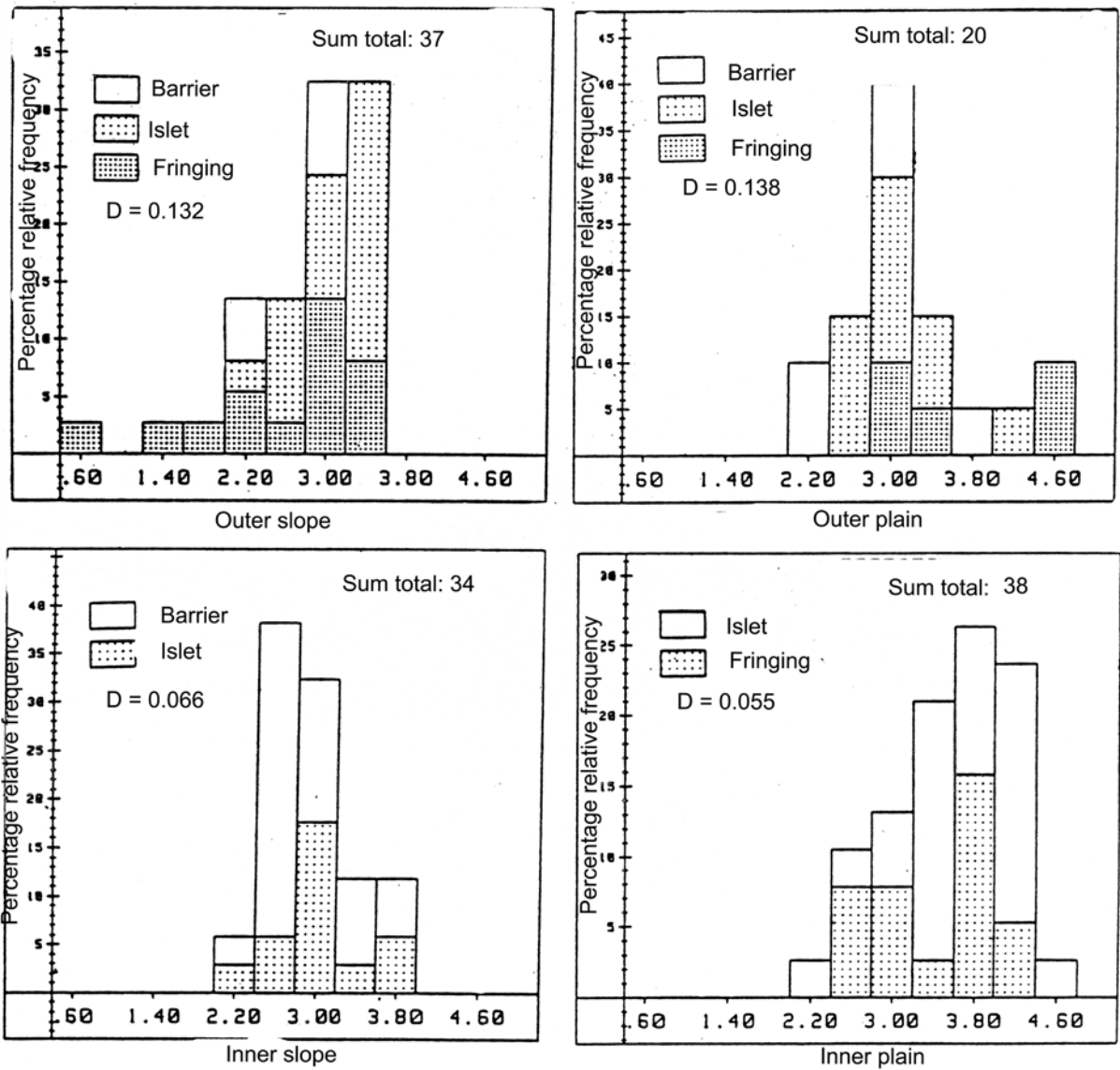


Figure 41B: Biomass frequency distributions by reef complex. Log-converted data; D: value calculated by the Kolmogorov-Smirnov test.

Table 16: Variance analysis with two controlled factors: types of reef formations and complexes. *: significant, P= 0.05, **: highly significant, P = 0.01.

CLASSIFICATION	VARIABLE	F observation	V1	V2	F theoretical
Type (geomorphology)	Density	8,88**	3	197	2,68
	Biomass	2,86*	3	197	2,68
Assemblages (Functional structure)	Density	27,58**	4	184	2,37
	Biomass	9,53**	4	184	2,37

Table 17: Differences between mean densities and biomasses in reef formations and complexes by 't' tests. NS: not significant, S: significant P = 0.05.

		Density				Biomass					
		1	2	3	4	1	2	3	4		
Reef Formations	Lagoon		S	NS	NS	1		S	NS	NS	1
	Barrier reef			S	S	2			S	NS	2
	Islet				NS	3				NS	3
	Fringing reef					4					4

		Density					Biomass						
		1	2	3	4	5	1	2	3	4	5		
Assemblages	Lagoon		S	NS	S	S	1		S	NS	S	S	1
	Inner reef flat			S	S	S	2			S	S	S	2
	Outer reef flat				S	S	3				NS	NS	3
	Inner reef slope					NS	4					NS	4
	Outer reef slope						5						5

Density comparison between formations makes it possible to define: lagoon, islet, fringing > barrier (1), whereas the comparison of complexes determines: inner reef flat > lagoon, outer reef flat > slopes (2).

Biomass comparisons between structures gives: lagoon, islet > barrier reef (3) and the comparison between complexes shows:

Inner reef flat > lagoon, outer reef flat, slopes (4) and lagoon > slopes (5).

These analyses clearly show that grouping by complex type is more likely to differentiate than grouping by type of structure. They also highlight the productivity of the inner reef flats, where mean density and biomass values were respectively 312 specimens and 6.93 kg fresh weight per 100 m². The observed differences between fringing reefs and islets are minor and not significant. Next comes the lagoon complex, with a mean density of 12 specimens and a biomass of 3.3 kg. These parameters vary greatly within this grouping between the 'slab-floor' lagoon setting, where mean biomass is 4.59 kg and the outer lagoon, where it is only 2.08 kg. The outer reef flats sit in an intermediate position. The inner and outer slopes are resource-poor groupings, with biomasses of 1.36 and 1.48 kg respectively.

5.3 MAIN TAXOCENOSES

5.3.1 Qualitative analysis

The qualitative analysis is performed on the observations, using the Ochiai Index; the other choices were defined earlier (see 5.1.2). The results are presented in Annex 3 and illustrated by Fig. 42 A and B. For the first three axes selected here, the variance percentages extracted are respectively 15.3%, 11.1% and 6.7%. These values are quite low, which comes from the high number of variables (48), as all the species have been kept, and from the scale of the study, which covers the whole lagoon.

5.3.1.1 Biotopes configuration

The absolute contributions of the barycentres of the observations grouped by biotope show that the passages, inner reef flats and inner lagoon return the highest values. The largest relative contributions for Axis 1 come from the inner lagoon, the inner slope of the barrier reef and the passages. This axis corresponds therefore to a coast-offshore gradient, or a terrigenous-coral one, as the inner lagoon and passages are opposite it through their coordinates.

On the second axis, the inner reef flats of islet and fringing reefs are opposite the inner lagoon. This axis therefore expresses a 'dry-wet' gradient.

Figure 42, showing the projection of the barycentres of the observations onto the plane (1,2) was drawn using the symbols already defined for the biotopes and also by plotting 'super-barycentres' that correspond to the two classifications. This representation reveals the opposition between a reef complex (flats, slopes, passage) and a lagoon complex. The position of the outer lagoon, near the reef slopes, is to be noted. Within the reef system the two classifications are apparent. The passages are situated at the edge of the 'fringing, islet, barrier' gradient or of the 'inner reef flat, outer reef flat, outer slope' gradient. In this analysis, the outer reef flat of the fringing reef is close to the inner reef flat and the outer slope is not very far from the origin. In the lagoon system, the bays are very close to the 'slab' lagoon.

5.3.1.2 Species configuration

In this type of analysis of the distances between samples, it is quite common for the most frequent species to come to the fore (Blanc *et al.*, 1976). It is therefore not surprising that the absolute contributions do correspond to the species occurrence frequencies.

The relative contributions oppose the species *S. variegatus* and *H. edulis* to *H. nobilis* and *B. argus* on Axis 1. On Axis 2, *H. atra* is isolated at the end of the positive values. It also provides the biggest contribution to Axis 3.

Projection of the species onto the plane (1,2) does not correspond to the optimum configuration. Some species nevertheless appear to be 'discriminating' while the rare species are located at the origin. The four batches of characteristic species, according to this analysis, are:

- species of passages, coral slopes and outer lagoon, somewhat scattered along the negative values of Axis 1, comprising *B. argus*, *H. nobilis*, *T. ananas*, *H. fuscopunctata*, *A. palauensis*, *P. graeffei*, *H. fuscogilva* and *T. anax*;
- species of the inner lagoon and bays, evident from their positive values on Axis 1 and less so by their negative values on Axis 2, comprising *H. edulis*, *S. variegatus*, *A. spinea* and *Holothuria sp. 1*;
- species of inner islet reef flats and fringing reefs along Axis 2, with *H. atra* on the one hand and also *A. miliaris*, *H. coluber* and *H. leucospilota* on the other;
- species of outer reef flats on the barrier reef and the islets, *S. chloronotus* and *A. mauritiana*.

In this representation, the semi-planes demarcated by Axis 2 correspond to two batches of species. In the positive segment of Axis 1 are those with terrigenous affinities, while the coral species are in the negative segment of Axis 1. Each batch can then be subdivided by depth along Axis 2.

5.3.2 Quantitative analysis

This was done on the matrix of correlation between variables, using either density or biomass.

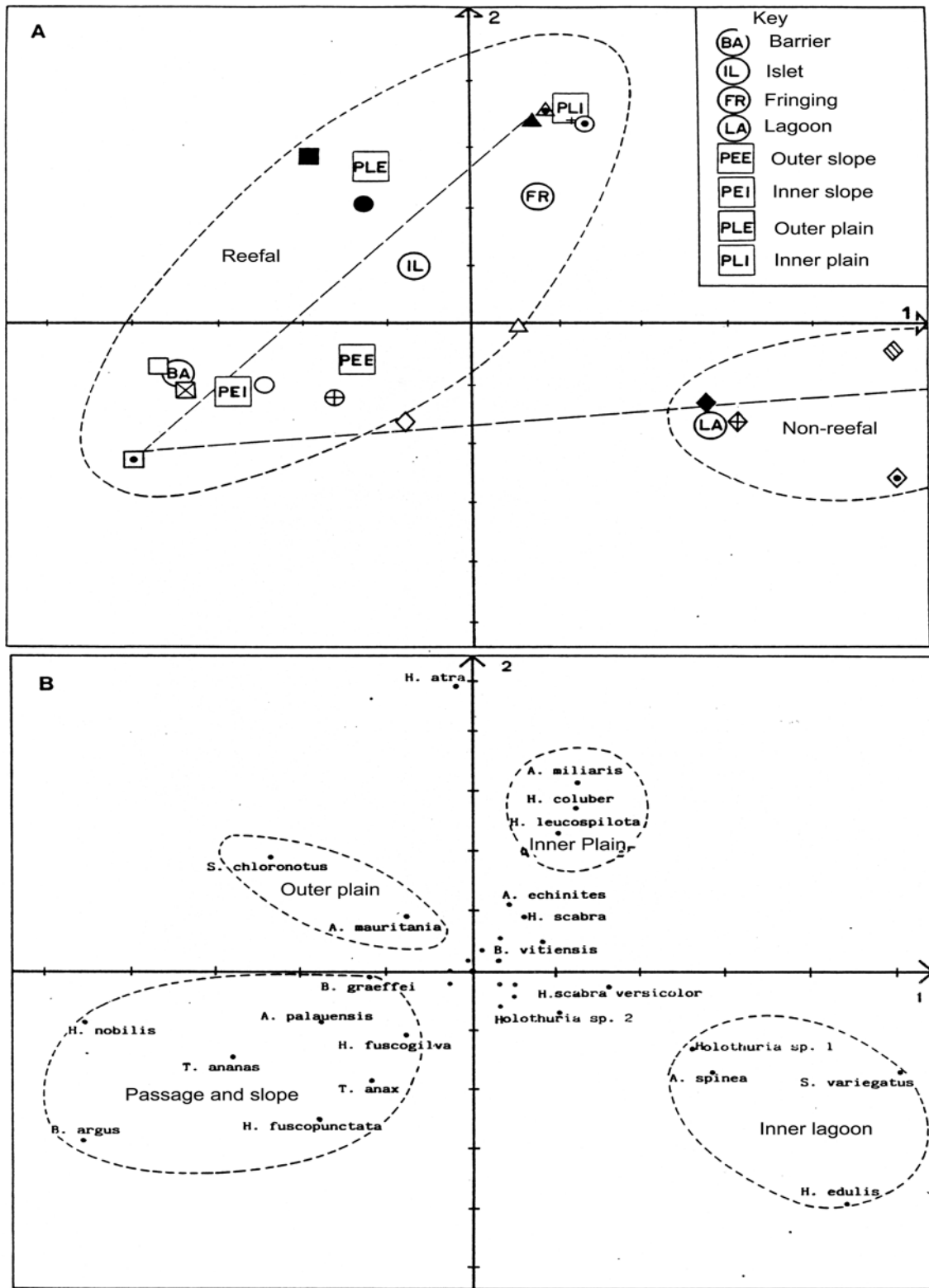


Figure 42: Inertia analysis; qualitative analysis.
 A: biotope configuration, for symbols see Fig. 12; B: species configuration, dotted lines = taxocenoses.

5.3.2.1 Densities

The results are presented In Annex 3 and Fig. 43. The variance percentages extracted by each of the first three axes are 9.6%, 7.8% and 5.5%.

Biotope configuration

The absolute and relative contributions show the same gradients as the qualitative analysis and the projection onto the plane (1,2) is little different.

As in the qualitative analysis, the observation barycentres with the highest absolute concentrations are the inner reef flats, the inner lagoon and the passages. These locations show the highest relative contributions on Axis 1, while the inner reef flats are preponderant for Axis 2.

Projection of the barycentres onto the plane (1,2) shows, in the same way as with the previous analysis, a V-shaped structure, with the passages at the tip. However, the gradient from inner reef flat to passage is clearer, with the inner reef flats emerging more clearly on an individual basis. Also, the slopes are more homogenous whatever the type of reef concerned. The outer reef flats follow the gradient from fringing to barrier reef. The reef gradient is more elongated close to Axis 1. The outer lagoon is more clearly distinguished whereas it was close to the islet slopes. Lastly, in the lagoon complex, the bays are now far from the inner lagoon, slab-floor lagoon and channel. These three barycentres are grouped around the positive values of Axis 1 and negative values of Axis 2; the depth gradient is therefore steeper.

Species configuration

This analysis is less influenced by species frequency. The relative contributions of the species differ slightly in comparison with the previous analysis, as apparently influenced by the slight rotation of the gradients in relation to axes 1 and 2.

Projection of species onto the plane (1,2) however shows the same general characteristics. On Axis 1, the species of the inner lagoon, quite closely grouped together, are opposed to passage species; on Axis 2, the inner lagoon species are opposed to those of the inner reef flats and less clearly to those of the outer reef flats. Axis 3 opposes species of the compact reef flat subject to strong water movement, such as *H. cinerascens*, *A. echinites* and *H. hilla* to species of shallow muddy sand bottoms, such as *H. pardalis* and *H. scabra*.

The four batches of species are found, but more evenly distributed than in the qualitative analysis. *H. atra*, for example, is no longer isolated, but is found with species of the inner reef flat.

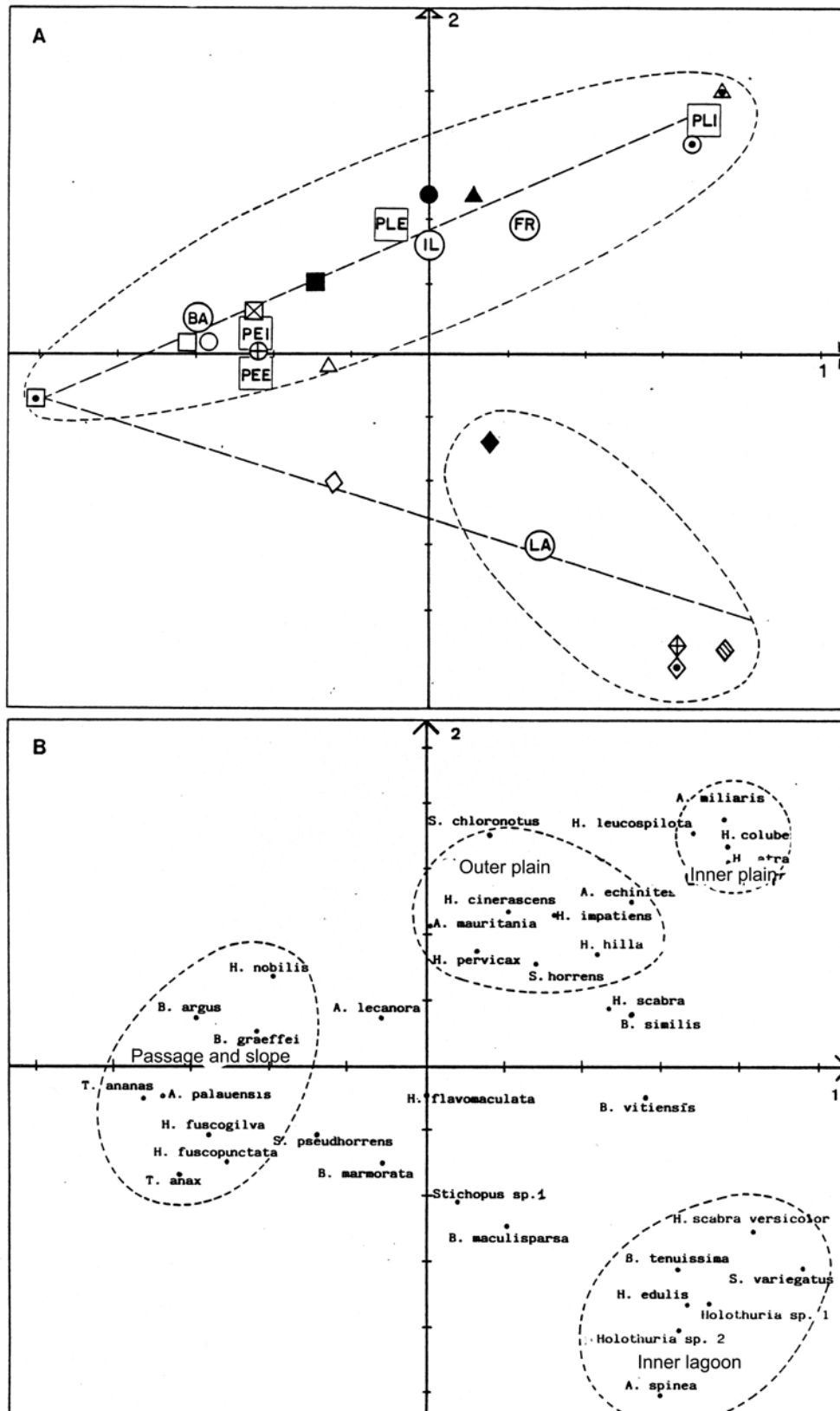


Figure 43: Inertia analysis: quantitative analysis of densities.
 A: biotope configuration; B: species configuration, dotted lines: taxocenoses.

The outer reef flats are slightly more clearly identified in this analysis. Within passage and slope species as a whole, as with the inner lagoon group, a depth gradient is apparent, opposing for example

H. nobilis to *T. anax* and *A. spinea* to *H. scabra* var. *versicolor*. The coastal lagoon is always unclearly distinguished in holothurian studies, but it should be noted that it does contain heterogenous environments such as bays, estuaries and deeper rias.

5.3.2.2 Biomasses

Lastly, in the inertia analysis performed on the biomasses, the variance extracted by the first 3 axes represents 9.6%, 8.6% and 5.2%. The contributions are shown in Annex 3.

The species and biotope configurations are very close to those of the previous analyses. The differences at the detail level relate to small species; in fact, despite the logarithmic conversion, in this analysis the preponderant role is given to the major abundant species.

Also, the ranking classification makes it possible to divide these species into homogenous classes. The biotope classification (Fig. 44) confirms the existence of 4 groups, passage and barrier and islet slopes (1), inner lagoon (2), inner islet and fringing reef flats (3) and outer reef flats (4). The division between the outer lagoon (5), the bays (6) and the fringing reef slopes is less clear.

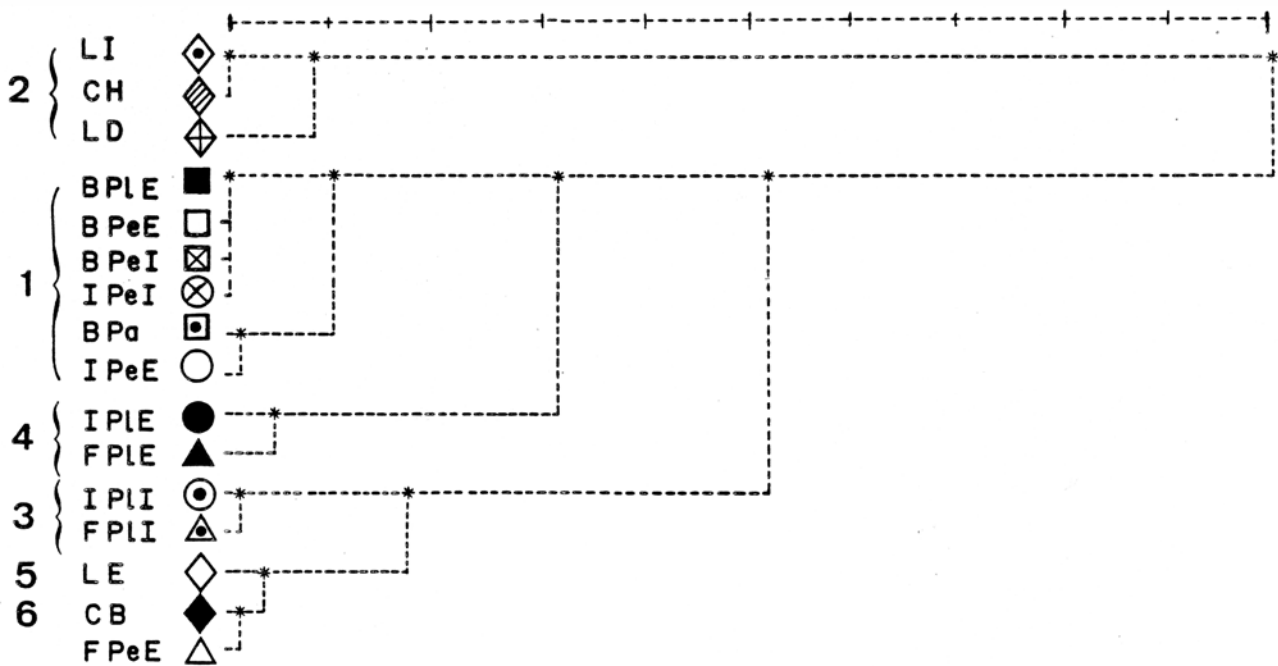


Figure 44: Ascending ranking analysis: biotope classification. For symbol key see Fig. 12.

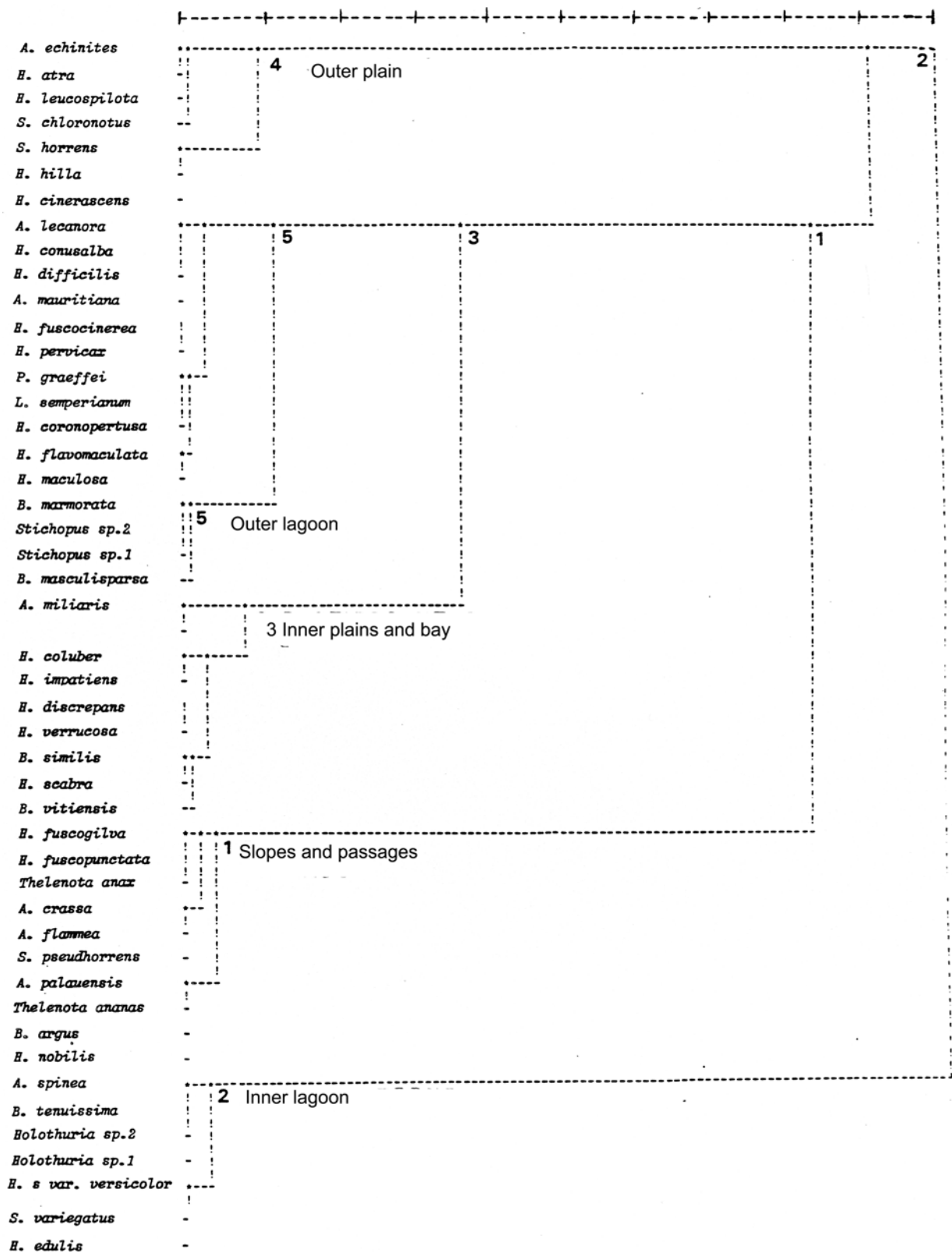


Figure 45: Ascending ranking analysis: species classification.

The species classification (Fig. 45) shows groupings that correspond to the same categories. The coastal zone species are partly found with inner reef flat species and partly with outer reef flat species, showing the importance of their terrigenous affinity.

5.3.3 Control variables

The relative contributions of the axes to the elements of each of the three categories of control variable are presented for each factor analysis (Annex 3).

Only the projection of these variables onto the plane (1,2) is detailed and illustrated by Figure 46, because the position of these variables in relation to the barycentres of the observations and to the species is very close in the various analyses.

The physical environmental factors confirm the significance of the axes. To the negative values of Axis 1 correspond the large distance offshore, the steep slope of the biotope and the presence of currents, which characterize the slopes, passages and barrier reef. At the tip of Axis 2 are mean depth and periods of drying-out, which oppose the inner lagoon and the reef flats. Exposure to wind is significant for the outer reef flats.

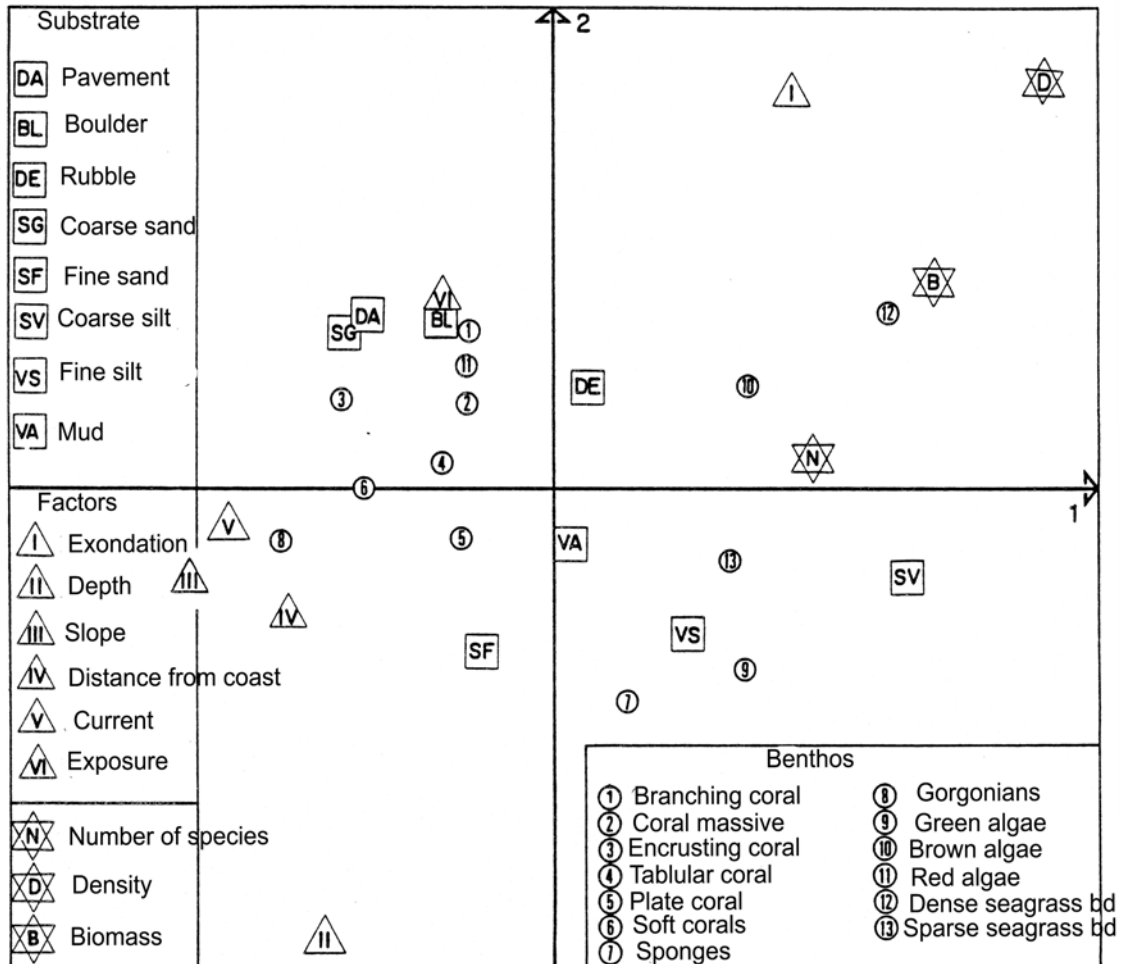


Figure 46: Inertia analysis: control variables in the quantitative analysis of densities.

The edaphic factors show that the inner lagoon is characterised by muddy sands and sandy muds, with muds not being a determining factor in these analyses. Fine coral sand is associated with the outer lagoon. Slabs, blocks and coarse sand are grouped and characterize outer reef flats and slopes while rubble is not a very determining factor.

Lastly, the accompanying flora and fauna make it possible to describe the biotopes more accurately. Green algae, sponges and sparse seagrass beds develop on the sandy muds and muddy sands of the inner lagoon. The inner reef flats, with often very varied substrates, sustain dense seagrass beds and brown algae. The outer reef flats are characterised by red algae of branching and brain corals. The various types of coral and alcyonaria develop on slopes, but are not clearly distinguished. Lastly, the gorgonians are well developed in the passages.

The synthetic variables, i.e. number of species, density and biomass, are aligned along the reef axis and show the richness of the inner reef flats.

5.4 DISCUSSION

5.4.1 Synopsis of results obtained in New Caledonia

Analysis of the abundance of holothurians in the main biotopes has yielded a classification, which jointly involves the two gradients, coast-offshore and functional organization of reefs. The inner reef flats and bays are the richest environments, followed by the inner lagoons. The reef flats and outer lagoons occupy intermediate positions. The passages and coral slopes are the poorest environments, from both the qualitative and quantitative points of view.

The qualitative and quantitative inertia analysis and the ascending ranking analysis carried out on these populations have provided quite convergent results. The inertia percentages of the first axes are always relatively low, which is probably due to the high number of variables and the scale of the study. They reflect the main features of the general characteristics of the lagoon, clearly showing the organization of the gradients, first of the lagoon (from inner lagoon to passages) then of the reef (from inner reef flats to passages). This expresses the classification both by reef type and by functional system.

On the basis of the presence or abundance of species, three main environments with their taxocenoses and three environments less clearly identifiable by some dual-affinity species can be distinguished.

The **coral slopes** and **passages** (1) correspond to an infra-littoral reef complex. They are characterised by species *A. palauensis*, *B. argus*, *H. fuscogilva*, *H. nobilis*, *T. ananas* and *T. anax* and scarce species *A. flammea* and *A. crassa*.

The **inner lagoon** (2) is a terrigenous infra-littoral system. The characteristic species here are: *A. spinea*, *B. tenuissima*, *H. edulis*, *H. scabra* var. *versicolor*, *S. variegatus*, and *Holothuria* sp. 1. and sp. 2.

The **inner flats of islet and fringing reefs** (3) in fact amount to a terrigenous medio-littoral system. These are characterised by: *A. miliaris*, *H. atra*, *H. coluber* and *H. leucospilota*. Their separation from outer reef flats on the one hand and bays on the other is liable to vary slightly depending on the analytical method used. The results of the quantitative analysis were chosen to define the other three populations.

The **outer reef flats** (4) correspond to a medio-littoral reef system whose affinity is intermediate between the inner reef flats and the upper horizon of the slopes. The characteristic species are: *A. mauritiana*, *A. echinites*, *H. cinerascens*, *H. hilla*, *H. impatiens*, *H. pervicax*, *S. chloronotus* and *S. horrens*.

The **outer lagoon** (5) is intermediate between the coral slopes, as it lies at their foot, and the inner lagoon. It can be considered as an infra-littoral reef complex with a soft bottom. The most frequent species are: *B. maculisparsa*, *B. aff. marmorata*, *H. fuscopunctata*, *S. pseudohorrens*, *Stichopus sp. 1* and *sp. 2*.

Lastly, the **bays** (6), which, in New Caledonia, cover a very wide range of environments, mangrove areas, sometimes deep rias and sandy beaches. The conditions here are often intermediate between the less coastal inner lagoon and the inner reef flats, as emerges from the ranking analysis (see Fig. 45). The frequent species here are: *B. vitiensis*, *B. similis*, *H. scabra* and *H. flavomaculata* specifically in the areas silted up with mud and containing coral shoals.

There seemed to be merit in assessing, even in a very approximate manner, the energy equivalent of these taxocenoses (Table 18). The calculations should have been made on the basis of the dosages of total dry organic matter or tegument organic matter, as this is usually considered as the essential compartment (Giese, 1966). In the absence of exact data on the relationship between the tegument weight and total weight and on the water and spicule content, as the main component of the ash, the assessment was made from the fresh weight, using mean values of 0.50 kcal per gram of tegument weight and 0.55 for the relationship between its weight and total weight (see Table 6).

Table 18: Mean energy equivalent, in holothurians, of the main biotopes.

BIOTOPE	BIOMASS	
	kg / 100 m ²	kcal / 100 m ²
Inner reef flat	6,93	1905
Inner Lagoon	3,66	1007
Outer lagoon	2,08	572
Passage and slope	1,33	366

5.4.2 Comparison with other tropical Indo-Pacific populations

Little research has so far been carried out on the zoning of all holothurian populations on a reef complex. Levin (1979), using a biotope coding system based on a classification by structural groupings and a similarity coefficient between stations spread throughout the Indo-Pacific, concluded that some environments, such as atoll lagoons and outer reef flats, were very specific, but also that there was resemblance between zones offering quite varied topographical and water movement conditions, where species could nevertheless be quite clearly zoned. It is possible that an inertia analysis would have clearly illustrated the general zonal distribution of populations.

Hammond *et al.* (1985) attempted to classify three categories within the Great Barrier Reef, inner, median and outer, using a ranking analysis of species density based on the Bray Curtis coefficient of similarity. In this study, only the inner and outer reef flats and the surface horizon of the inner slope were sampled at night. The results show very low general densities (see Table 13), perhaps due to the methods used, and the surprisingly low diversity of the inner reefs. The authors conclude that there is no general zoning pattern, because of the difference in size of reefs, the highly variable distribution of microhabitats and/or species' flexibility as regards habitat. This analysis basically relates to reef flats not very subject to terrigenous influences, which have just been shown in New Caledonia to be poor

environments, in which distributions follow gradients in which the classes are less clearly differentiated than elsewhere.

The older work by Yamanouchi (1939) in Palau comprises a qualitative description of the populations on a radial from the barrier reef to the fringing reef that corresponds to the species characteristic of New Caledonia; he points out the absence of species in the mangrove areas.

Most other research, Baker (1929), Sloan (1979, 1982), Lawrence (1980), Harriot (1980) and Massin and Doumen (1986) refers to reef flats or even a subdivision thereof, outer reef flat, inner reef flat or micro-atoll. The same batch of species is reported, usually corresponding to populations (3) and (4) as defined for the reef flats of New Caledonia.

Definition of the scale on which research is conducted is essential for recognizing populations. At the scale of a system as extensive and complex as the New Caledonian lagoon, populations have been defined for the main biotopes. The majority of holothurian species are characteristic of biotopes but infrequently exclusive; rather, they tend to occupy a specific zone, each with flexible variability, on the main coast-offshore and slope-reef flat gradients.

5.5 DISTRIBUTION FACTORS

The distribution of species and populations over the gradients already referred to above is not restricted to holothurians in New Caledonia. In fact, certain pelagic populations of small fish (Conand *F.*, 1987) zooplankton communities (Binet, 1984) or benthic foraminifer communities (Debenay, 1985) are distributed along the coast-offshore gradient. Other studies of the fauna of the south-west region (Intès and Menou, 1979; Dugas and Debenay, 1980) also show such a gradient-based distribution, which is particularly marked in New Caledonia because of its topography, with narrow elongated lagoons along the coast, in comparison with the Great Barrier Reef, for example, which has less clearly demarcated and more homogenous sections.

According to the functional reef gradient in which water movement plays a major role, research in New Caledonia relates to the zoning of Scleractinia (Faure *et al.*, 1982, Thomassin, 1984), while many studies on the Indo-Pacific domain describe the zoning of other benthic groups.

While most authors who have studied holothurian distribution agree that there is an influence from coast-offshore and reef gradients, the nature of the determining factors in macro- and micro-distribution is however still at issue.

5.5.1 Factors in macro-distribution

Most of the studied populations were located on reef flats and it is therefore not surprising that water movement was usually considered to be a determining factor in zonation.

Some authors even oppose species associations in sheltered areas to those occurring in exposed habitats (Sloan and Von Bodungen, 1980; Massin and Doumen, 1986). But water movement is a complex factor, which in addition to mechanical agitation, determines water quality and substrate particle size and also influences the fixation of organisms, in particular larvae and juveniles.

The influence of the nature of the substrate, both physical and by particle-size and also in chemical terms through its organic matter content, is perhaps less explicitly recognized by those who have studied the macro-distribution of holothurians in coastal areas. In fact, the same species may be found in or on various substrates, which may themselves vary from area to area (Levin, 1979; Hammond *et al.*, 1985). Some current contradictions on this point are linked to the controversy on the presence or absence of selectivity in diet. In the deeper zones, however, density is clearly correlated to organic matter content (Sibuet, 1985).

The coast-offshore gradient, which this study clearly identifies, basically corresponds to terrigenous influences acting on the substrate's properties.

Depth is not frequently used to explain the distribution of coastal species, whereas its influence on the richness of abyssal populations is major (Sibuet, 1985). Even for coastal species this composite factor is a determining one, because only some species are subject to drying-out at low water and also there is apparently a bathymetric zonation in congeneric species of a biotope, such as *H. nobilis*, and *H. fuscogilva*, *T. ananas* and *T. anax*.

Salinity has a clear influence by eliminating species in areas like mangrove swamps where the salt content drops.

The influence of biotic factors on distribution or recruitment is not well known. Predation probably occurs to the detriment of juveniles. Competition could have an effect on micro-distribution.

5.5.2 Micro-distribution and diet selectivity

In order to explain the coexistence of more than one species in the same biotope, which is especially the case in the Indo-Pacific domain, where diversity is very high on reef flats where the highest densities are observed, distribution by micro-habitat has been considered. To resolve the issue of resource sharing in reef environments, Kohn (1971) theorized that carnivores specialize in a particular type of prey, while detritus-feeders shared one or more microhabitats. A number of studies have tried to test this theory with holothurians. Sloan (1979) shows that the availability of micro-habitats on beach rock would appear to be more determining than food resource availability.

Diet selectivity, whether physical, depending on the substrate particle size or chemical, depending on organic matter content, can also enable species to co-exist.

Particle-size selectivity

This type of selectivity has been found in various groups of detritus-feeders, polychetes, amphipods, sipunculans and mollusks. It is however controversial with regard to holothurians (Hammond *et al.*, 1982; Massin and Doumen, 1986).

Selectivity observations have been described by a number of authors: Bertram (1936) and Yamanouchi (1939) for certain species, but not for *H. atra* or *S. variegatus*, Emery *et al.* (1954), Rhoads and Joung (1971), Hauksson (1979) for *S. tremulus* in opposition to Jespersen and Lützen (1971), Roberst (1979) and Franklin (1980) for *S. chloronotus*, contrary to *H. leucospilota*. More recently, Roberts and Bryce (1982) showed the existence of a number of strategies including selectivity for finer or coarser particles than the characteristics of the surrounding sediment or the lack of selectivity in *H. atra*, already observed by Trefz (1958), Lawrence (1980) and confirmed by Massin and Doumen (1986). Some authors have observed variable results from different locations, which could result from opportunistic behaviour in the presence, or absence, of competition. During our own sampling work, although no particle-size survey was carried out, it emerged that a number of *Actinopyga*, in particular *A. mauritiana* and *A. miliaris*, had digestive contents formed of fine particles, but the possibility of chemical selectivity for the epiphytic felt of the phanerogam leaves can also be envisaged in this case.

The lack of particle-size selectivity, apart from the examples already referred to, has been shown by Gardiner (1904), Choe (1963), Glynn (1965), Yingst (1974, 1982), Powell (1977), Levin (1979), Sloan and von Bodungen (1980), Bouland *et al.* (1982) and Hammond (1982). This author re-examines and criticizes certain results proving the existence of selectivity. He concludes that the differences observed are more likely to come from a relatively stable preference for a microhabitat.

Further research, analyzing the respective roles of availability of sediment, interspecific and even interindividual competition, which scenario has never been envisaged, remain necessary in order to resolve these contradictions. During a species' life cycle, a change of diet may occur. Juvenile *S. japonicus*, for example, ingest relatively higher quantities of microalgae and detritus than adult specimens (Choe, 1963). This is also probably the case with *H. fuscogilva*, whose juveniles live among the stalks of phanerogams or *Halimeda* (Gentle, 1979 and pers. obs.). With the adults, on the other hand, the lack of a relationship between individual size and the particle-size composition of the ingested sediment has been shown by Levin (1979), Hammond (1982) and Massin and Doumen (1986).

Chemical selectivity

This type of selectivity has frequently been demonstrated in aspidochirote holothurians, as shown in the references in Table 19, classified by species and geographical zone. For some species, in particular *S. tremulus* (Jespersen and Lützen, 1971) and *P. parvimensis* (Yingst, 1982), it has not been identified, but it does seem that only the upper layer of the sediment, the richest in bacteria, microfauna and meiofauna is exploited for nutrition purposes. Chemical selectivity is particularly obvious in the species inhabiting environments that are relatively poor in organic matter.

Table 19: Chemical selectivity in aspidochirote holothurians.

SPECIES	ZONE	AUTHOR	OBSERVATIONS: surrounding sediments – digestive contents and sediments - faeces
<i>H. atra</i>	Indo-Pacific (tropical, coastal)	Webb <i>et al.</i> , 1977	Faeces approx. 3 times richer in organic C. than the sediment.
		Moriarty, 1982	Digestive content 16 to 34% higher than the sediment in organic C., 35 to 111% in N., 33 to 300% in muramic acid (bacterial biomass).
<i>S. chloronotus</i>		Moriarty, 1982	ditto
<i>H. arenicola</i> <i>H. mexicana</i> <i>I. badionotus</i>	Atlantic, (tropical, coastal)	Hammond, 1983	Relation between digestive contents and sediment in organic C. 2.0; 1.4; 1.4; in N 2.0; 1.9; 3.0; in pigments 2.0; 2.2; 1.3; in ATP 1.2; 1.7; 1.9. Faeces not richer in O. M. than sediments.
<i>H. tubulosa</i>	Temperate, coastal	Massin and Jangoux, 1976	Digestive contents more than twice as rich in O. M. than the sediments.
		Massin, 1980	Faeces rich in organic matter
<i>S. tremulus</i>		Hauksson, 1979	Digestive contents richer in O. M. than the sediments by selection of faeces of other benthic organisms and sediment aggregates.
<i>S. japonicus</i>		Tanaka, 1958	Digestive contents with 4 times more N than the environment.
<i>P. pallens</i> <i>P. villosus</i>	Atlantic, abyssal	Kripounoff and Sibuet, 1980 Sibuet, 1984	Digestive contents 4 times richer in organic C., 6 times richer in N., 7 times richer in proteins than the environment.
<i>P. atlanticus</i>		Briggs, 1985	Selection of the faeces of other organisms.

6 CONCLUSION

The distribution and abundance of aspidochirote holothurians was studied by means of quadrats performed by diving or on foot in the various reef and lagoon biotopes of New Caledonia. This complex is characterized by high habitat diversity due to the general topography of the lagoons and barrier reefs, stretching out parallel to the coastline, by water movement, terrigenous inputs from the many watercourses and by the functional organization of the reefs which are the site of construction activities and of sources of mechanical and biological destruction. Sixteen major biotopes have been identified and classified both by type of structure and type of functional complex.

Habitats, affinities and abundance, both numerical and in weight terms, were determined for the 41 species of Holothuridae and eight species of Stichopodidae concerned. They were classified according to their frequency of occurrence, biomass and density, while also taking their commercial value into consideration. Their affinity for the main environmental factors made it possible to oppose species with a reef affinity to others with a terrigenous affinity, intertidal species to infralittoral species and to define the particle-size preferences of each. Despite inaccuracies due to the study method and the scattered mode of distribution of most species, these results should be useful for the assessment of resources and the exploitation of commercial species.

The aspidochirote holothurian populations of the reef complex were identified using ascending factor and ranking analyses, the results of which are reasonably convergent. Three biotope groupings with their characteristic species were clearly identified. A reef group, undergoing little terrigenous influence, comprises the coral slopes of the barrier and islet reefs and the passages (1). The inner lagoon and the channels and the slab-bottomed lagoon (2) are under terrigenous and infralittoral influence. The third group, also under terrigenous, but intertidal, influence is formed of inner islet and fringing reef flats (3). Three other groups of biotopes show transitional characteristics between the others and their species have dual affinities. Outer reef flats (4) subject to strong water movement are intermediate between the outer slopes and the inner reef flats. The outer lagoon (5) with organogenic sand is intermediate between the reef slopes and the inner lagoon. The bays (6), which contain varied environments, are less clearly characterised by holothurians.

Species abundance in each of these groups, expressed in density, biomass or energy equivalent, shows the richness of the inner islet and fringing reef flats and that of the inner lagoon. These are accumulation environments, as opposed to the reef systems.

An estimation of commercial holothurian resources could be made on the basis of the map of the various biotopes concerned (see Chap. 4 – 3.3). Production, however, would require knowledge of species biology that will be developed in the following chapter. From the point of view of the functioning of the coral ecosystems, the role of holothurians can be examined both on the basis of their place in the trophic chains and also by studying their bioturbation role. This has an influence on the stratification of sediments and the associated meiofauna. In the many trophic chains of coral complexes depicted by Lewis (1981), holothurians are an important element in the detritus-feeder group, as a consumer of bacteria and detritus.

CHAPTER III: BIOLOGY OF THE MAIN COMMERCIAL SPECIES

1 INTRODUCTION

1.1 PURPOSE OF THE STUDY

An understanding of the biology of holothurian populations is necessary in order to envisage rational management of the exploited stocks. Regular sampling over time makes it possible to study their demographic structures, growth, reproduction, migration and mortality.

As it is not possible to determine the age of sea cucumbers, the demographic structures cannot be presented and this study will be restricted to presenting a description of the metric characteristics, sizes and weights, of the sampled populations, together with the relationships between these characteristics. This information will be used during the growth study and also in order to facilitate comparisons with the results obtained by other authors.

Sexual reproduction for each of these species and asexual reproduction through fission in *H. atra* will then be looked at with the sex ratio, gonad anatomy, sexual cycles, first maturity and fertility examined in detail.

Growth and mortality are particularly difficult to study in these soft-bodied organisms. Various methods have been used with results that can only be considered as initial approximations.

1.2 MATERIALS

1.2.1 Choice of species

When this work was started, there was no holothurian trade in New Caledonia that could have guided the choice of species for research. The SPC Handbook (Anonymous, 1975) lists 13 commercial species. Of these, two species *Bohadschia argus* and *B. marmorata* throw out their Cuvier organs so quickly that they are unlikely to be of commercial value. Further market research confirmed that they were not in fact exploited. Of the *Actinopyga*, species *A. lecanora* seems to be too scarce to enable consistent sampling, while the black-coloured species proved too difficult to identify. The following nine species and were therefore selected:

- The teatfish, *H. nobilis* and *H. fuscogilva* (see Fig. 1);
- The sandfish, *H. scabra* and *H. scabra* var. *versicolor* (see Fig. 1);
- *H. fuscopunctata* (see Fig. 2);
- *echinites* and *A. mauritiana* (see Fig. 2);
- *H. atra*. (see Fig. 2);
- Lastly, the Stichopodidae, *T. ananas* and *S. variegatus*. (see Fig. 3).

1.2.2 Harvests

In order to study the biometrics and sexual reproduction, a monthly sampling programme was carried out for each species from November 1978 to May 1980 and continued until 1981 for certain species, so as to confirm and enhance the initial results obtained. Growth was addressed particularly by means of tagging, which will be presented later (see 4.2).

Of the first observations on the distribution of some species in the vicinity of Nouméa, by Intès and Menou (1979) made it possible to select some stations close to the ORSTOM laboratory. A number of harvests were carried out by means of diving in the same day. Other stations, from reef flats to fringing reefs, accessible by road, were visited at low water.

For each population, the monthly sample generally comprised twenty specimens harvested at random. Material constraints prevented us from the collecting larger specimens: firstly, the length of diving time could not exceed half an hour to an hour and these animals are fairly widely scattered, and also some of the largest species were difficult to collect because of their weight, while others tended to eviscerate if they were tightly packed into the harvesting bags. In order to remedy this, each specimen of *T. ananas* and *S. variegatus* had to be individually captured in a plastic bag full of water, making it possible to collect the various organs and possibly Carapidae fish sheltered by *T. ananas*. On board, the specimens were placed in large tanks full of water, to which magnesium chloride was added to facilitate their relaxation. They were then brought back to the laboratory and stored in a cold room at 4 degrees centigrade for dissection the next day.

1.2.3 Research stations (Fig. 47)

The characteristics of each of the 17 stations are given in Annex 4, using the same descriptors as for the ecological study. Some samples were occasionally harvested elsewhere. The knowledge gained on distribution made it possible to group the species according to biotope: coral slope, outer reef flat, inner reef flat and inner lagoon.

1.2.3.1 Species of coral slopes

Holothuria nobilis

Because of its low abundance, but also in order to enable comparisons, this species was harvested from five main stations:

- Ilôt Amédée (Station 1): inner islet reef flat situated close Boulari Passage;
- Bancs de l'Ouest (Station 2): lagoon reef slope, to windward;
- Grand Récif Aboré (Station 3): inner slope;
- Ilôt Croissant (Station 4): leeward drop-off;
- Unia fringing reef (Station 5): inner reef flat.

This station was the only one located outside the southwestern lagoon, but it was chosen for its large population of various holothurian species. It is in fact a wide fringing reef with little protection from the influences of water movement, as the barrier reef is submerged in this area.

Holothuria fuscogilva

Sampling of this species was carried out on a bi-monthly basis, because of the remote location of the station:

Passe de Uitoë (Station 6): windward passage edge.

Holothuria fuscopunctata

Monthly sampling of this species was performed while harvesting other species and is therefore distributed between 4 outer lagoon bottom stations, near islets. Station 4 has already been described:

- Ilôt Signal (Station 7): foot of leeward slope;
- Ilôt Laregnère (Station 8): slab-bottomed lagoon;
- Ilôt Amédée (Station 9): foot of slope.

Thenelota ananas

To Reef (Station 10): submerged passage reef.

1.2.3.2 Species of outer reef flats

Actinopyga mauritiana

This species, which is characteristic of outer reef flats, was sampled on a bi-monthly basis from December 1979 to April 1982, at 2 stations, in order to compare their characteristics:

- Grand Récif Aboré (Station 11): outer reef flat;
- Unia fringing reef (Station 12): outer reef flat.

Actinopyga echinites

This species has a more widespread distribution than the previous one and offers high densities from outer slopes to inner reef flats. It was sampled, especially at Ilôt Maître, from November 1978 to May 1980 and then from February 1981 to April 1982 in order to confirm the initial results, and study the calcareous ring and fertility:

- Ilôt Maître (Station 13): upper part of windward slope;
- Ricaudy fringing reef (Station 14): outer reef flat. This station has been covered in a more detailed study through data analysis and remote sensing (see Chapter 4 - 5.3).

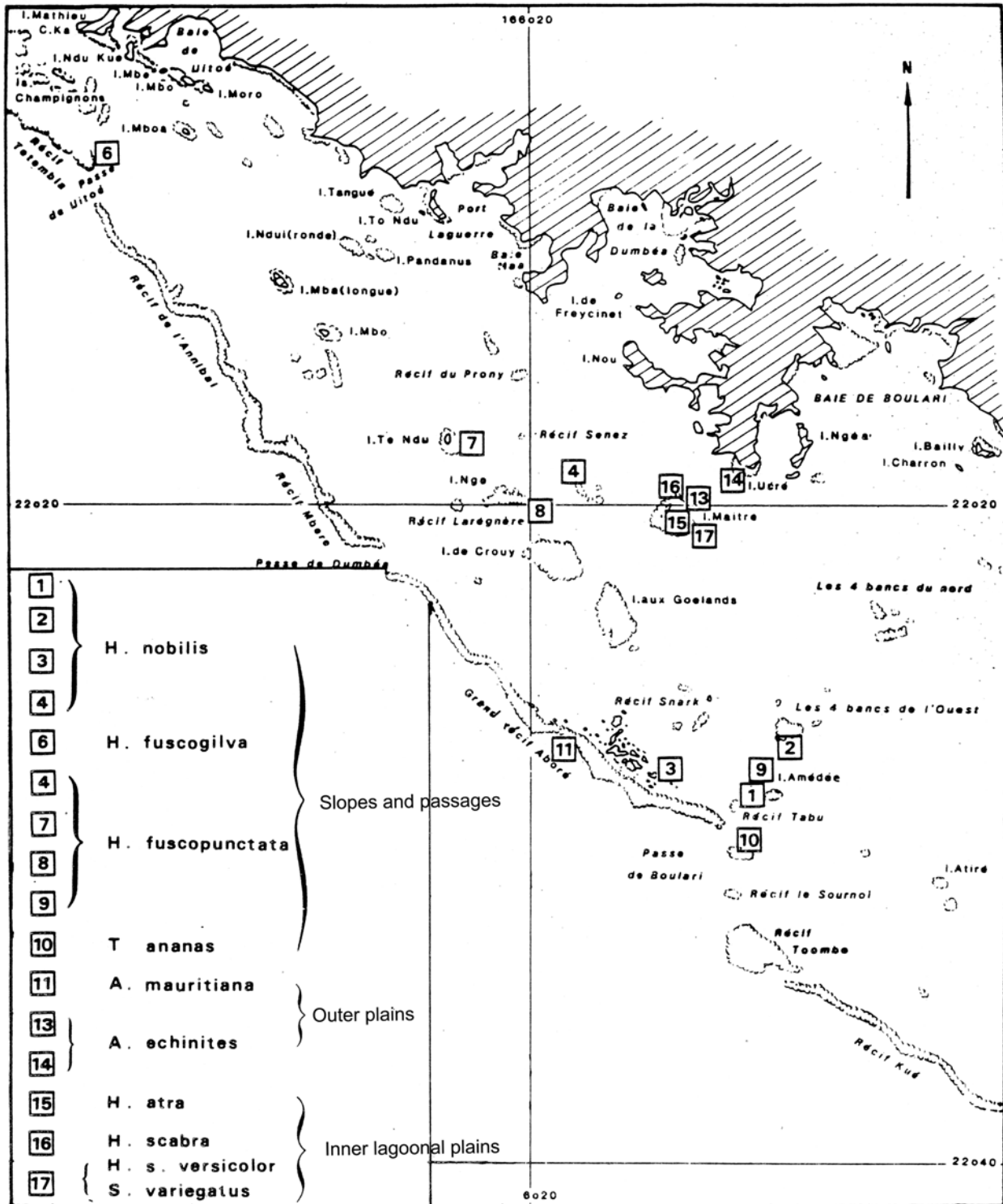


Figure 47: Monthly sampling stations in the southwestern lagoon.

1.2.3.3 Species of the lagoons and inner reef flats

Holothuria atra

- Ilôt Maître (Station 15): inner reef flat.

Holothuria scabra

- Ilôt Maître (Station 16): inner reef flats with seagrass beds.

Holothuria scabra var. *versicolor*

- Channel of Ilôt Maître (Station 17): inner lagoon at foot of outer slope.

Stichopus variegatus

- This species was harvested at the same time as *Holothuria scabra* var. *versicolor* at the previous station, where in the daytime it was found near coral rocks, whereas *H. s. versicolor* was more or less buried in the sediment.

2 BIOMETRICS

2.1 INTRODUCTION AND METHODS

The biometrics of holothurians is particularly difficult to study because of the variability of the measurements. The consistency of the body is soft, as the skeleton is not very developed and the morphometric parameters depend on the animal's degree of contraction, the amount of water in the cloaca and the respiratory trees, of the celiac liquid and sediment in the digestive tube. It is therefore necessary to precisely define the measurement conditions because they are not as yet available in a standard format. Choe (1963) in his research on *Stichopus japonicus* shows that length is a very variable parameter with a mean coefficient of variation of 7.3%, whereas it is only 2.8% for total weight. He does however recommend the use of drained weight. This has the disadvantage of not being usable in experiments using live holothurians. Other authors use either contracted length (Lawrence, 1980), or a size index defined by the product of length by contracted weight (Yingst, 1974; Cameron and Fankboner, 1986). Lastly, total fresh weight is also used (Harriet, 1980; Franklin, 1980).

In this study, the following parameters were measured for each individual:

- **L_t**, total length after relaxation, to the nearest 0.5 cm by default, measured with a tape measure dorsally from the mouth to the anus; it was sometimes measured under water on undisturbed animals and did not appear to be any more variable than the contracted length;
- **PT**, total weight;
- **PO**, drained weight, after a medio-dorsal incision to remove the celiac liquid and that contained in the respiratory trees;
- **PE**, gutted weight, which apart from the tegument also includes the five radial muscular bands and the oral bulb. The last three parameters are wet weights, measured to the nearest 5 g by default.

The genital glands (Fig. 48) are removed, drained onto blotting paper, weighed to the nearest dg by default (Pg), then fixed with neutralized 5% formol to determine sex and stage of maturity. It should be noted that, because of their distribution, samples from a number of species are difficult to collect and numbers are low, approximately 20 specimens per month of sampling.

A data processing programme called 'HOLOT', comprising a histogram section and a regression section, with a characteristic selection option, was used to create species files. Frequency distributions for the measured parameters were thus obtained. The biometric relationships between these parameters are necessary in order to convert these data. The various relationships that can be established and their applications are presented and discussed by Fréon (1979). They were calculated here by the method of the reduced major axis, from all the value pairs available.

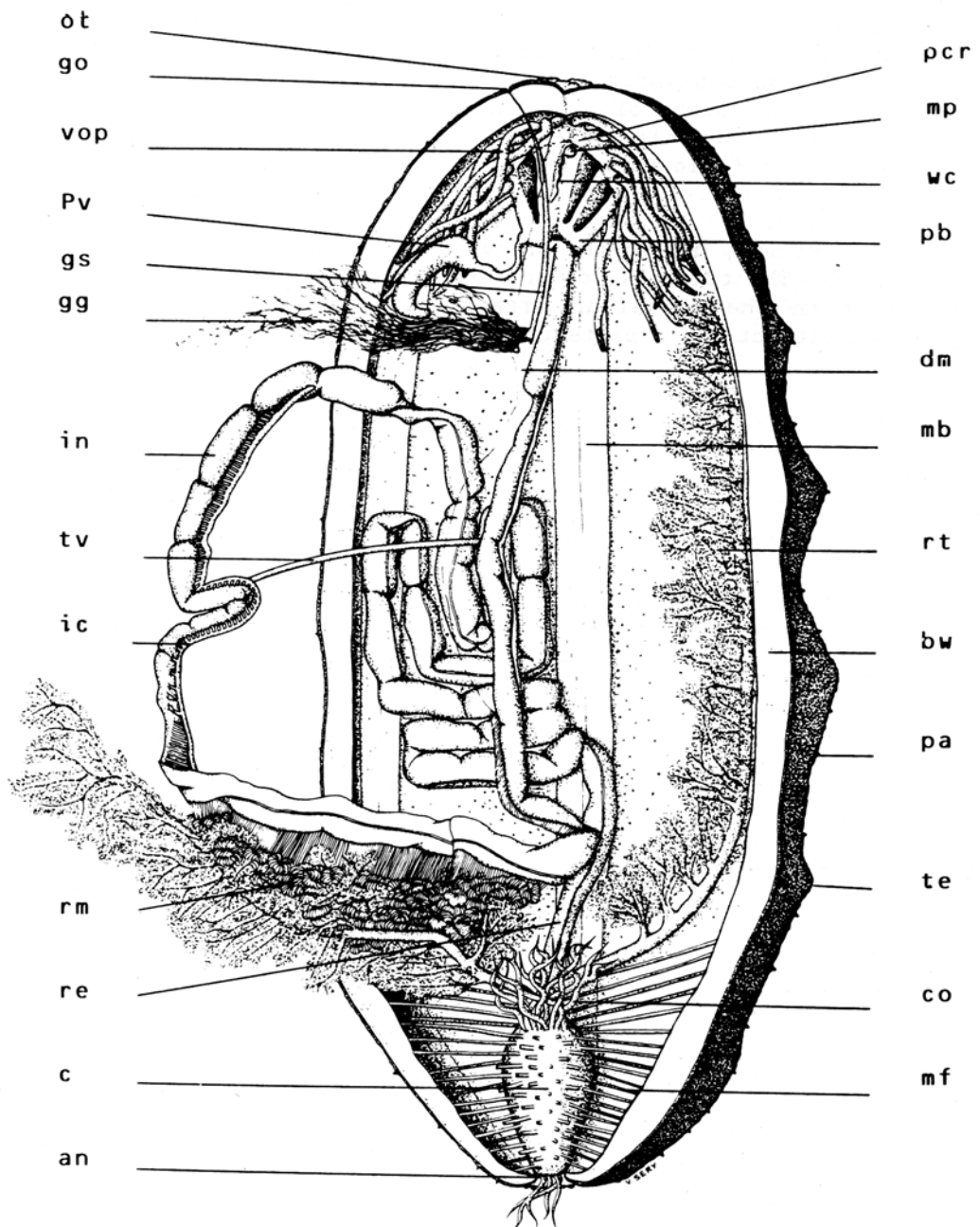


Figure 2: Anatomy of *Holothuria nobilis*

ot: oral tentacles go: genital orifice vop: vesicles of the oral podia mp: madreporite wc: water ring canal Pv: Polian vesicle pcr: peripharyngeal calcareous ring mb: radial muscular band gs : genital stolon gg: genital gland co: cuvierian organs c : cloaca an: anus re: rectum rt: right respiratory tree pb: pharyngeal bulb rm: rete mirabile tv: transverse vessel ic: intestinal cavity dm: dorsal mesentery mf: muscle fibres bw: body wall in: intestine pa: papillae te: teats

2.2 DISTRIBUTION OF LENGTH AND WEIGHT FREQUENCIES

2.2.1 Slope species

In order to provide an overall picture of the populations of each species, the results are first presented in bulk (Table 20). The samplings carried out over the two years of the study do not make it possible to identify evolution over time. This stability may be real, due to very slow growth, or apparent, due to the variability of measurements or from the low numbers of animals concerned. It will be discussed in the chapter on growth.

It clearly emerges that these four species are large in size, 40 cm approximately in length and have a mean total weight of 2 kg. The results are given in a more detailed manner for each species.

Holothuria nobilis

From all the stations (Fig. 49), 518 specimens were studied. The distributions of parameters are plurimodal; small specimens are scarce. They often have cream or orange coloured patches. Further to the initial observations (Conand, 1981) on this species, sampling was continued for a further year, in order to enable comparison of different populations, in particular those of stations 1 and 4.

Table 20: Distribution of measured characteristics of slope and passage species.
n = number; I = value interval; m = mean value; s = standard deviation.

	<i>Holothuria nobilis</i>				<i>Holothuria fuscogilva</i>			
	n	I	\bar{m}	s	n	I	\bar{m}	s
LT (mm)	518	180-560	370	57	125	230-570	401	46
PT (g)	509	300-4300	1829	644	108	1005-3600	2111	530
PO (g)	507	250-2450	1238	398	120	685-2590	1463	308
PE (g)	516	200-1900	938	283	124	320-2000	1209	253
	<i>Holothuria fuscopunctata</i>				<i>Theleota ananas</i>			
	n	I	m	s	n	I	m	s
LT (mm)	252	200-760	447	76	298	180-670	430	75
PT (g)	238	500-5750	2489	914	265	220-6250	2180	854
PO (g)	248	350-3250	1658	556	290	205-5850	1979	723
PE (g)	249	250-2250	1169	403	298	175-4800	1600	565

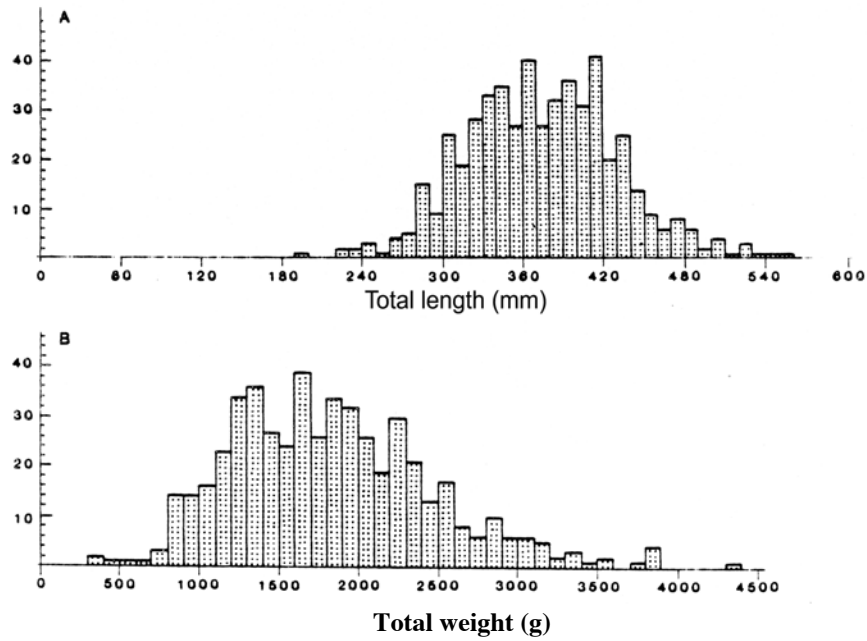


Figure 49: length and total weight distributions for *H. nobilis*.

The distributions of total weights shows three types of station, corresponding to different biotopes (Fig; 50):

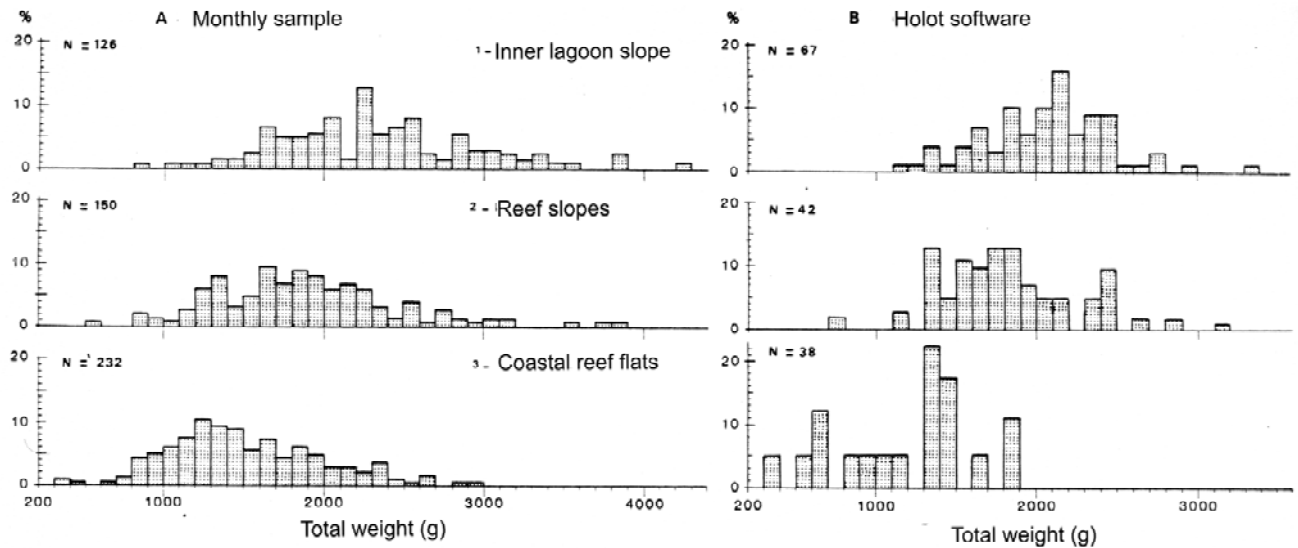


Figure 50: Distribution of the weights of *H. nobilis* depending on biotope. *n* = number; A = monthly sampling; B = HOLOT research programme.

- the first (stations 2 and 3, Poum reefs and Belep reefs) is formed of reef flat and inner barrier reef slope stations; the weight of individual animals is between 1 000 and 3 800 g;
- the second (Station 4 at Anse Vata) includes islet and lagoon slopes; the weights are more variable;
- the third (stations 1 and 5) corresponds to shallow stations on the coastal reef flats; the animals are smaller, weighing from 400 to 2 600 g.

These three types of distributions by biotope would appear to be confirmed by the observations performed during the HOLOT programme, the results of which are summarised in Fig. 50. It is difficult to clarify the origin of these differences. Various theories can be entertained, based on variable growth or mortality rates, different recruitment periods or migration.

Holothuria fuscogilva

The parameters of the sampled population of *H. fuscogilva* are given in Fig. 51. The absence of small specimens is worth noting. In Fiji, Gentle (1979) studied a population in a dense seagrass bed, at a depth of 5-10 m, whose weight distribution was very similar to that observed in New Caledonia, with specimens weighing from 1 to 3kg, with the being approximately 2 kg. On same reef, however, in deeper water, the animals were smaller, weighing 500 g on average. Lastly, juveniles less than 1 cm in length and weighing just a few grams, were observed in February at the base of the *Syringodium* leaves. In this area therefore the various size classes did not have the same bathymetric distribution and the proximity of stations could enable migration during growth.

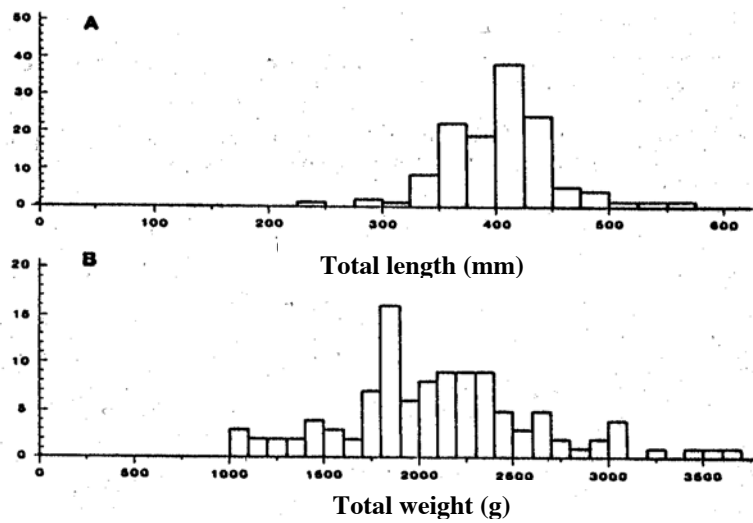


Figure 51: Total length and weight distributions for *H. fuscogilva*

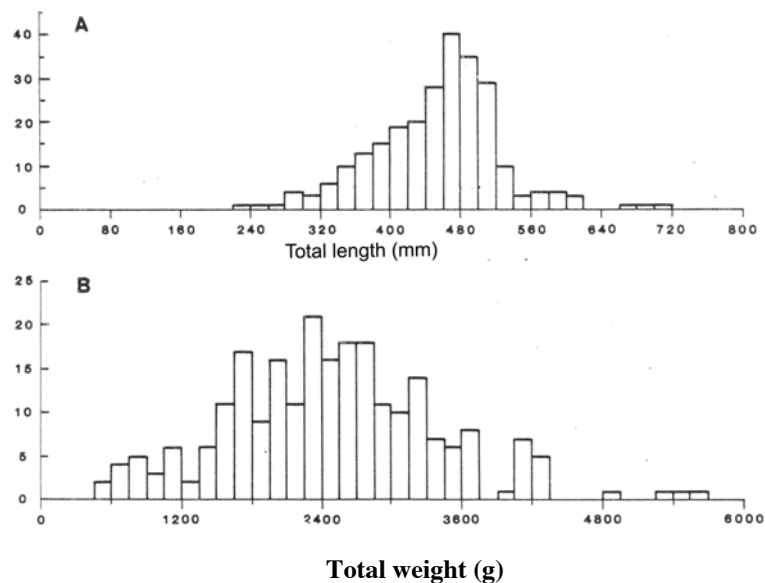


Figure 52: Total length and weight distributions for *H. fuscopunctata* at all stations.

Holothuria fuscopunctata

No research would seem to have been done on this species' biology. Despite the heterogeneity of the sampling, the distribution of the characteristics of the 256 animals studied shows that this is a large-sized species and that specimens under 24 cm in length are very rare at these stations (Fig. 52).

Presented separately for each station (Fig. 53), these distributions would appear to be plurimodal. Average-sized individuals are always present, but the proportions of the smallest to the biggest vary from one station to another.

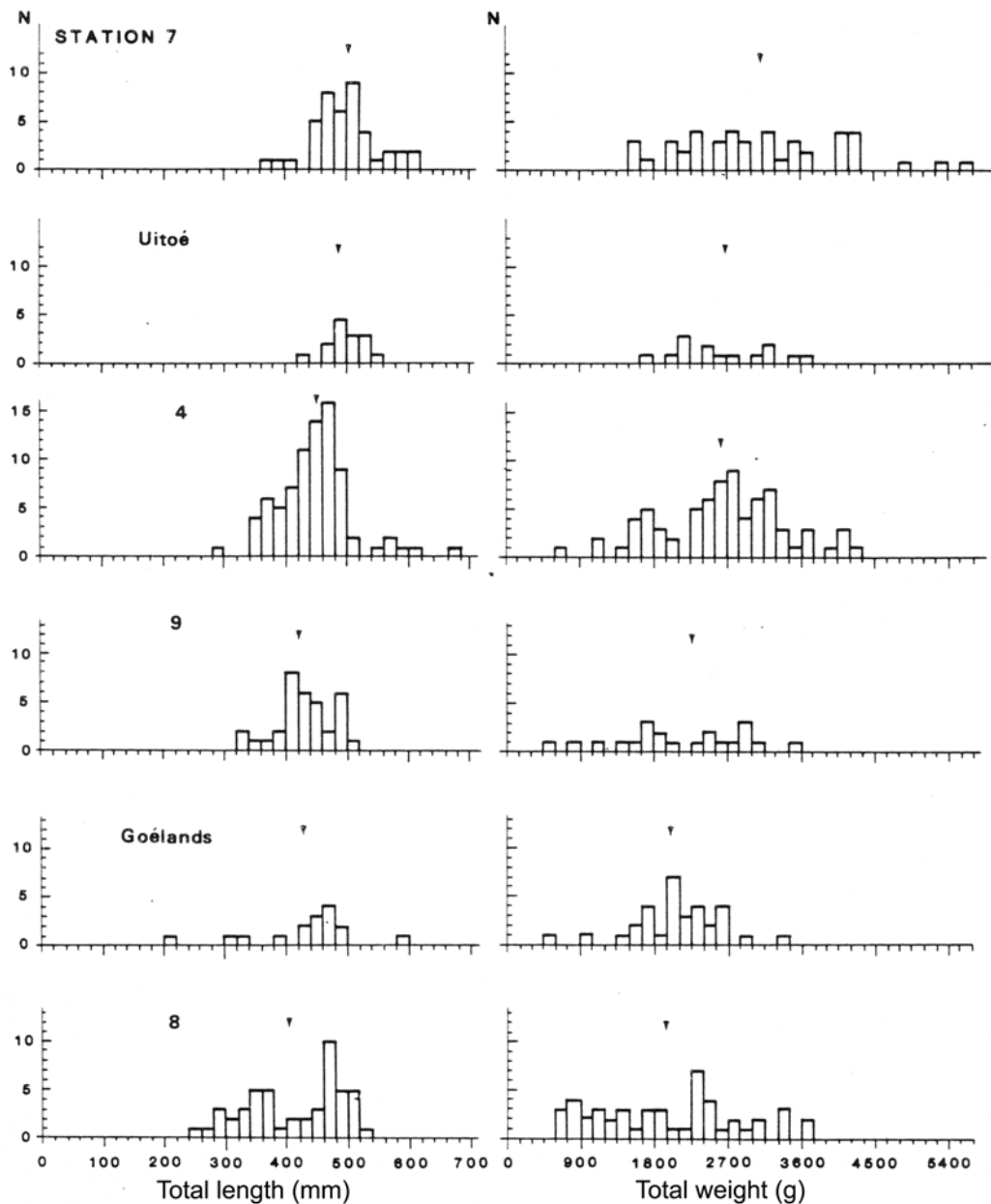


Figure 53: Distribution by station of total lengths and weights for *H. fuscopunctata*

Thelenota ananas

The results of sampling on that the 298 specimens of this large species are given in Fig. 54. The distribution of total weights would appear to be plurimodal, with the most frequently encountered animals weighing approximately 2 kg.

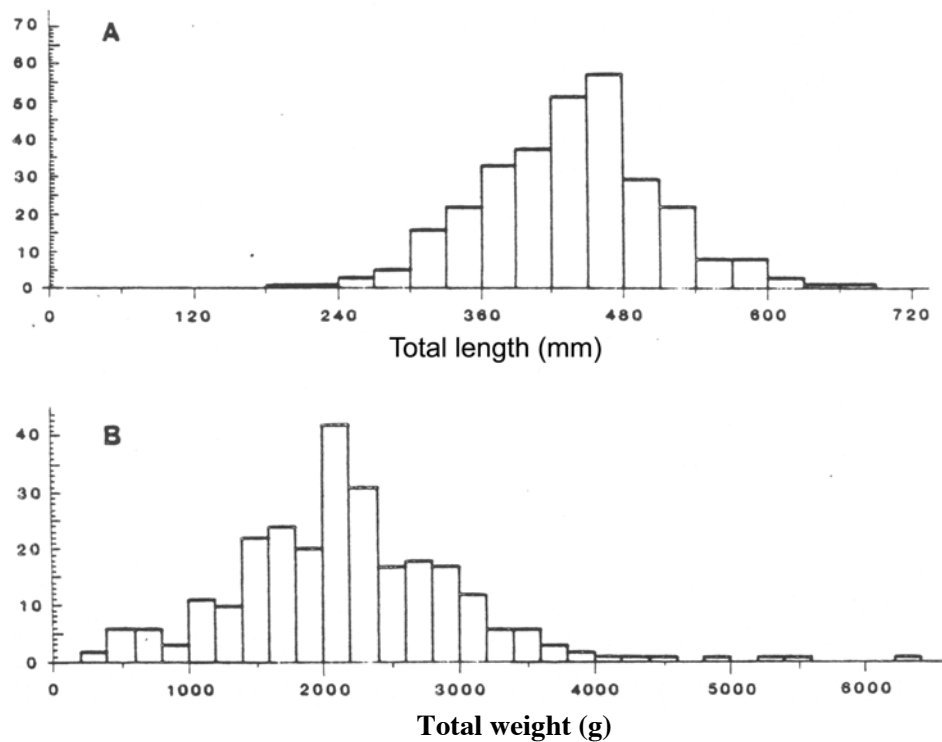


Figure 54: Distribution of total lengths and weights for *T. ananas*.

2.2.2 Species of the outer reef flats

As with slope-dwelling species, the results are given in synoptic table 21. The two species *A. mauritiana* and *A. echinites* are smaller than the slope species, approximately measuring 20 cm in length and having a total weight of 400 g.

Actinopyga mauritiana

The sampling was restricted to Station 12 from December 1978 to April 1980 and then extended from April 1981 to 1982 at Station 11. The distribution of the parameters of a total of 472 specimens is presented in Fig.55; it is presented by station on Fig. 55. Whereas at Station 11 the distributions are roughly speaking unimodal and small individuals scarce, at Station 10 small animals are present and it in fact represents an important mode.

Comparison of these two stations shows the very clear difference between these two populations. That of the barrier reefs, low in density, is formed of large specimens, whereas that of the coastal reef, high in density, is made up of several size groups. It is not yet possible to determine whether these differences come from biotic or abiotic factors.

Table 21: Distributions of measured characteristics of species of outer reef flats.

<i>Actinopyga mauritiana</i>					<i>Actinopyga echinites</i>				
	n	I	m	s		n	I	m	s
LT (mm)					LT (mm)				
T	469	60-400	224	69	T	602	40-380	207	51
St 11	138	160-400	279	42	St 13	486	40-380	217	44
St 12	331	60-340	203	64	St 14	79	40-280	151	52
PT (g)					PT (g)				
T	468	5-1500	452	293	T	599	0-1410	396	208
St 11	139	300-1500	733	252	St 13	483	0-1410	437	189
St 12	329	5-1100	333	218	St 14	79	0-630	168	143
PO (g)					PO (g)				
T	466	5-800	297	165	T	595	0-600	260	99
St 11	138	200-800	433	98	St 13	480	0-600	283	75
St 12	328	5-650	240	153	St 14	78	0-450	120	94
PE (g)					PE (g)				
T	469	5-650	229	124	T	600	0-420	188	69
St 11	140	175-650	335	73	St 13	484	0-420	205	54
St 12	329	5-500	184	114	St 14	79	0-390	96	79

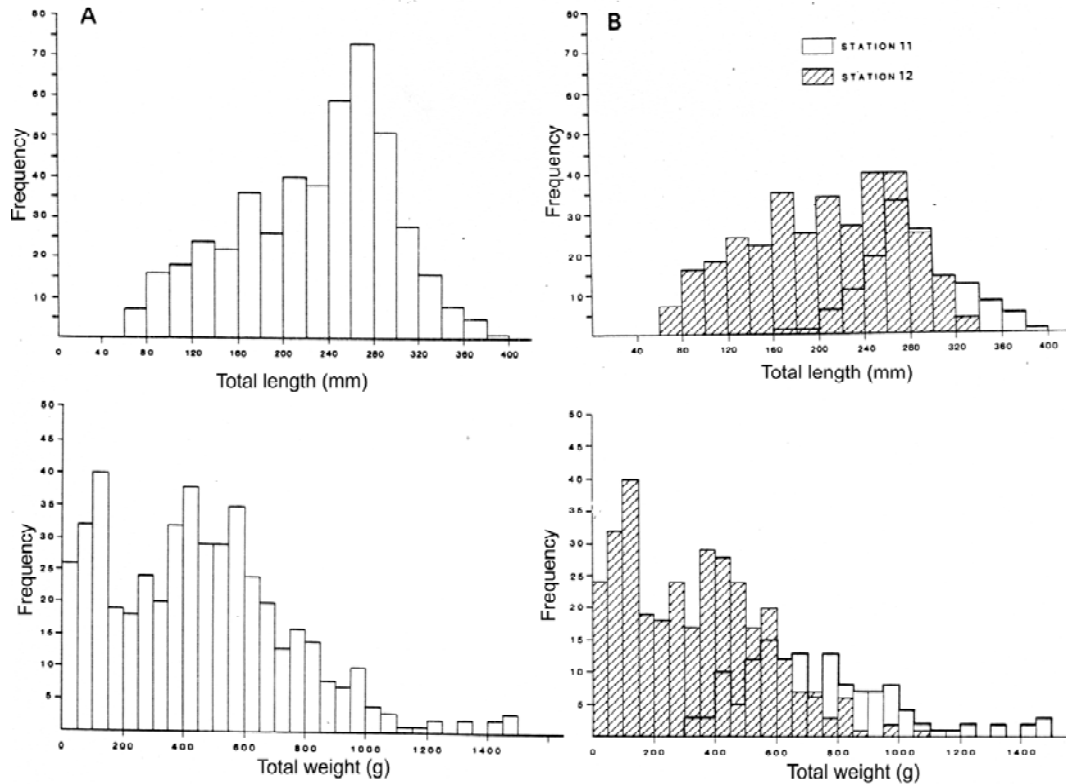


Figure 55: Distribution of total lengths and weights for *A. mauritiana*.
A = all stations; B = by station.

Actinopyga echinites

The preliminary results (Conand, 1982) were supplemented through continued sampling at Station 13 (Ilôt Maître) and some samples were also collected from the reef flats of the Ricaudy reef for comparison purposes (Fig. 56). At Station 13, the distributions appear to be unimodal and the main parameter values are quite comparable to those of the population studied by Shelley (1981, 1985) in Papua New Guinea, i.e. a length of 22 cm and an average total weight of 340 g. On reef flats at Station 14, on the other hand, despite the low number of animals present, various modes are observed because of the presence of smaller specimens. In the same way as for *A. mauritiana*, the coastal reef flat population comprises individuals of various sizes, including smaller specimens.

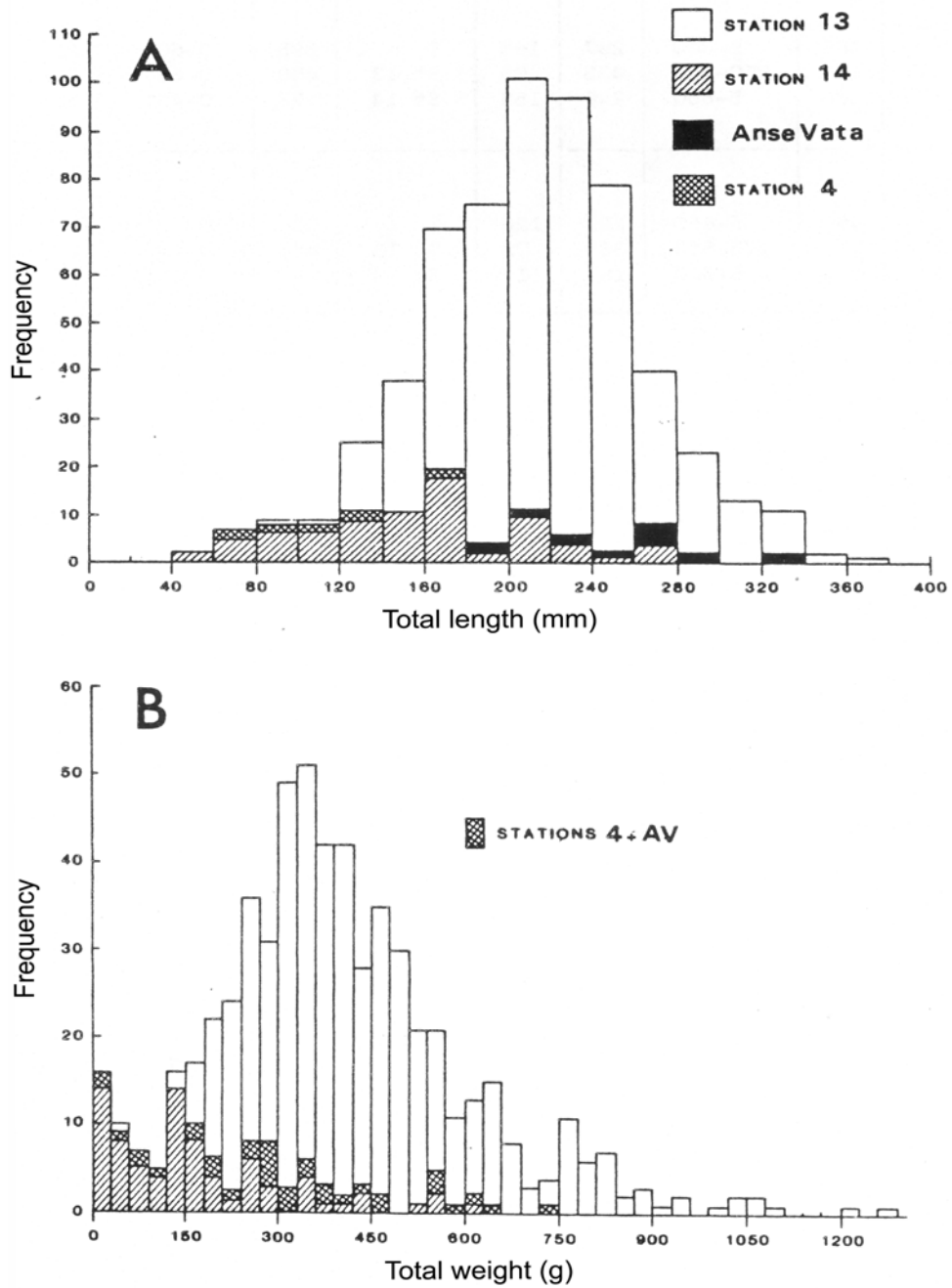


Figure 56: distribution of total lengths and weights for *A. echinites*.

2.2.3 Species of inner reef flats and lagoons

The parameters for *H. atra*, *H. scabra*, *H. scabra* var. *versicolor*, and *S. variegatus* harvested from the inner reef flats of Ilôt Maître or at their foot in the channel, are given in Table 22.

Table 22: distribution of measured characteristics of inner reef flat and inner lagoon species.

	<i>Holothuria scabra</i>				<i>H. scabra</i> var. <i>versicolor</i>			
	n	I	m	s	n	I	m	s
LT (mm)	325	120- 390	241	44	272	180- 480	350	46
PT (g)	325	50-1400	484	196	270	100-2800	1452	409
PO (g)	324	50-1100	381	157	272	100-1900	969	276
PE (g)	324	0- 850	270	111	272	100-1400	732	181
	<i>Stichopus variegatus</i>				<i>Holothuria atra</i>			
	n	I	m	s	n	I	m	s
LT (mm)	272	175- 575	392	58	240	40-320	133	48
PT (g)	237	160-2440	1427	393	240	0-500	138	96
PO (g)	240	160-2080	1144	307	235	0-340	94	61
PE (g)	241	40-1840	981	256	238	0-190	50	32

Holothuria atra

The sampling was carried out over a one-year period, on the inner reef flat. Specimens at this station were generally small (Fig. 57) and the average length is 13 cm. This value is very close to those observed by Ebert (1978) and Bonham and Held (1963). A number of authors, such as Harriot (1980, 1982) and Massin and Doumen (1986) observed some unimodal and some bimodal distributions at neighbouring sites. Also, Clark (1921) and Pearse (1968) observed a relationship between the size of individuals and depth. These variations are often related to the fission process, which will be detailed later (see 3.7).

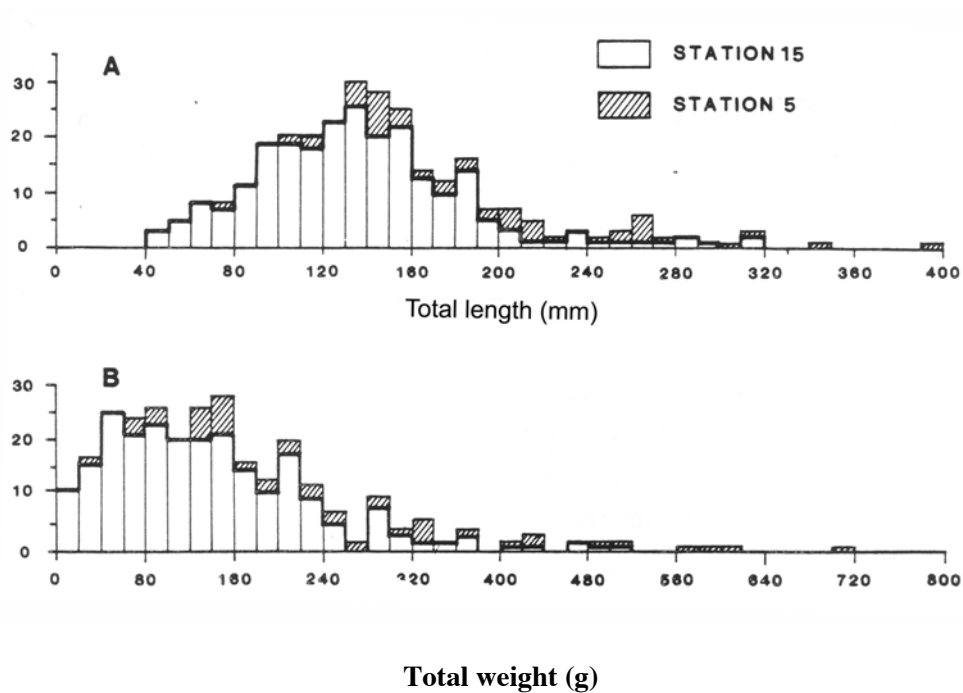


Figure 57: Total length and weight distributions for *H. atra*.

Apart from these reef flat or lagoon populations, in which specimens are usually small and covered with a layer of fine sand, except in certain circular areas where the tegument remains uncovered, we observed at various stations in New Caledonia populations of very large specimens with a modal size between 25 and 45 cm, whose tegument was uniformly covered in sand and instead of being smooth was covered in wart-like protrusions on the dorsal area. These populations were not located at deep stations, but rather on barrier reef flats with strong water movement. It would probably be useful to define the populations of this variety more accurately, using electrophoresis for example.

Holothuria scabra* and *H. scabra versicolor

The sampling conducted for *H. scabra* at two sites very close to an inner reef flat, concerning 325 specimens, showed similar parameter distributions (Fig. 58 A), which is confirmed by the weight distributions observed when tagging at these stations (see Fig. 100). The mean values are also very comparable to those observed respectively by Harriet (1980) and Shelley (1981) during their monthly sampling work on this species. Populations composed of smaller animals have been observed on Ouano reef flats and in the vicinity of mangroves in northern New Caledonia.

The variety *H. scabra versicolor* was basically sampled at Station 17 (Fig. 58B). A number of animals harvested from the reef flats here were smaller in size.

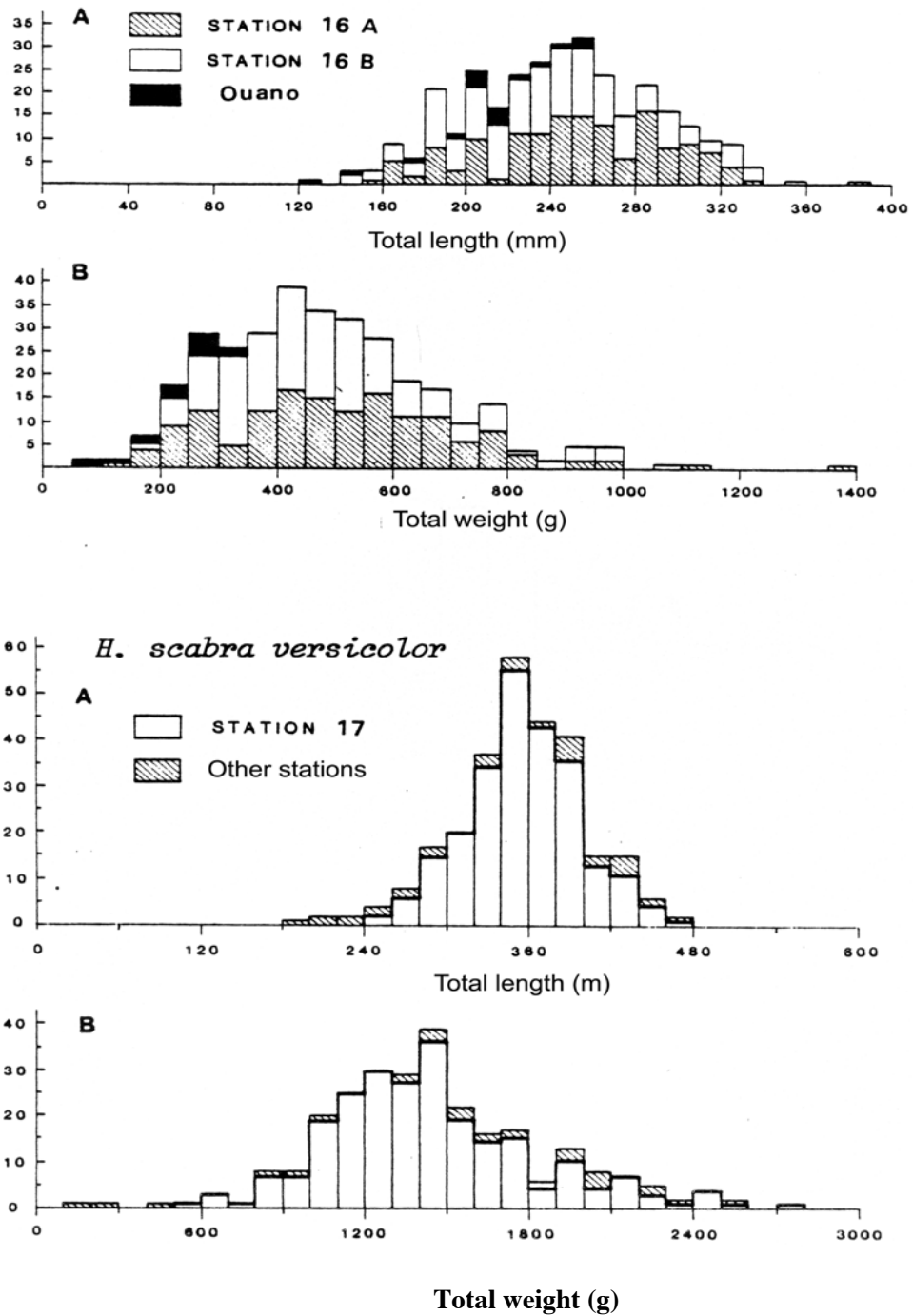


Figure 58: Total length and weight distributions for *H. scabra* and *H. scabra* var. *versicolor*.

Stichopus variegatus

Sampling of 275 specimens at the same Station 17 also shows the scarcity of small animals (Fig. 59) whereas they were present on the neighbouring reef flats, as indicated by the tagging data (see Fig. 100).

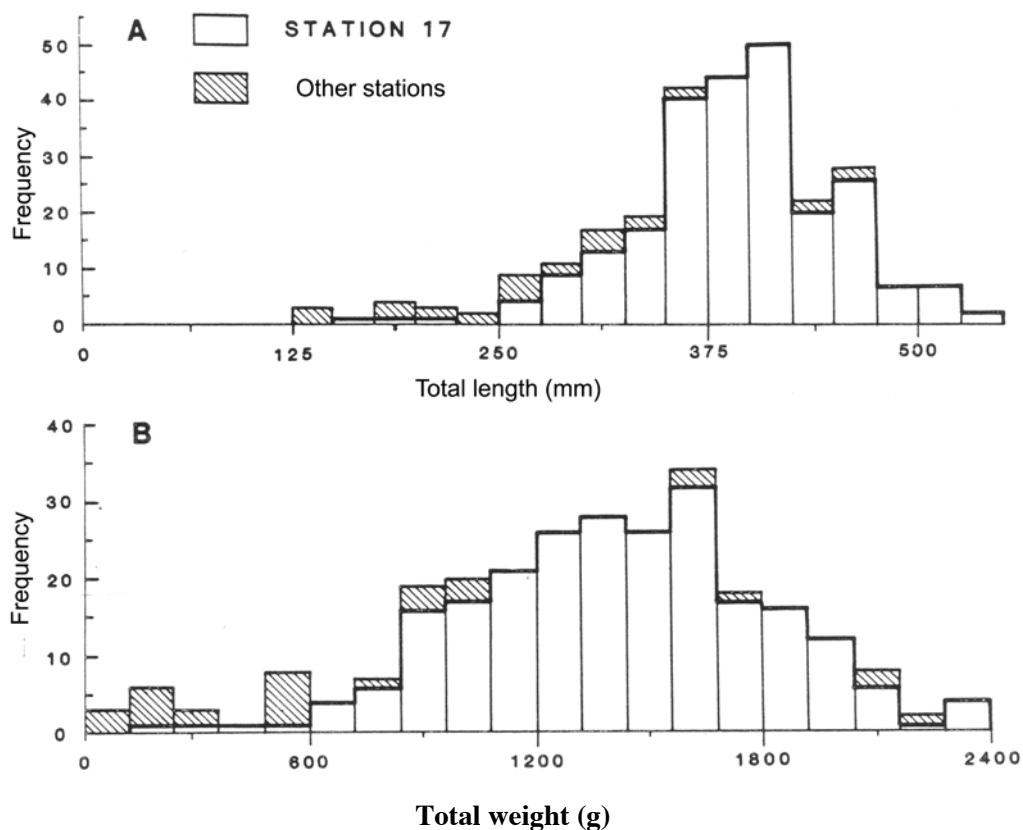


Figure 59: total length and weight distributions for *S. variegatus*.

2.3 BIOMETRIC RELATIONSHIPS

The biometric relationships are presented, in the same order, for the species of slopes, outer reef flats and inner reef flats and lagoons.

2.3.1 Slope species

Table 23 is a synopsis of the relationships between the length and weight parameters for each species.

These are exponential relationships between length and total weight, whether open or eviscerated. The correlation coefficient values, despite the variability of the measurements, are high between length and total weight, but diminish with open and eviscerated weight. The relationships between the weights are linear in nature; the correlation coefficient values are high, in particular between the open and eviscerated weights.

For each species, the dispersal of the experimental points is shown by Fig.60 for the relationships between total weight and length (A) and gutted weight - open weight (B).

When sampling was carried out at a number of different stations, the relationships calculated for each are not different and there is justification for grouping them. The dispersal of points is illustrated by the example of *Holothuria nobilis* (Fig. 60).

Table 23: Biometric relationships of slope and passage species.
 dl = degrees of freedom; r = correlation coefficient.
 i = confidence interval of the slope, probability threshold = 0.05.

X	Y	<i>Holothuria nobilis</i>				<i>Holothuria fuscogilva</i>			
		dl	r	Equation	i	dl	r	Equation	i
LT	PT	506	0,80	Log Y = -6,39 + 2,34 Log X	2,22-2,46	106	0,71	Log Y = -6,81 + 2,41 Log X	2,10-2,72
LT	PO	504	0,65	Log Y = -5,80 + 2,18 Log X	2,04-2,33	118	0,67	Log Y = -4,79 + 2,01 Log X	1,76-2,27
LT	PE	513	0,61	Log Y = -4,97 + 1,99 Log X	1,86-2,13	112	0,74	Log Y = -4,87 + 1,99 Log X	1,77-2,25
PT	PO	497	0,82	Y = 104,44 + 0,62 X	0,59-0,65	105	0,80	Y = 217,7 + 0,58 X	0,52-0,65
PT	PE	505	0,77	Y = 132,04 + 0,44 X	0,42-0,46	104	0,78	Y = 292,7 + 0,43 X	0,38-0,49
PO	PE	504	0,96	Y = 56,71 + 0,71 X	0,69-0,73	119	0,97	Y = 75,54 + 0,78 X	0,75-0,81
X	Y	<i>Holothuria fuscopunctata</i>				<i>Theleota ananas</i>			
		dl	r	Equation	i	dl	r	Equation	i
LT	PT	236	0,90	Log Y = -7,55 + 2,50 Log X	2,37-2,63	263	0,89	Log Y = -6,67 + 2,36 Log X	2,23-2,49
LT	PO	246	0,78	Log Y = -7,04 + 2,36 Log X	2,18-2,54	288	0,87	Log Y = -6,51 + 2,32 Log X	2,19-2,45
LT	PE	247	0,76	Log Y = -7,95 + 2,45 Log X	2,26-2,64	296	0,86	Log Y = -6,28 + 2,25 Log X	2,12-2,38
PT	PO	233	0,84	Y = 116,18 + 0,62 X	0,58-0,66	259	0,97	Y = 92,78 + 0,86 X	0,83-0,89
PT	PE	233	0,81	Y = 56,85 + 0,44 X	0,41-0,47	263	0,94	Y = 117,76 + 0,68 X	0,65-0,71
PO	PE	243	0,98	Y = -21,49 + 0,72 X	0,70-0,74	288	0,98	Y = 58,12 + 0,78 X	0,76-0,80

Table 24: Biometric relationships of species of outer reef flats.

X	Y	<i>Actinopyga echinites</i>				<i>Actinopyga mauritiana</i>			
		dl	r	Equation	i	dl	r	Equation	i
LT	PT	597	0,89	Log Y = -7,98 + 2,60 Log X	2,51-2,70	463	0,90	Log Y = -7,34 + 2,46 Log X	2,36-2,55
LT	PO	593	0,84	Log Y = -6,74 + 2,30 Log X	2,20-2,40	461	0,87	Log Y = -7,30 + 2,38 Log X	2,27-2,48
LT	PE	598	0,83	Log Y = -6,61 + 2,21 Log X	2,11-2,31	464	0,88	Log Y = -7,19 + 2,31 Log X	2,21-2,41
PT	PO	293	0,83	Y = 55,00 + 0,53 X	0,50-0,56	462	0,88	Y = 42,11 + 0,56 X	0,54-0,58
		590	0,94	Log Y = 0,32 + 0,88 Log X	0,86-0,90	462	0,96	Log Y = -0,19 + 0,96 Log X	0,93-0,99
PT	PE	294	0,80	Y = 43,18 + 0,37 X	0,35-0,39	463	0,87	Y = 37,97 + 0,42 X	0,40-0,44
		595	0,93	Log Y = 0,18 + 0,85 Log X	0,83-0,87	463	0,96	Log Y = -0,26 + 0,94 Log X	0,91-0,96
PO	PE	591	0,96	Y = 5,30 + 0,70 X	0,69-0,71	461	0,98	Y = 6,49 + 0,75 X	0,74-0,76

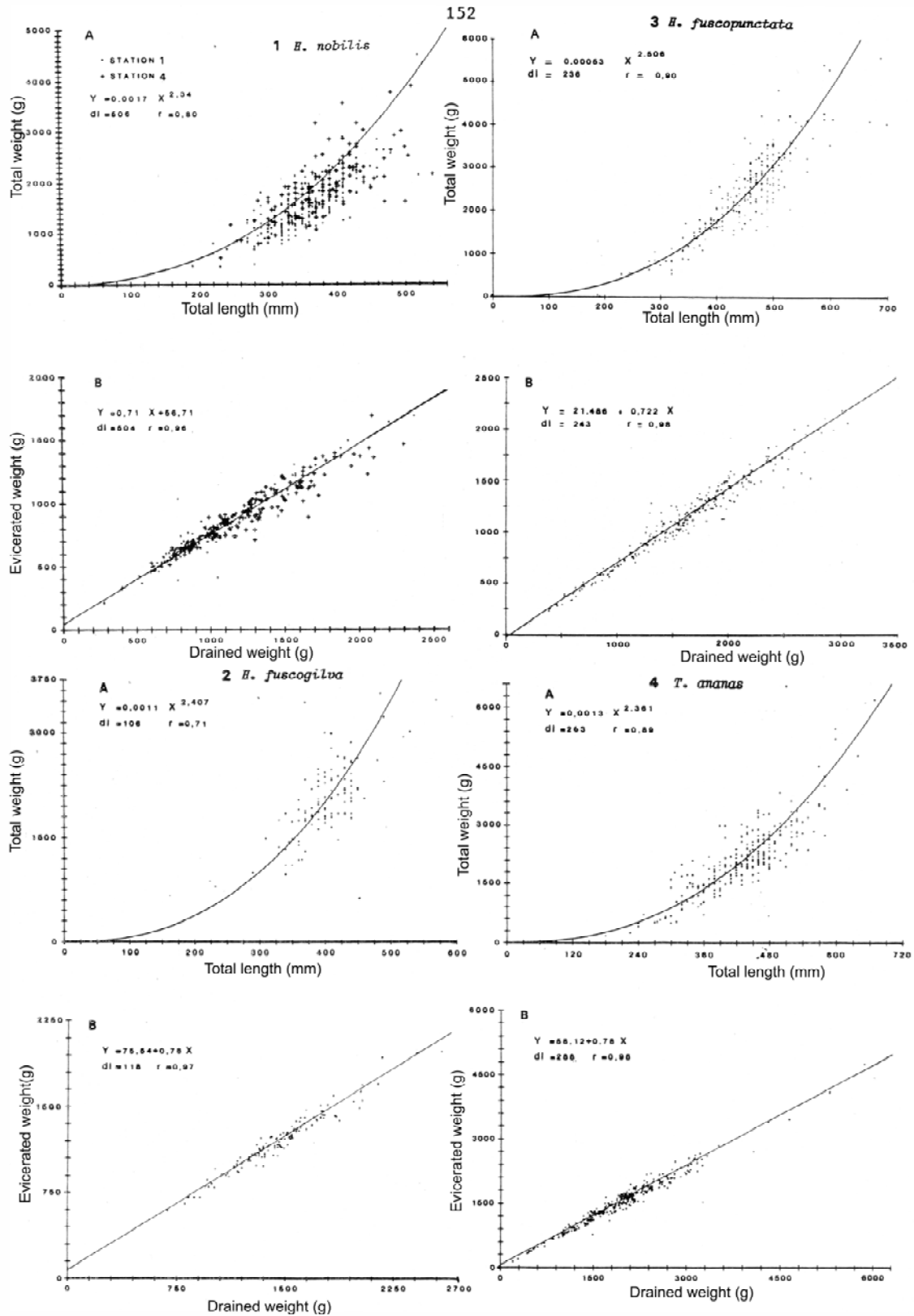


Figure 60: Biometric relationships of slope species.
 A = total weight minus length;
 B = open weight minus eviscerated weight.
 The relationship is calculated for the points as a whole.

2.3.2 Species of outer reef flats

Similarly, the biometric relationships are presented for *A. mauritiana* and *A. echinites* in Table 24 and Fig. 61.

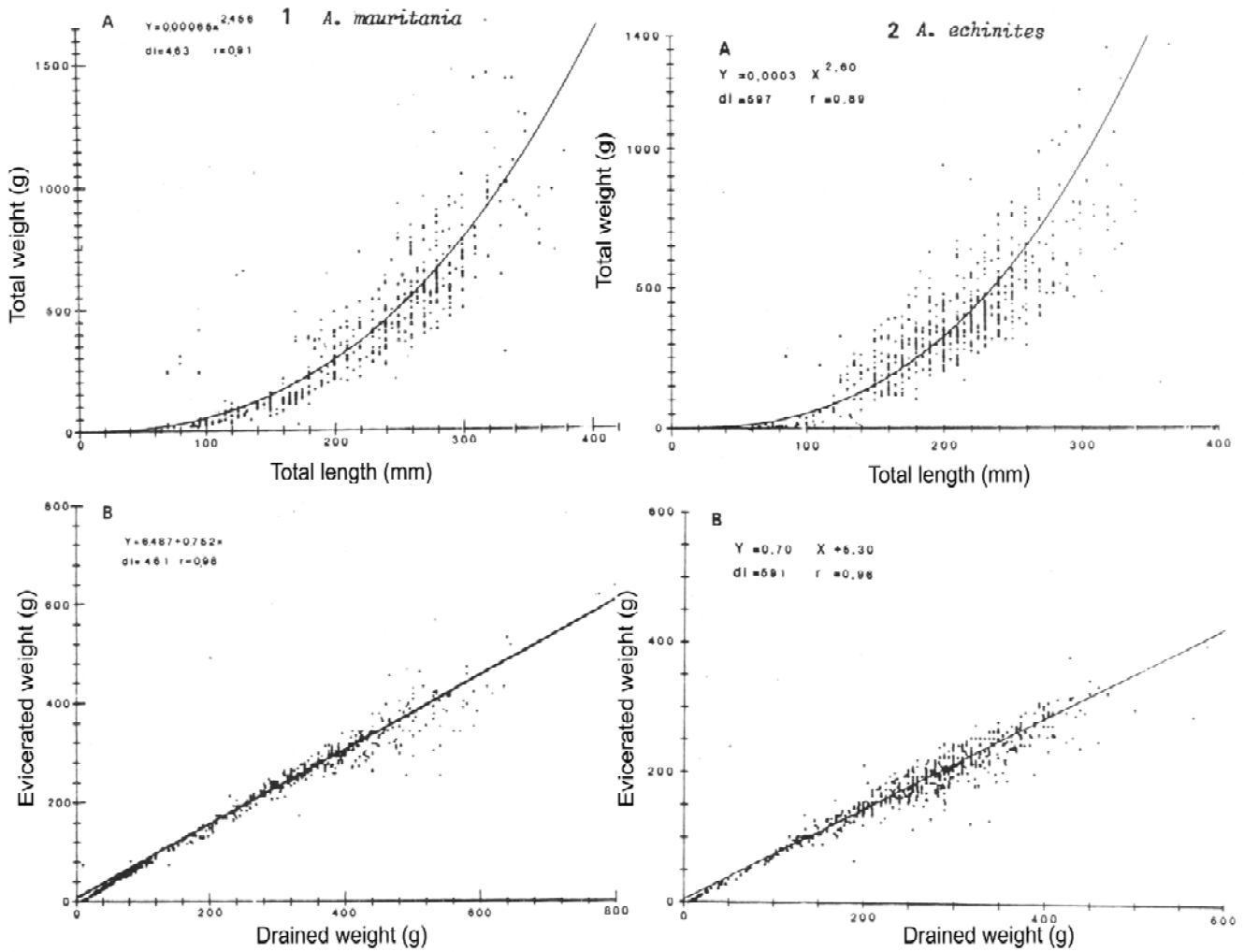


Figure 61: Biometric relationships of outer reef flat species.

2.3.3 Species of inner reef flats and inner lagoons

For this group of species, *H. atra*, *H. scabra*, *H. scabra* var. *versicolor* and *S. variegatus*, the biometric relationships are given in Table 25 and Fig. 62.

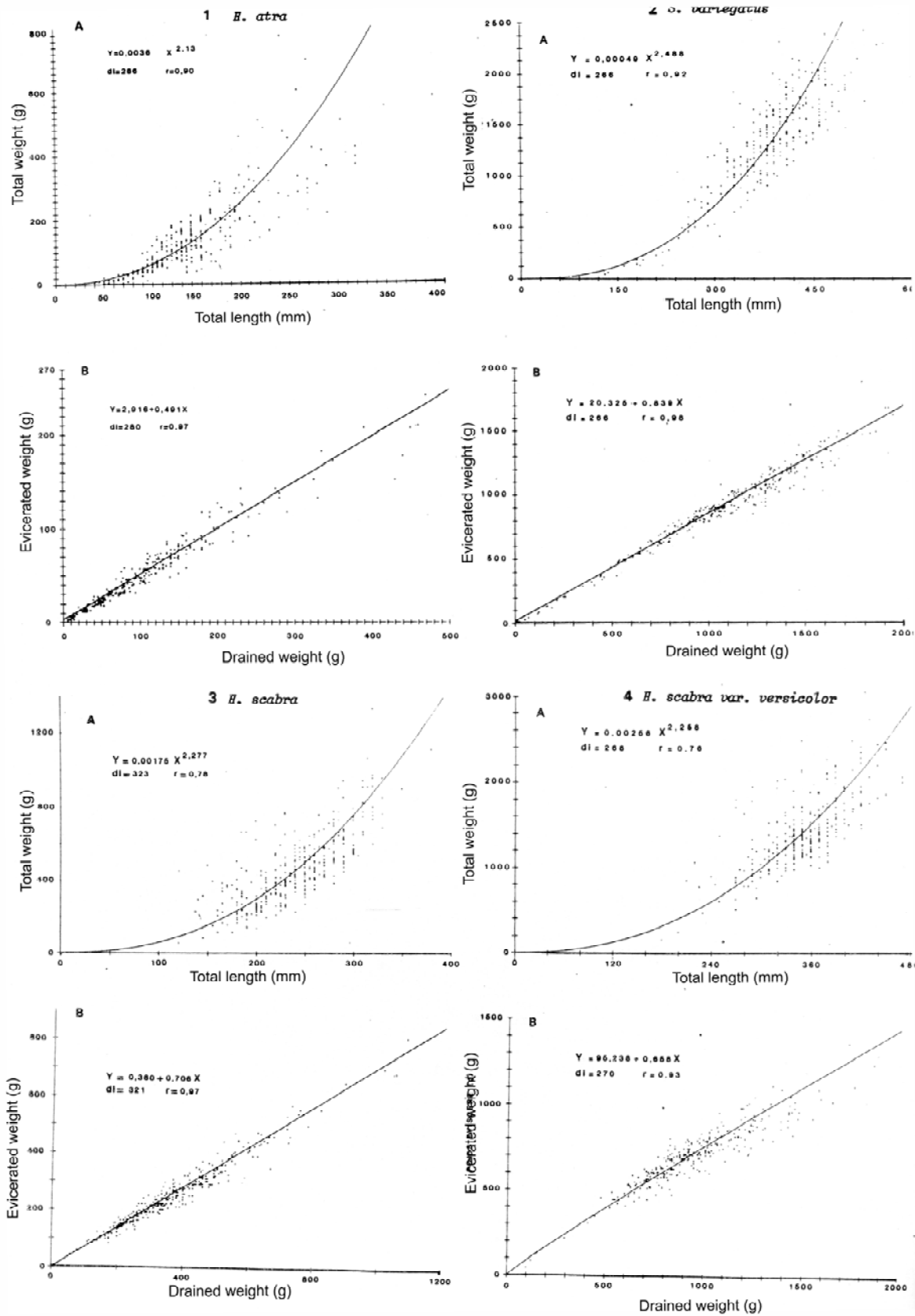


Figure 62: Biometric relationships of species of inner reef flats and inner lagoons.

Table 25: Biometric relationships of species of inner reef flats and inner lagoons.

X	Y	<i>Holothuria scabra</i>				<i>H. scabra</i> var. <i>versicolor</i>			
		dl	r	Equation	i	dl	r	Equation	i
LT	PT	323	0,78	Log Y = 2,28 Log X - 6,35	2,13-2,44	268	0,76	Log Y = 2,26 Log X - 5,97	2,09-2,44
LT	PO	322	0,74	Log Y = 2,29 Log X - 6,65	2,12-2,46	270	0,63	Log Y = 2,44 Log X - 7,42	2,22-2,67
LT	PE	322	0,73	Log Y = 2,23 Log X - 6,67	2,07-2,40	270	0,64	Log Y = 2,29 Log X - 6,83	2,09-2,51
PT	PO	322	0,95	Y = 0,80 X - 7,10	0,78-0,83	268	0,84	Y = 0,68 X - 13,47	0,63-0,73
PT	PE	322	0,93	Y = 0,57 X - 4,69	0,55-0,59	268	0,75	Y = 0,44 X + 86,56	0,41-0,48
PO	PE	321	0,97	Y = 0,71 X - 0,36	0,69-0,72	270	0,93	Y = 0,66 X + 95,24	0,63-0,69
X	Y	<i>Holothuria atra</i>				<i>Stichopus variegatus</i>			
		dl	r	Equation	i	dl	r	Equation	i
LT	PT	286	0,90	Log Y = -5,64 + 2,13 Log X	2,02-2,24	266	0,92	Log Y = -7,62 + 2,49 Log X	2,37-2,60
LT	PO	281	0,87	Log Y = -5,95 + 2,12 Log X	2,00-2,24	267	0,91	Log Y = -7,60 + 2,45 Log X	2,32-2,56
LT	PE	284	0,83	Log Y = -5,89 + 1,97 Log X	1,85-2,10	269	0,90	Log Y = -7,79 + 2,45 Log X	2,33-2,57
PT	PO	281	0,96	Y = 1,58 + 0,68 X	0,65-0,70	261	0,97	Y = 0,56 + 0,80 X	0,78-0,82
PT	PE	284	0,94	Y = 3,59 + 0,33 X	0,32-0,35	264	0,94	Y = 19,85 + 0,67 X	0,64-0,70
PO	PE	279	0,97	Y = 2,92 + 0,49 X	0,48-0,50	266	0,98	Y = 20,32 + 0,84 X	0,82-0,86

2.4 DISCUSSION

2.4.1 Morphometric characteristics

Despite the variability of holothurian measurements, the frequency distributions of the morphometric characteristics, lengths and weights, for nine species, do make it possible to identify some general features of these populations.

Species size

The three groups of species characteristic of the three habitats, coral slopes, outer reef flats, inner reef flats and inner lagoons, are distinguished in general by their size. The slope species are large in size, those of the inner reef flats and inner lagoons are often medium-size, while species of outer reef flats are smaller. These distinctions relate to the nine main species making up the majority of the densities and biomasses calculated at a lagoon-wide scale. The other species present in abundance also seemed to comply with this classification. By referring to the parameter values given in Chapter 1 as part of the species descriptions, it would appear that the species of inner reef flats, *A. miliaris* and *H. leucospilota*, and those of inner lagoons, *A. spinea*, are often medium-sized. On the other hand, *S. chloronotus*, of the outer reef flats, is smaller and the slope species *B. argus* and *A. paluaensis* are large-sized species.

Distribution characteristics

In the majority of species sampled, length distributions are unimodal. This type of distribution will be more thoroughly researched in connection with growth (see 4.4). Also, it emerged that small individuals were scarce or even completely lacking, except at a few coastal reef flats stations. This has already been reported with echinoderms and in particularity with holothurians by Crozier (1918), Bacchus (1973) and Muscat (1983). It is especially marked here in the larger species and will be addressed in the conclusion in connection with the recruitment issue.

Spatial variations

With regard to the species studied at a number of stations in the southwestern lagoon, the modal values of distributions are generally different. These variations cannot be explained by a simple general hypothesis. In fact, in some cases, they would appear to be linked to abiotic factors: for example, the relationship with depth could exist for *S. variegatus* or *Holothuria scabra versicolor*, whose inner reef flat specimens are smaller than those found at stations near the inner lagoon. Migrations during the life cycle could also be a factor, that they were not identified by tagging. Water movement and the organic matter content of the sediment are certainly influential abiotic factors. The biotic factors, predation and interspecific competition, have not yet been analysed.

2.4.2 Biometric relationships

Despite the variability of measurements, the correlation coefficient values for the relationships between length and weight are high. They will be used later in this study to enable the conversion of measurements and to compare the results with those obtained by other authors.

The relationships between length and total weight have also been established, during the HOLOT research programme on other frequent species in the lagoon, from a smaller total number (Table 26). It would appear that the allometric coefficient values are between 1.8, the lowest value calculated for *H. coluber*, and 3.1 with *Holothuria* sp.2. The intervals between parameter values and the different numbers of specimens involved do not make it possible to draw a comparison, that it would nevertheless appear that with species having the shape of a narrow cylinder, the allometric coefficient shows lower values, about 2.2, than with broad cylinder-shaped species OR parallelepiped-shaped species.

The allometric coefficient values in the relationships between length and eviscerated weight are lower, as are those of the correlation coefficient. The linear relationship between weights shows high correlation coefficient values, in particular between the open weight and the eviscerated weight. Generally speaking, a reduction in the open weight in comparison with the total weight is approximately one-third and not very different from that of the open weight to the eviscerated weight. The latter is therefore slightly lower than half of the total weight.

For species sampled at a number of stations, the biometric relationships do not appear any different, taking into account the variability of measurements. Similarly, no sexual dimorphism appears in the biometric relationships, with the sex ratio generally being balanced (see 3.2).

Table 26: Relationships between total weight and length $PT (g) = a L^b (mm)$,
for the main species of holothurian found in the lagoon.
*relationships established from the monthly sampling activity.

Species	d.l.	r	a	b	L min	L max
<i>A. echinites</i> *	597	0,89	$0,342 \cdot 10^{-3}$	2,600	58	365
<i>A. mauritiana</i> *	463	0,91	$0,647 \cdot 10^{-3}$	2,456	60	420
<i>A. miliaris</i>	118	0,96	$0,824 \cdot 10^{-3}$	2,441	75	380
<i>A. spinea</i>	31	0,95	$1,014 \cdot 10^{-3}$	2,402	170	380
<i>B. argus</i>	84	0,98	$0,925 \cdot 10^{-4}$	2,802	100	510
<i>B. similis</i>	18	0,95	$0,755 \cdot 10^{-3}$	2,411	52	290
<i>B. vitiensis</i>	17	0,98	$0,562 \cdot 10^{-4}$	2,961	120	350
<i>P. graeffei</i>	56	0,94	$1,521 \cdot 10^{-3}$	2,217	150	490
<i>H. coluber</i>	34	0,91	$5,797 \cdot 10^{-3}$	1,835	76	600
<i>H. atra</i> *	286	0,90	$3,555 \cdot 10^{-3}$	2,128	40	340
<i>H. edulis</i>	90	0,81	$0,208 \cdot 10^{-3}$	2,554	100	320
<i>H. leucospilota</i>	25	0,98	$0,164 \cdot 10^{-3}$	2,513	80	480
<i>H. scabra</i> *	323	0,78	$1,750 \cdot 10^{-3}$	2,277	140	370
<i>H. s. versicolor</i> *	268	0,76	$2,560 \cdot 10^{-3}$	2,258	180	470
<i>H. nobilis</i> *	506	0,80	$1,677 \cdot 10^{-3}$	2,344	190	550
<i>H. fuscogilva</i> *	106	0,71	$1,102 \cdot 10^{-3}$	2,407	280	575
<i>H. fuscopunctata</i> *	236	0,90	$0,530 \cdot 10^{-3}$	2,506	220	700
<i>H. flavomaculata</i>	11	0,73	$0,911 \cdot 10^{-3}$	2,201	280	480
<i>H. hilla</i>	17	0,76	$0,225 \cdot 10^{-3}$	2,373	130	340
<i>Holothuria</i> sp.1	19	0,86	$2,252 \cdot 10^{-3}$	2,177	120	370
<i>Holothuria</i> sp.2	25	0,96	$0,037 \cdot 10^{-4}$	3,138	200	510
<i>S. chloronotus</i>	142	0,96	$2,221 \cdot 10^{-3}$	2,102	55	340
<i>S. variegatus</i> *	266	0,92	$0,489 \cdot 10^{-3}$	2,488	130	565
<i>Stichopus</i> sp. 1	22	0,94	$2,701 \cdot 10^{-3}$	2,112	110	270
<i>T. ananas</i> *	263	0,89	$1,266 \cdot 10^{-3}$	2,361	180	660
<i>T. anax</i>	29	0,96	$2,034 \cdot 10^{-4}$	2,654	300	740

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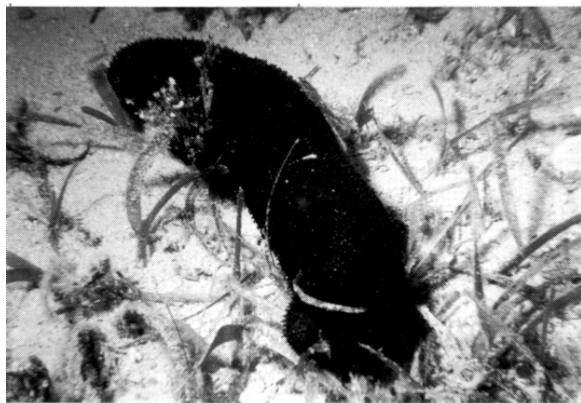
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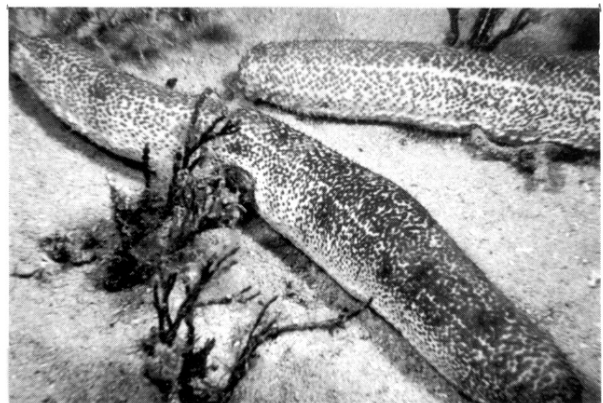
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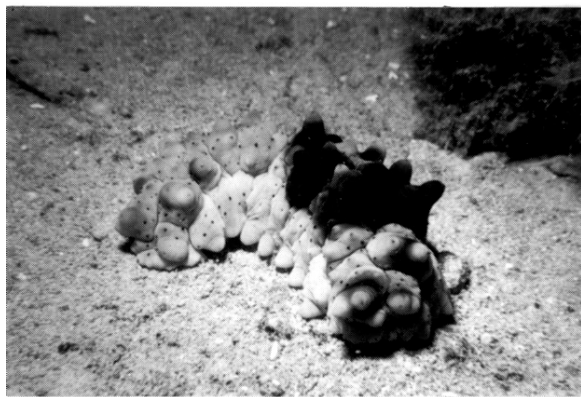
APPENDIX I: Some relevant figures and tables from parts of the thesis that have not been translated.



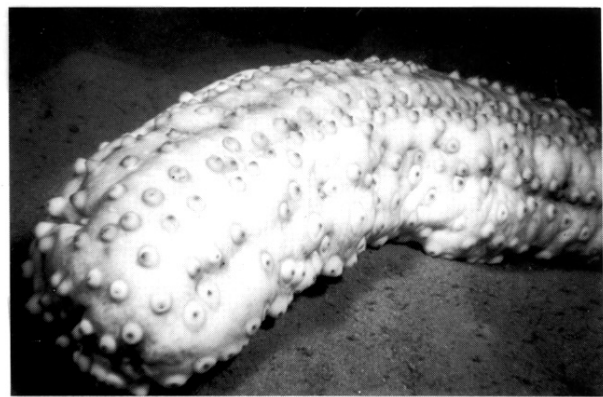
Holothuria sp.1



Holothuria sp.2



Stichopus sp.1



Stichopus sp.2

Figure 4. Unidentified species of the genus *Holothuria* and *Stichopus*

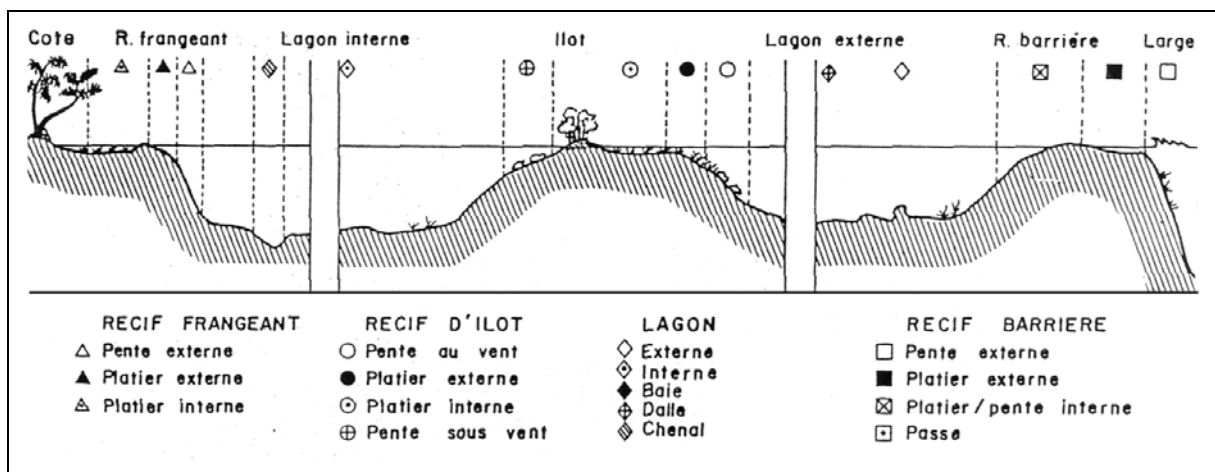


Figure 12. Main biotopes of reefal and lagoonal complexes, classified by type of structure.

Table 9: Geographical distribution of the HOLOT. campaigns.
S: stations with holothurians

REGION	CAMPAGNE	LIMITES GEOGRAPHIQUES A LA COTE	STATIONS EFFECTUEES	S
Sud-Ouest	Holot 5	La Tontouta-Plum	48	48
Centre-Ouest	Holot 1	La Tontouta-Voh	32	25
Nord-Ouest	Holot 3	Voh-Poum	25	23
Nord-Est	Holot 4	Arama-Tao	28	28
Centre-Est	Holot 2	Hienghène-Canala	31	28
Sud-Est	Holot 6	Canala-Goro	26	24
Sud	Holot 7	Goro-Plum	26	26
TOTAL			216	202

Table 10: Distribution by biotope of the sampling stations.
n: stations with holothurians

BIOTOPE		SYMBOLE	STATIONS EFFECTUEES	n
Barrière	pente externe	B Pe E □	7	6
	platier externe	B Pl E ■	6	5
	platier + pente interne	B Pe I ⊠	23	22
	passee	Pa ◻	12	12
Ilot	pente externe	I Pe E ○	18	18
	platier externe	I Pl E ●	11	10
	platier interne	I Pl I ⊕	23	23
	pente interne	I Pe I ⊕	12	12
Frangeant	pente externe	F Pe E △	14	14
	platier externe	F Pl E ▲	5	5
	platier interne	F Pl I ▴	14	14
RECIFAL			145	141
Lagon externe	L E ◇	16	14	
Lagon interne	L I ◆	16	15	
Côtier	C B ◆	26	19	
Lagon à dalles	L D ⊕	10	10	
Chenal	C H ⊞	3	3	
LAGONAIRE			71	61