Helgoländer wiss. Meeresunters. 28, 51–65 (1976)

Feeding behaviour of the felt-, sponge-, and coral-feeder sea stars, mainly *Culcita schmideliana*

B. A. THOMASSIN

Station Marine d'Endoume et Centre d'Oceanographie; Marseilles, France

RESUME: **Ethologie alimentaire des Stéllérides mangeuses de film épibenthique, d'éponges et de madréporaires, principalement de *Culcita schmideliana*.** Sur les récifs coralliens de la région de Tuléar (Madagascar), les éthologies alimentaires des Stéllérides de l'épifaune ont été étudiées, particulièrement celle de *C. schmideliana*. Cette espèce colonise habituellement les herbiers de Phanérogames des platiers récifaux internes; dans ce biotope, elle se nourrit toujours en extroversant son estomac, soit sur le film épipsammique ou épiphytique (riche en algues microscopiques, diatomées, bactéries, foraminifères et méiofaune), soit sur les colonies de *Gellius cymiformis*, éponge associée à une algue filamenteuse et qui vit à la surface du sédiment. Récemment (en 1971–72) des populations de *C. schmideliana* se sont développées dans les formations coralliennes du platier récifal interne (platier compact, platier à éléments dispersés, platier à alignements coralliens et couloirs sableux); dans ces biotopes particuliers, cette étoile de mer se nourrit du film épibenthique croissant à la surface des colonies mortes (algues et faunule associée), ou bien de madréporaires vivants *(Galaxea, Goniopora)*, d'éponges ou d'alcyonnaires *(Xenia)*. Ce comportement nutritionel particulier et non dévut est analysé; des hypothèses sur les causes de cette migration sont avancées. Par ailleurs, la distribution et les éthologies alimentaires d'autres Stéllérides épibenthiques habitant les récifs coralliens, telles que: *Acanthaster planci, Linckia laevigata* et *L. multifora, Nardoa variolata, Echinaster purpureus, Monachaster sanderi, Asterina burtoni, Choriaster granulosus, Protoreaster nodosus* et *P. linckei, Pentaceraster mammillatus*, sont décrites et discutées.

INTRODUCTION

As an integral part of our studies on the coral reef ecosystem, the feeding behavior of the more common sea stars was observed during field trips and in the laboratory during the 1965–66, 1969 and 1972 surveys on the coral reefs in the vicinity of Tuléar, Madagascar, especially the "Grand Récif" (Fig. 1).

During these surveys we noticed changes in the population densities of two species, *Culcita schmideliana* (RETZIUS) (including typical specimens of this species, and the varieties *ceylanica* and *africana* (GOTO, 1914) and *Acanthaster planci*. Densities of other species of sea stars have remained unchanged during these seven years. Aspects of the predation on sea stars by gastropods were also examined.

FEEDING BEHAVIOR OF THE CUSHION-STAR *CULCITA SCHMIDELIANA*

Observations

During the 1965–66 (July–February) and 1969 (July–November) field seasons, we observed *Culcita schmideliana** (typically yellow or light-brown in color, or blue or pink-colored, as in var. *africana*) mainly colonizing the intertidal sea-grass beds on the inner coral reef flats. A few scattered specimens were also encountered in the

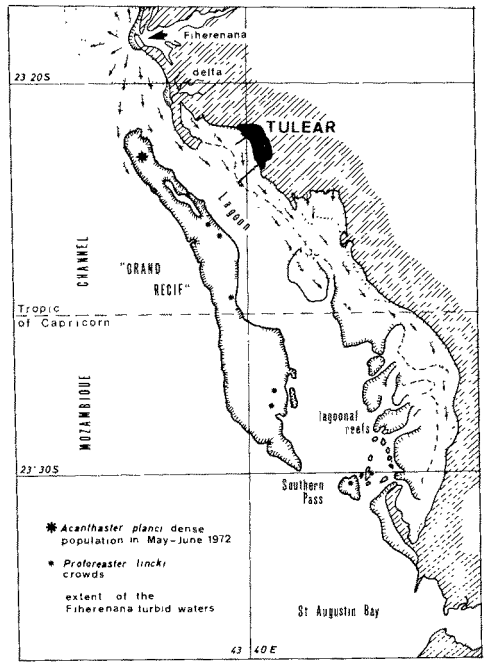

Fig. 1: Map of the Tuléar region

coral reef pass (Southern Pass) on coarse sand bottoms with never more than 5 % of silt at depths of 13 m. Others were also observed living in residual pools just behind the boulder tracts, or sometimes in sandy tidal couloirs between boulder banks. During the 1972 survey (April–August), populations of *Culcita schmideliana* in the sea-grass beds seemed to be more scattered and were generally concentrated in the high-leaved sea-grasses, *Cymodocea rotundata, C. serrulata, Halodule uninervis* (form with high leaves) or *Syringodium isoetifolium.* They were uncommon on the top of the sea-grass

* *C. schmideliana* is the only species of this genus reported from the coral reef of Tuléar. It is apparently restricted to the western Indian Ocean from the Mozambique coast to the Ceylon area (CLARK & ROWE, 1971). Pichon (1973) reports the presence of *Culcita coriacea* MÜLLER & TROSCHEL (one specimen sampled) in the coral-built formations of the inner reef flat.

flats, but more frequent in small pools and along tidal channels opening into the lagoon.

Individuals were observed feeding during the day extruding their stomachs either on the sandy substrates or on the sea-grass leaves (Fig. 2a, b), and also feeding on the branching green sponge, *Gellius cymiformis* (ESPEER), frequently located in small funnels (burrow entrances of squills or of thalassinids) among the tumuli-and-funnels fields. Generally, however feeding on *G. cymiformis* was observed more frequently at

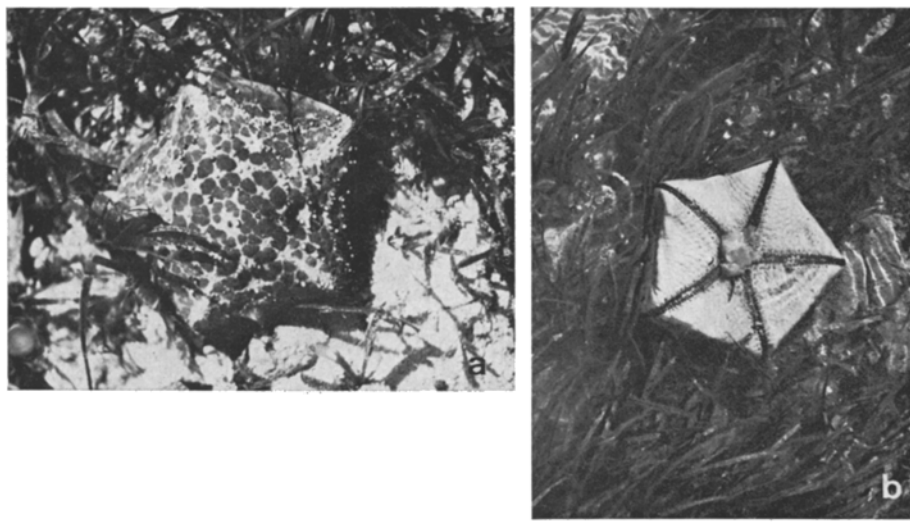

Fig. 2: *Culcita schmideliana* feeding in the sea-grass beds on the epipsammic and epiphytic felt, "Grand Récif"; *a* upper view; *b* the sea star overturned to show the stomach extruded. (1972-survey, ph. B. THOMASSIN)

night. In this case the cushion-star climbs on the colony to eat the branches (Fig. 3). On one occasion, in a tidal channel of the lagoon edge where a *Thalassodendron ciliatum* bed with numerous coral bowls (*Porites)* occurred, *Culcita* was observed feeding on another sponge, *Pachychalina* sp., but never on the Didemnidae which are frequent on sea-grass stems.

In 1972, *Culcita schmideliana* (more frequently the variety *africana*) was commonly observed in the coral-growth formations of the inner reef flats (reticulate flat, coral alignments with sandy couloirs, scattered growth flat) (Fig. 5a–c). In addition they were more abundant than in previous years in the tidal channels of the boulder tract and on the bottom of the residual pools behind them. In these biotopes, *C. schmideliana* was observed, at midday as well as during midnight spring low tides, feeding: (a) on the epibenthic felt growing on dead coral substrates; (b) sometimes on soft coral colonies with large polyps, *Xenia* sp., *Lemnalia humesi* VERSEVELDT and *Paralemnalia digitiformis* MACFADYEN, which are common in these coral reef flats; (c) more frequently on living coral colonies of small size and with large polyps, such as *Galaxea fascicularis* (LINNÉ) or *Goniopora stokesi* MILNE EDWARDS & HAIME; and less commonly on small *Acropora* growths.

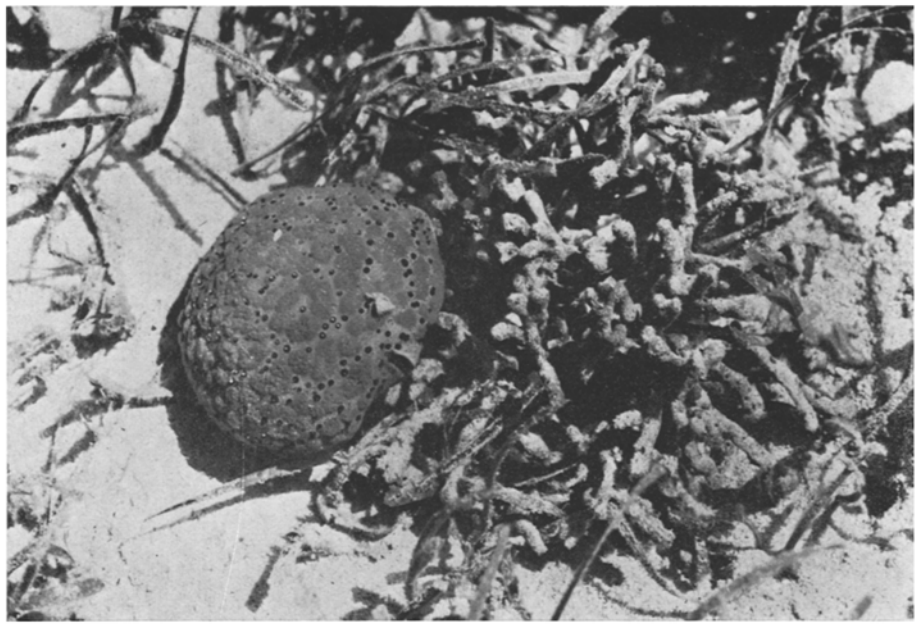

Fig. 3: *Culcita schmideliana* feeding on the green-sponge, *Gellius cymiformis,* in the sea-grass beds, "Grand Récif". (1972-survey, ph. B. THOMASSIN)

Fig. 4: *Culcita schmideliana* feeding on the yellow-sponge, *Paratetilla bacca,* on the beach rock, Nosy Vé I. (1972-survey, ph. B. THOMASSIN)

On another hard substrate biotope (on the Nosy Vé cay-reef, 30 km south of Tuléar), a specimen of *Culcita schmideliana* was caught at day-time eating over half of a colony of the yellow sponge, *Paratetilla bacca* (SELENKA), growing on the low part of the beach-rock near *Halophila ovalis* patches (Fig. 4).

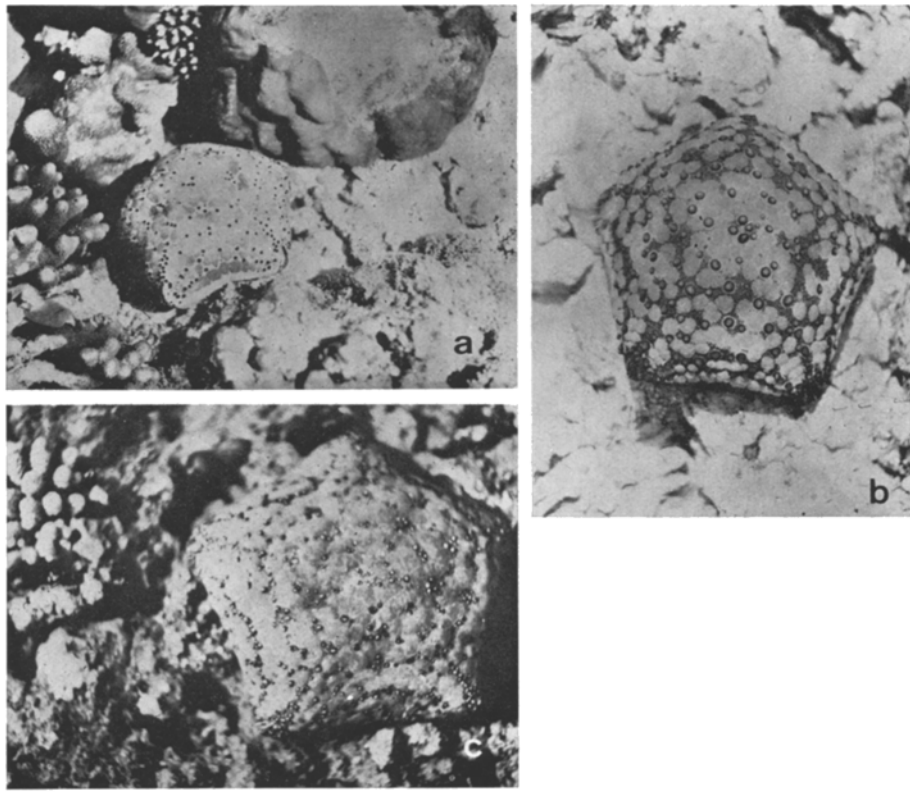

Fig. 5: *Culcita schmideliana* feeding in the coral-built formations of the inner reef flat, "Grand Récif", *a C. schmideliana* feeding on the epibenthic film growing on dead coral substrates; *b C. schmideliana* var. *africana*; *c C. schmideliana* near an *Acropora* colony recently eaten. (1972-survey, ph. B. THOMASSIN)

Comments

The feeding behavior of *Culcita schmideliana* shows in conclusion various diets, but all are generally mixed animal-vegetal foods. When *C. schmideliana*, as other known cushion sea stars (e. g. *Patiria miniata*, in: FEEDER & CHRISTENSEN, 1966), feeds by extrusion of the large cardial stomach (the digestion being direct or the stomach playing the role of a ciliary mucous-feeding organ) on epipsammic, epiphytic or epibenthic felt, it is omnivorous, all the rich small fauna (Nematoda, micro-crustaceans, small Foraminifera, Protozoa) as well as the micro-algae being consumed.

However it is very curious that the sponge eaten by *Culcita schmideliana* in the sea-grass beds, *Gellius cymiformis* (= *Spongia cymaeformis;* very close to *Sigmadocia symbiotica* BERGQUIST & TIZARD and to *Gellius ridleyi* (HENTSCHELL) (in: LÉVI, 1959) lives in symbiotic association with the green alga, *Ceratodictyon spongiosum* ZANARDINI, (RIDLEY, 1884; LÉVI, 1959, 1967; SARA & VACELET, 1974). The algae represents principal component, the sponge merely coating and encrusting all the algal surface. This sponge is widely distributed in the Indopacific, occurring in Madagascar, Ceylon, Phillipines I., Formosa, Hong Kong, Torres Strait, Queensland, Darwin Bay (as *S. symbiotica* associated with another red alga, *Gracilaria*), and New Caledonia. It is generally found growing on muddy sandy bottoms. But the alga is also encountered free in the infralittoral zone on corals and rocks under the sea-grass patches (DAWSON, 1954; PHAM HOANG HO, 1958), or in association with other sponge species (LÉVI, 1959, 1961).

Thus when *Culcita* feeds on didemnid ascidia (just one observation) growing along sea-grass stems or on molluscan shells *(Arca)*, the ascidian species are green in color.

In the coral growths of the inner reef flat, *Culcita schmideliana* seems to adhere to its common diet of animal food associated with vegetal material, feeding either on the epibenthic felt of dead corals (the feeding place is marked by a white patch), or more commonly on living corals, generally those with large easily-digestible polyps, such as *Galaxea* and *Goniopora* (animal food associated with zooxanthellae).

Sea stars feeding commonly on sponges are not well known. Definite sponge-eating asteroids are reported from the Antarctic bottoms (MacMurdo Sound) by DAYTON et al. (1970) and DAYTON et al. (1974); they are: *Acodontaster hodgsoni, A. conspicuus, Perknaster fuscus antarctica* and *Odontaster meridionalis.* VASSEROT 1961) showed that *Henricia sanguinolenta* and *Echinaster sepositus* (Echinasterids), from the English Channel coasts, are specific eaters of axinellid sponges, whereas *Asterina gibbosa* seems to be a sponge predator but also feeds on composed ascidia. This latter feeding ethology is more frequent, and RODENHOUSE & GUBERLET (1946), MACGINITIE (1949), FEDER & CHRISTENSEN (1966), and SALVINI-PLAVEN (1972), report several species which are omnivorous scavengers of both plants and animals (Table 1).

However, *Culcita schmideliana* from Java is reported doubtfully by SLUITER (1889) to eat echinoids (*Echinometra lucunter sic,* more probably. *E. mathei* or *Tripneustes gratilla,* the first one being an Atlantic species). This may be an accidental case.

Among the cushion sea stars, *Culcita novaeguinae* MÜLLER & TROSCHEL (a species restricted to E. Indian Ocean and Pacific Ocean, from the Bay of Bengal to Hawaiian I., in: CLARK & ROWE, 1971) is reported to be a coral predator by ENDEAN (1971) from Great Barrier Reef and by GOREAU et al. (1972) from Saipan. But *C. novaeguinae,* as well as *C. schmideliana* on the Tuléar "Grand Récif", just attacks the small colonies with a low or encrusting form *(Acropora, Polcillopora);* it does not climb, as does the other coral predator *Acanthaster planci* (LINNAEUS), to eat on the branching colonies.

About the distribution of *Culcita schmideliana* a further question might be asked: does the population observed during the 1972 survey in the coral – built formations of the inner reef flat represent a normal distribution or a cyclic phenomenon?

On the other reef flats of the Indian Ocean, *C. schmideliana* is generally reported

Table 1

List of the other sea stars feeding on sponges

Sea star	Localisation	Type of food	Reference
Oreaster reticulatus	West Indies	sponges?	THOMAS (1960)
Pteraster tessulatus	Bering Sea, North American coast to Washington state	sponges and hydroids	RODENHOUSE & GUBERLET (1940)
Odontaster validus	Antarctic (MacMurdo Sound, Terre Adélie)	sponges + hydroids, detritus feeder, necrophagous when insufficient supply of vegetal food	DAYTON et al. (1970); DAYTON et al. (1974); ARNAUD(1970)
Pycnopodia helianthoides	Alaska to San Diego	occasionally algae + sponges, truly omnivorous diet	KJERSKOG-AGERSBORG (1918); REESE (1966)
Hacellia attenuata	Mediterranean Sea (Marseilles region) coralligenous bottoms	sponges + others materials	ZIBROWIUS (pers. comm.)
Asterina burtoni	Madagascar (Tuléar), boulder tracts	sponges + ascidiacea	this paper

from the sea-grass beds (PICHON, MIREILLE, 1964, from Nosy Bé, N. W. of Madagascar MACNAE & KALK, 1958, from Inhaca I., Mozambique; TAYLOR & LEWIS, 1970, from Mahé I., Seychelles I.; TAYLOR, 1971, from Diego Garcia atoll), with *Protoreaster lincki* and *Pentaceraster mammillatus*.

From the Tuléar surveys, it seems that the population of *C. schmideliana* increased from 1969 to 1972 in the living coral flats. It is strange, because at the same time, an increase of the *Acanthaster planci* in a restricted area occurred.

Thus, in 1966, just one specimen of *Acanthaster planci* was observed along a 300–350 m long transect crossing the coral-built formations of the inner reef flat. In 1969, few additional specimens were found (1 to 3) along the same transect. However, more important populations were reported from the Songoritelo reef, 15 km north of Tuléar, on a reef affected by silty and fresh flows of the Fiherenana River (PICHON, 1973, last observation 1971 survey). In 1972 (May–June), I discovered a more important aggregation of *A. planci* (up to 1/16 m^2, with numerous juveniles hidden in holes of the coral flat, abundant in this zone, with dense population of *Echinometra mathei*) in the northern part of the "Grand Récif", near a rubbly coral flat with flourishing algal growth. This peculiar area supported an abnormal number of *Acanthaster*, feeding mainly on *Acropora* and *Pocillopora*. In 1973 (personal communication, J. LABOREL), this infestation had disappeared and the population had returned to a normal level. This phenomenon can be equated with condition 6 of CHESHER's classification (1969) of *Acanthaster* infestation (cf. ENDEAN, 1973).

An hypothesis of a disturbance of the normal conditions affecting this part of the reef flat could be put forward to explain this phenomenon, on an area limited southwards by a rubble flat resulting from the strong surge beating on this reef front line.

During the spring of 1972 the rainfall season, normally from December to February, was prolonged until August and the Fiherenana River (which is a kind of wadi normally, with high run-off only in January-February) was flowing during all 6 months, transporting large quantities of terrigenious material. Moreover, since 1968, the Fiherenana valley has been deforested for cotton field expansion (field surfaces multiplied by $^2/_3$, in: Ader, 1972), and the suspended flow of the river characterized by montmorillionitic silts (CHAMLEY et al., 1967) has increased since this time. Insecticide treatment residues (endrin, feldrin, D.D.T.), which are very important in cotton culture (principally in Februar–April) (LAGIÈRE, 1966), are carried to the sea if the rainy season is prolonged, and fixation of these residues is favoured by the expansion properties of the montmorillionit silt (ARNOUX & CHAMLEY, 1974). As the silty fraction is generally deposited in the sea-grass beds (the leaves acting as sediment baffles), the epipsammic felt of this biotope perhaps becomes toxic for *Culcita* feeding. This could explain the concentration of this species, as *Protoreaster lincki*, in better flushed zones along stream channels, and perhaps the migration of specimens in the coral growth flat. Such cases of disturbance of coral reef communities have been reported by STODDART (1969) from the Solomon I., by PEARSON & ENDEAN (1969) from the Great Barrier Reef of Australia, by DANA et al. (1972), and by NISHIHIRA & YAMAZOTO (1973) from Okinawa I. Thus chemical pollution by pesticides was advanced as an hypothesis to explain *Acanthaster planci* infestations in the Pacific regions (DANA, 1970; JOHANNES, 1971; RANDALL, 1972; ENDEAN & CHESHER, 1973).

FEEDING BEHAVIOR OF OTHER OREASTERID SEA STARS

Among the other oreasterid sea stars are the following: *Protoreaster nodosus* (LINNAEUS, 1758), *P. lincki* DE BLAINVILLE, 1834), *Pentaceraster mammillatus* (AUDOUIN, 1826), which are commonly encounted in the coral growths and in the sea-grass beds *(P. nodosus)* or restricted to the sandy bottoms of the inner reef flats with or without sea-grass beds *(P. lincki)* or on the inner slope with dense or scattered sea-grass meadows *(P. mammillatus)*, where it seems their feeding behavior is restricted to sucking and ingesting of the the epibenthic felt of micro-organisms and perhaps dissolved organic substances (see Fig. 6).

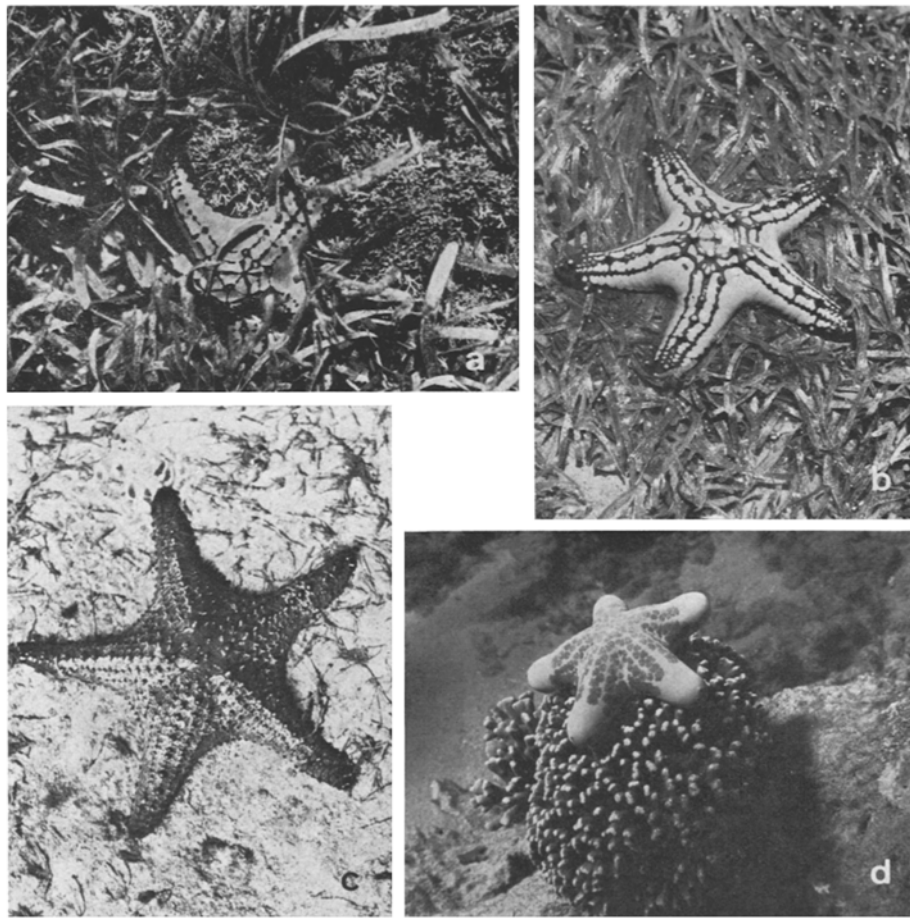

Fig. 6: *a Protoreaster nodosus* feeding on the felt growing on calcareous algae *(Lithothamnion* and *Lithophyllum)* in the sea-grass beds, "Grand Récif"; *b* idem feeding on the epiphytic film of *Cymodocea rotundata* beds, "Grand Récif"; *c Pentaceraster mammillatus* in the scattered sea-grass beds *(Halodule uninervis)*, lagoonal edge, "Grand Récif"; *d Choriaster granulosus*, enclosed lagoon slopes, "Grande Vasque" of the "Grand Récif", 5–6 m deep. (photogr. *a, b, c*, 1972-survey, B. THOMASSIN; photogr. *d* 1969-I.B.P. survey, J. G. HARMELIN)

In the coral-built formations of the inner reef flat, or on dead corals in the sea-grass flats, individuals of *Protoreaster nodosus* feed on algal felt and on the sand meiobenthos of the patches and couloirs. In the sea-grass beds, they were commonly encountered eating film on *Halimeda* colonies or the felt growing on the calcareous algae, *Lithophyllum molluccense* and *Lithothamnium erubescens,* and also accidentally feeding on broken sea-urchin tests *(Tripneustes gratilla)**. On the sandy bottoms of the lagoon, 13 m deep, with few *Halophila ovalis* and free living scleractinia, such as *Heteropsammia michelini, P. nodosus* was observed feeding on the large foraminifera associated with zooxanthelles, *Marginopora vertebralis* (= *Amphisorus hemprichii), Operculinella venosa* and O. *complanata.*

Distribution of *Protoreaster lincki* is more restricted than that of *P. nodosus.* This species has generally been observered in the sea-grass beds in the stream zones in the vicinity of the sea-grass bed channels where it is very abundant (up to 20 individuals by 100 m²) (Fig. 7). It seems to have a different feeding mechanism to *P. nodosus,* using the stomach more as a ciliary mucus-feeding organ.

No observations were made on the feeding behavior of another oreasterid sea star, *Choriaster granulosus* LÜTKEN, 1869. This species is generally restricted to the silty inner slopes of lagoon and enclosed lagoons, between 1 to 8 m deep, in coral and rubble zones (the rubble being covered by small filamentous algae mixed with a clay fraction). In contrast to the other oreasterids (rate of locomotion of *Protoreaster nodosus:* 20 cm/min., OHSHIMA, 1940), *C. granulosus* has a slow rate of locomotion (marked specimens were observed during the course of a week at the same place in the "Grande Vasque" enclosed lagoon in July 1972). This species may be a necrophagous feeder, according to Yamaguchi (1973).

FEEDING BEHAVIOR OF OTHERS SEA STARS (OPHIDIASTERIDAE, ECHINASTERIDAE, GONIASTERIDAE, ASTERINIDAE)

Others sea stars encounted in the growth flats and less commonly on coarse sandy flats (except *Astropecten* and *Luidia,* which catch their prey in the sediments) are: *Linckia laevigata* (LINNAEUS)**, *L. multifora* (LAMARCK), *Nardoa variolata* (RET-

* Accidental necrophagous feeding by asteroids is reported by EDMONDSON (1946) from Hawaii I. for *Culcita* sp.; by H. ZIBROWIUS (*pers. comm.*) from the Mediterranean Sea (Marseilles region) for *Methasterias glacialis;* by ARNAUD (1970) from Antarctic bottoms for *Odontaster validus, Cuenotaster involutus* and *Saliasterias brachiata* (in this latter case this peculiar feeding is the consequence of insufficient supply of vegetal food during the winter season).

** *Protoreaster nodosus* was found to be preyed upon by the gastropod *Charonia tritonis* (pers. comm., P. VASSEUR), whereas *Linckia variegata, Nardoa variolata* and *Monachaster sanderi* were observed to be preyed upon by *Bursa lampas.* VINE (1970) reported that *C. tritonis* feeds more commonly on *L. laevigata* than on *Acanthaster planci.* I agree with this opinion (*C. tritonis,* always up to 30 cm long, is rare in the Tuléar region, in contrast to *B. lampas,* which is common – young and large adults up to 27 cm long – in the coral built formations of the inner reef flats).

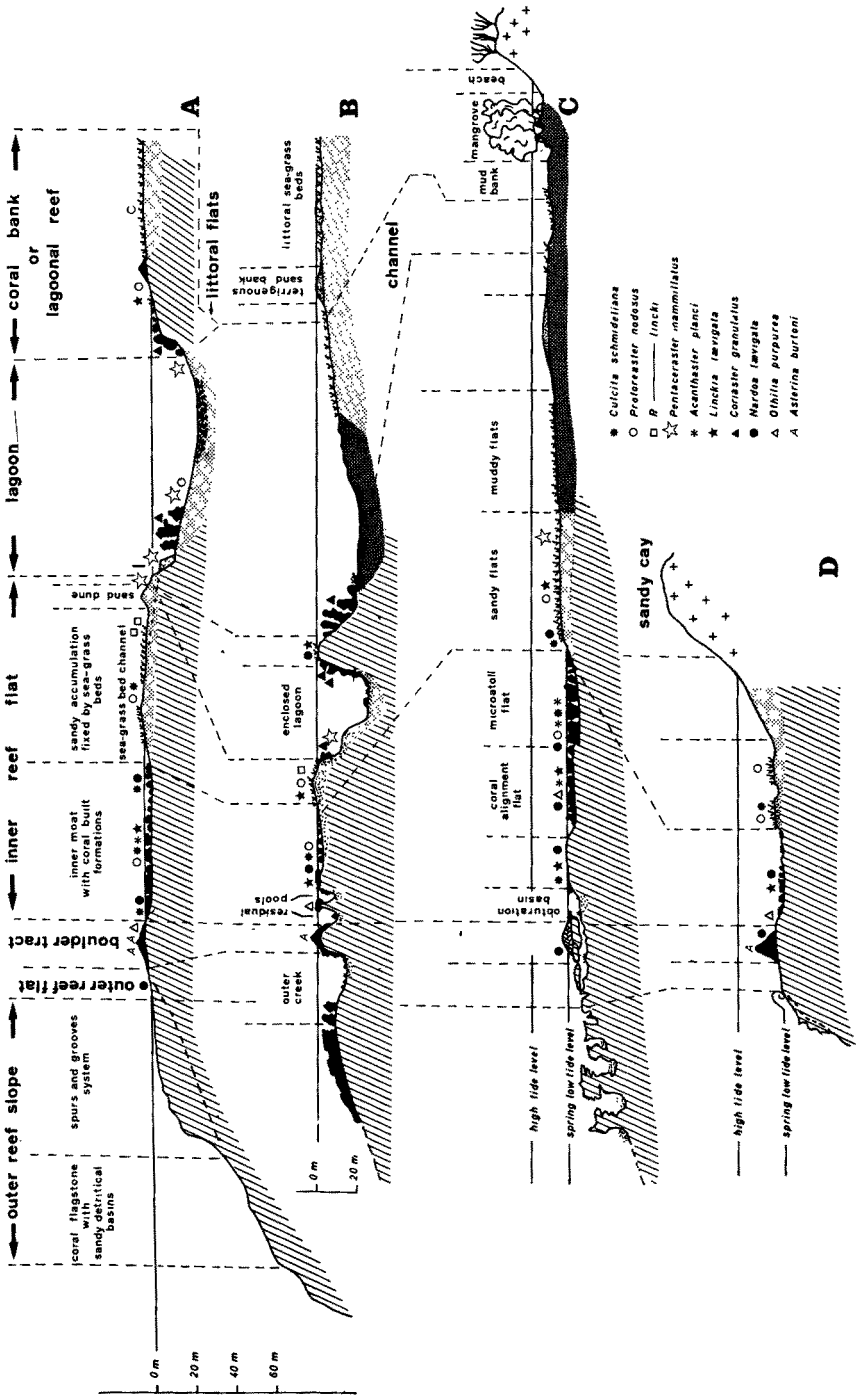

Fig. 7: Distribution of the sea stars on the coral reefs of the Tuléar region

ZIUS)*, *Echinaster purpureus* (GRAY), *Monachaster sanderi* (MEISSNER)* and *Asterina burtoni* GRAY. Few observations were made on these species (Fig. 8).

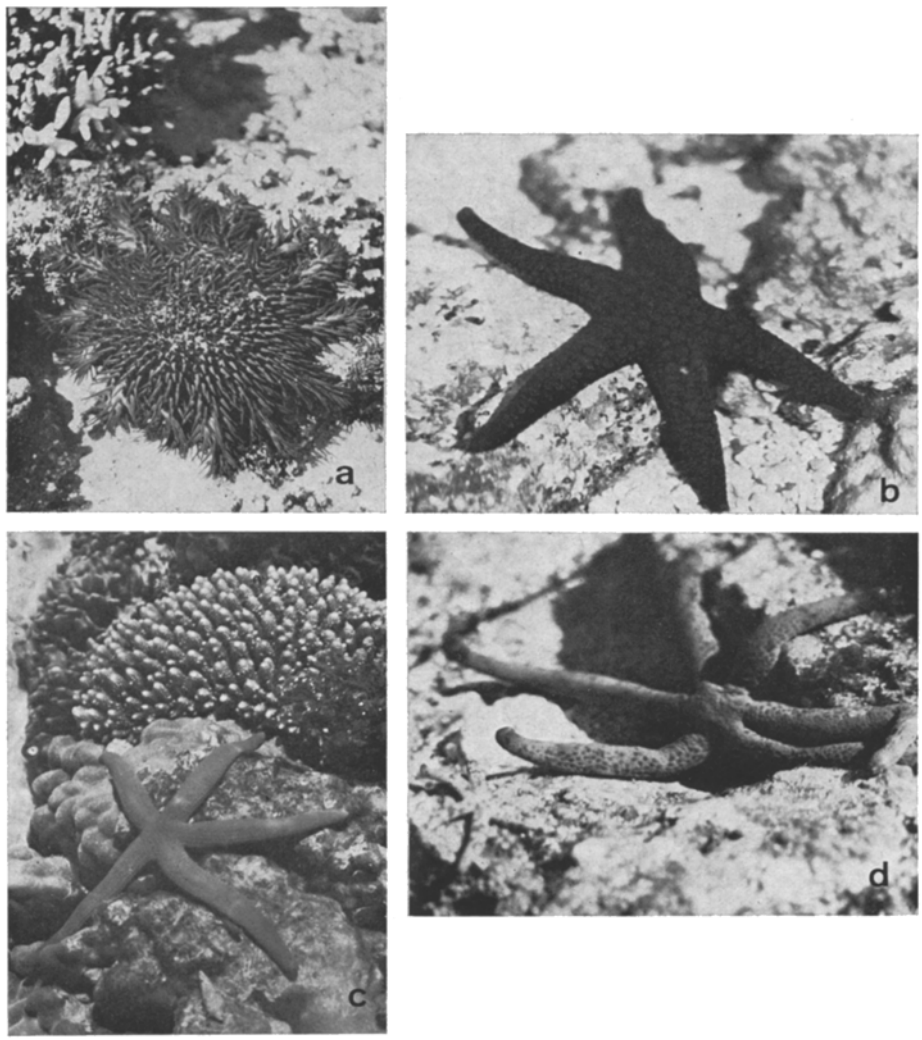

Fig. 8: *a Acanthaster planci* just leaving a part of *Acropora* colony eaten, N. "Grand Récif", *b Nardoa variolata* in the coral-built formations of the inner reef flat, "Grand Récif"; *c Linckia laevigata* in the latter biotope (1966 and 1972-surveys, ph. B. THOMASSIN); *d Linckia multifora* in the coral-built formations of the inner reef flat, "Grand Récif"

However *Asterina burtoni*, living under the blocks of the boulder tracts or of the sea-grass beds, less commonly in the gravel tails and gravelly hydraulic banks, seems to feed on the rich sciaphilic populations of the blocks, sponges (Spirastrellids, as *Spirastrella* and *Timea* spp.) or ascidiacea *(Tridemnum, Eudistoma).*

Linckia laevigata, Nardoa variolata and *Echinaster purpureus,* seem to feed on the mucous of the corals on which they crawl *(Porites),* as well as on the epibenthic film of the hards (rarely soft) substrates of the coral built formations of the inner reef flat or of the outer reef flat *(E. purpureus),* or of the rubbly sea-grass beds *(L. variegata, N. variolata).*

SUMMARY

1. On the coral reefs of the Tuléar region (S. W. Madagascar), the feeding behaviour of sea stars, in particular the species *Culcita schmideliana* has been studied. It feeds in its usual biotope, the sea-grass beds of the inner reef flats, on the epibenthic film of the substrates, of the leaves, but also commonly on sponges, mainly the symbiotic *Gellius cymiformis* (associated with *Ceratodictyon spongiosum*);
2. In the moat (residual pools, coral-built formations) of the inner reef flat where the population was poor in 1965 but equal to that of the sea-grass bed in 1972, the cushion sea star feeds on the epibenthic felt, but also on the living corals (*Galaxea, Goniopora*) and on soft corals *(Xenia).* This latter diet is very close to that of the Pacific cogeneric species, *Culcita novaeguinae.*
3. *Acanthaster planci* populations are normal on the reef flats of the region (but a little more dense on the fringing reef under silty deposits). Only a beginning of an infestation was observed in May 1972, but it disappeared later (condition 6 of Chesher's classification).
4. Others Oreasterids feed mainly on epibenthic film, extruding their stomachs on the substrates. *Protoreaster nodosus* has a larger distribution than *P. lincki, Pentaceraster mammillatus* and *Choriaster granulosus.*
5. Among others sea stars, *Asterina burtoni* seems to be a large predator of species living under dead coral blocks (sponges, ascidiacea) of the boulder tracts and of the rubbly flats.

Acknowledgements. The opportunity to conduct surveys on the coral reefs of Madagascar was provided by grants of the D.G.R.S.T. (Délégation Générale à la Recherche Scientifique et Technique, COMEXO), of the C.N.E.X.O. (Centre National pour l'Exploitation des Océans) and the C.N.R.S. (Centre National de la Recherche Scientifique, L. A. nº 41) and the I.B.P. – Marine Productivity –. The author is grateful to Dr. G. CHERBONNIER (M.N. H.N., Paris) for his help in the identification of the sea stars, to Drs. J. VACELET and P. VASSEUR (Station Marine d'Endoume, Marseille) for the identifications of sponges, and to Dr. A. TIXIER-DURIVAULT (M.N.H.N., Paris) for identification of Octocorallia. Thanks are due to Drs. J. PICARD (Station Marine d'Endoume) and G. CHERBONNIER for their help during discussions and to my colleagues for useful information cited herein as personal communications. Dr. A. LOGAN (New Brunswick University) kindly corrected the English text. This paper (Station Marine d'Endoume et Centre d'Oceanographie Contribution no 660) was presented at the International Symposium on Indo-Pacific Tropical Reef Biology, Guam (June 23–July 5, 1974).

LITERATURE CITED

ADER, R. L., 1972. Statistiques socio-économiques. Madagascar, **21**, 133–139.

ARNAUD, P. M., 1970. Frequency and ecological significance of necrophagy among the benthic species of Antarctic coastal waters. In: Antarctic Ecology. Ed. by M. W. HOLDGATE. Acad. Pr., London **1**, 259–267.

ARNOUX, A. & CHAMLEY, H., 1974. Minéraux des argiles et détergents des eaux interstitielles dans les sédiments superficiels du golfe du Lion. C. r. hebd. Séanc. Acad. Sc., Paris, (D) **278**, 999–1002.

BANNER, A. H., 1968. A fresh-water "kill" on the coral reefs of Hawaii. Tech. Rep. Hawaii Inst. mar. Biol. **15**, 1–29.

CHAMLEY, H., PAQUET, H. & MILLOT, G., 1967. Minéraux argileux des sédiments marins littoraux et fluviatiles de la région de Tuléar (Madagascar). Bull. Serv. Carte géol. Als. Lorr. **19**, 191–204.

CHESHER, R. H., 1969. *Acanthaster planci* impact on Pacific coral reefs. Final Rep. Res. Lab. Westinghouse Electric Corp. to U. S. Dept. Interior 151 pp.

DANA, T. F., 1970. *Acanthaster:* A rarity in the past? Science, N. Y. **169**, 894.

— NEWMAN, W. A. & FAGER, E. W., 1972. *Acanthaster* aggregations: interpreted as primarily responses to natural phenomena. Pacif. Sci. **26**, 355–372.

DAWSON, E. Y., 1954. Marine plants in the vicinity of the Institut Océanographique de Nha Trang. Pacif. Sci. **8**, 373–481.

DAYTON, P. K., ROBILLIARD, G. A. & PAINE, R. T., 1970. Benthic faunal zonation as a result of anchor ice at McMurdo Sound, Antarctica. In: Antarctic ecology. Ed. by M. W. HOLDGATE. Acad. Pr., London, **1**, 244–258.

DAYTON, P. K., ROBILLIARD, G. A., PAINE, R. T. & DAYTON, L. B., 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol. Monogr. **44**, 105–128.

EDMONDSON, C. H., 1946. Reef and shore fauna of Hawaii. Spec. Publs Bernice Pauahi Bishop Mus. **22**, 1–381.

ENDEAN, R., 1971 (1972). The recovery of coral reefs devastated by catastrophic events with particular reference to current *Acanthaster planci* plagues in the tropical Indo-West Pacific region. J. mar. biol. Ass. India **13**, 1–13.

— 1973. Population explosions of *Acanthaster planci* and associated destruction of hermatypic corals in the Indo-West Pacific region. In: Biology and geology of coral reefs. Ed. by O. A. JONES & R. ENDEAN. Acad. Pr., New York, **2**, 389–438.

— & CHESHER, R. H., 1973. Temporal and spatial distribution of *Acanthaster planci* population explosions in the Indo-West Pacific region. Biol. Conserv. **5**, 85–95.

FEEDER, H. & CHRISTENSEN, A. M., 1966. Aspects of asteroid biology. In: Physiology of Echinodermata. Ed. by R. A. BOOLOOTIAN. Interscience, New York, 87–127.

GOREAU, T. F., LANG, J. C., GRAHAM, E. A. & GOREAU, P. D., 1972. Structure and ecology of the Saipan reefs in relation to predation by *Acanthaster planci* (LINNAEUS). Bull. mar. Sci. **22**, 113–152.

JOHANNES, R. E., 1971. Coral reefs and pollution. South Pac. Comm., Regional symp. on Conservation of nature – Reefs and lagoons. South Pacif. Commn, Nouméa, 37 pp.

KJERSKOO-AGERSBORG, H. P., 1918. Bilateral tendencies and habits in the twenty-rayed starfish *Pycnopodia helianthoides* (STIMPSON). Biol. Bull. mar. biol. Lab., Wood Hole **35**, 232–254.

LÉVI, C., 1959 (1961). Spongiaires des Iles Philippines, principalement récoltées au voisinage de Zamboanga. Philipp. J. Sci. **88**, 509–533.

— 1967. Démosponges récoltées an Nouvelle-Calédonie par la Mission Singer-polignac. Ed. Fond. Singer-Polignac **2**, 13–26.

LAGIÈRE R., 1966. Le Cotonnier. Maisonneuve & Larose, Paris, 306 pp.

MACGINITIE, G. E. & MACGINITIE, N., 1949. Natural History of marine animals. McGraw-Hill, New York, 473 pp.

MACNAE, W. & KALK, M., 1958. A natural history of Inhaca Island, Moçambique. Witwatersrand Univ. Pr., Johannesburg, 163 pp.

MARSH, J. A. & TSUDA, R. I., 1973. Population levels of *Acanthaster planci* in the Mariana and Caroline Islands 1969–1972. Atoll Res. Bull. **170**, 1–16.

NISHIHIRA, M. & YAMAZATO, K., 1974. Disturbance of coral reef communities and *Acanthaster* problem in Okinawa. Proc. 2nd. intern. symp. on corals and coral reefs. Great Barrier Reef Commn, Australia **1**, 577–590.

OHSHIMA, H., 1940. The righting movement of the sea-star, *Oreaster nodosus* (L.). Jap. J. Zool. **8**, 575–589.

PEARSON, R. G. & ENDEAN, R., 1969. A preliminary study of the coral predator *Acanthaster planci* (L.) (Asteroidea) on the Great Barrier Reef. Fish. Notes Dep. Harbours Mar. Queensland **3**, 27–55.

PICHON, MICHEL, 1973. Recherches sur les peuplements à dominance d'Anthozoaires dans les récifs coralliens de Tuléar (Madagascar). Thèse, Univ. Aix-Marseille, 445 pp.

PICHON, MIREILLE, 1964. Aperçu préliminaire des peuplements sur sables et sables vaseux, libres ou couvert par des herbiers de Phanérogames marines, de la région de Nosy Bé. Cah. O.R.S.T.O.M. (Océanogr.) **2** (4), 5–15.

PHAM HOANG HO, 1958. Aperçu sur le peuplement littoral de la Pointe de Câuda (Nhatrang). Bull. Soc. Bot. N. Fr. **105** (3–4), 1–4.

RANDALL, J. E., 1972. Chemical pollution in the sea and the crown-of-thorns starfish *(Acanthaster planci)*. Biotropica **4**, 132–144.

REESE, E. S., 1966. The complex behavior of echinoderms. In: Physiology of Echinodermata. Ed. by R. A. BOOLOOTIAN. Interscience, New York, 157–218.

RIDLEY, S. O., 1884. Spongiidae. Report on the zoological collections made in the Indo-pacific Ocean during the voyage of H.M.S. "Alert", 1881–1882, 366–482; 582–630.

RODENHOUSE, I. Z. & GUBERLET, J. E., 1946. The morphology and behaviour of the cushion star *Pteraster tassulatus* IVES. Univ. Wash. Publs Biol. **12** (3), 21–48.

SALVINI-PLAWEN, L. VON, 1972. Cnidaria as food-sources for marine invertebrates. Cah Biol. mar. **13**, 385–400.

SARÁ, M. & VACELET, J., 1974. Ecologie des Démosponges. In: Traité de Zoologie. Ed. by P. P. GRASSÉ. Masson, Paris **3** (1), 462–575.

SLUITER, C., 1889. Die Evertebraten aus der Sammlung des Kgl. Naturwissenschaftlichen Vereins in Niederländisch-Indien in Batavia. Echinodermen; 3. Asteroides. Natuurk. Tijdschr. Ned.-Indu **48**, 297–313.

STODDART, D. R., 1969. Geomorphology of Solomon Islands coral reefs. Phil. Trans. R. Soc. (B) **255**, 355–382.

TAYLOR, J. D., 1968. Coral reef and associated invertebrate communities (mainly Molluscan) around Mahé, Seychelles. Phil. Trans. R. Soc. (B) **254**, 129–206.

— & LEWIS, M. S., 1970. The flora, fauna and sediments of the marine grass beds of Mahé, Seychelles. J. nat. Hist. **4**, 199–220.

VACELET, J. & VASSEUR, P., 1971. Eponges des récifs coralliens de Tuléar (Madagascar). Téthys (Suppl.) **1**, 51–126.

VASSEROT, J., 1961. Caractère hautement spécialisé du régime alimentaire chez les Astérides *Echinaster sepositus* et *Henricia sanguinolenta*, prédateurs de Spongiaires. Bull. Soc. zool. Fr. **86** (6), 796–809.

VINE, P. J., 1970. Field and laboratory observations of the crown-of-thorns starfish, *Acanthaster planci*. Nature, Lond., **228**, 341–342.

YAMAGUCHI, M., 1973. Early life histories of coral reef asteroids, with special reference to *Acanthaster planci* (L.). In: Biology and geology of coral reefs. Ed. by O. A. JONES & R. ENDEAN. Acad. Pr., New York **2**, 369–387.

Author's address: Dr. B. A. THOMASSIN
Station Marine d'Endoume
Rue de la Batterie des Lions
F-13007 Marseille
France