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Molluscan Distribution Patterns in Fanning Island Lagoon and a Comparison of the Mollusks of the Lagoon and the Seaward Reefs[1]

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ABSTRACT: Lagoon molluscan assemblages at Fanning Island are described in terms of three topographical areas: the lagoon reef flat, the patch reefs, and the lagoon floor. Among the large mollusks, *Clypeomorus brevis*, *Rhinoclavis asper*, *Pupa sulcata*, *Pyramidella* sp., and two bivalves, *Fragum fragum* and *Tellina robusta*, are the principal components of the fauna of the reef flat; *Cypraea moneta* and *Trochus histrio* are the dominant epifaunal mollusks of rubble on patch reefs; and sessile bivalves, *Cardita variegata*, *Electroma* sp., *Ostrea sandvichensis*, and *Tridacna maxima*, are associated with coral. The micromolluscan assemblages of the lagoon reef flat are dominated by *Tricolia variabilis*, and patch reef and lagoon floor assemblages by *Diala flammea*. *Obtortio sulcifera* is the second most abundant mollusk on the patch reefs and *O. pupoides* the second most abundant mollusk on the lagoon floor. The patch reef and lagoon floor assemblages are distinguishable into assemblages associated with turbid water and clear water areas of the lagoon. Standing crops of micromollusks are greatest on the windward or southeastern periphery of the lagoon reef flat.

The lagoon mollusks are distinguished from the seaward reef mollusks in terms of species composition, modes of life, and feeding habits. The lagoon assemblages are predominantly herbivores and suspension feeders among the macrofauna, and are epifaunal herbivores among the microfauna. The seaward reef macrofauna is dominated by carnivores and herbivores, and the microfauna by faunal grazers. Standing crops of seaward reef micromollusks are less than those in the lagoon and the species diversity index is higher.

A SURVEY of the littoral marine mollusks of Fanning Island in 1970 reported a faunal list of 305 species and showed a clear distinction between the species composition of the seaward reefs and that of the lagoon (Kay 1971). Distribution patterns for the mollusks of the seaward reefs indicated discrete assemblages associated with various features of topography. It was suggested that species composition and distribution of the lagoon mollusks would also reflect the topographical structure of the lagoon.

A second expedition to Fanning Island in July and August 1972 gave opportunity to make a detailed survey of the distribution of the lagoon mollusks. In this report we explore the relationships between molluscan assemblages and lagoon parameters such as topography, sediment distribution, salinity, and algal distribution, and compare aspects of the species composition and modes of life of lagoon and seaward-reef mollusks.

METHODS

During July and August 1972, the 42-km perimeter of the Fanning Lagoon reef flat was surveyed on foot and observations and collections of mollusks and sediments were made at 98 stations. Twenty-three patch reefs were sampled by snorkel diving and estimates were obtained of distribution and abundance of the

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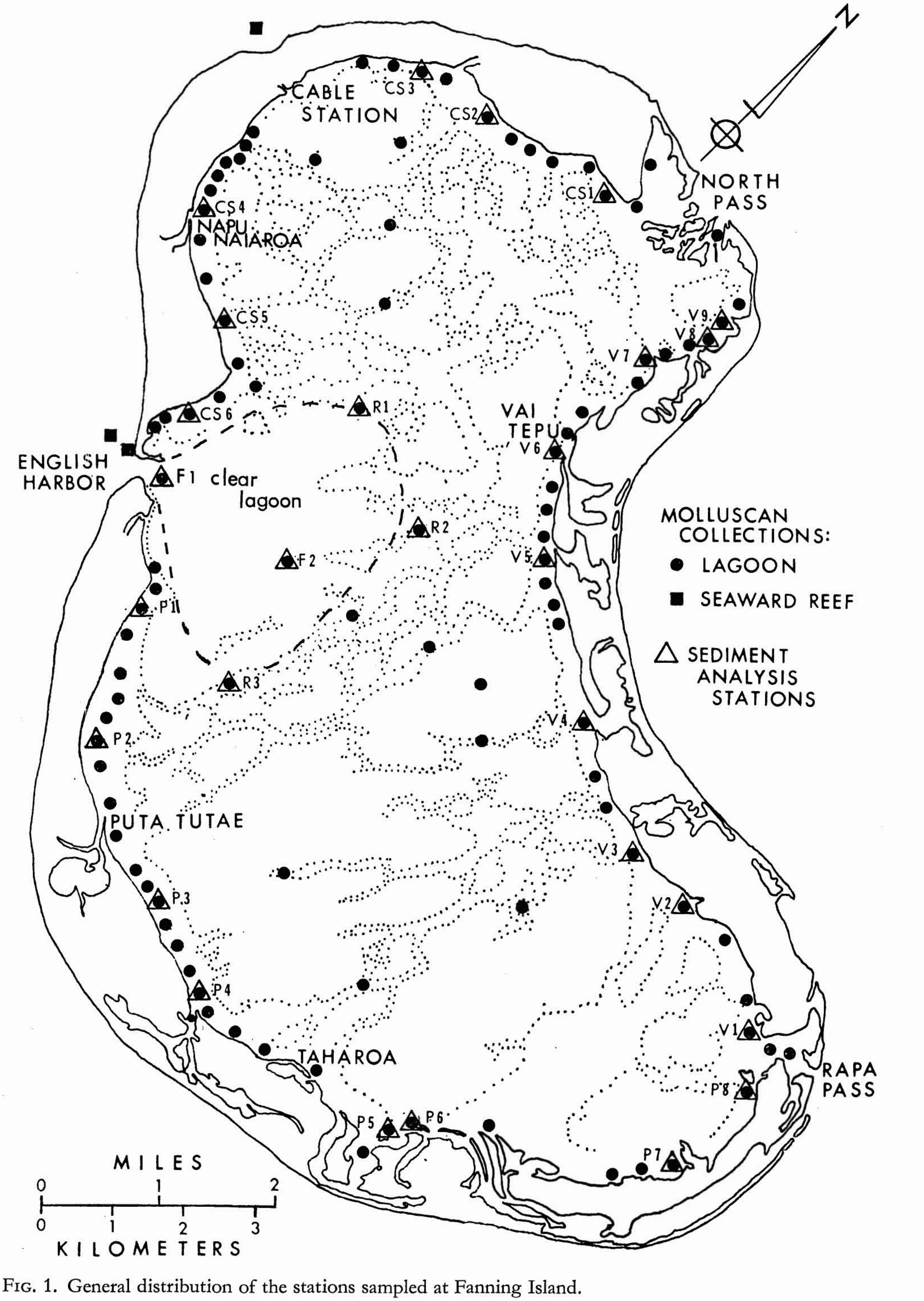

FIG. 1. General distribution of the stations sampled at Fanning Island.

mollusks by throwing a 0.25 m^2 quadrat on the surface of the reefs, counting all large mollusks visible in the quadrat, and recording substrate types. Fifteen stations on the lagoon floor were sampled by SCUBA diving and clam shell dredge. The general distribution of the stations sampled is shown in Fig. 1.

Sediments from all stations were put into plastic bags upon collection and returned to the laboratory where they were placed in open containers and air-dried. Sediment samples were processed in the laboratory for micromollusks, that is, for shells less than about 10 mm in greatest dimension. Shells were sorted under a binocular dissecting microscope from standard 25 cm^3 volumes. This volume produced standing crops as great as 77 shells per cm^3, and an average of 10 shells per cm^3. The samples were deemed sufficient for subsequent analysis, as larger samples would have been difficult to deal with in a routine manner. Although live/dead shell ratios were not determined, it is assumed, because living specimens of most species were found, that the dead biofacies patterns reflect the general occurrence of living populations.

A list of mollusks recorded from Fanning Island is presented in Table 1, and the most commonly encountered micromollusks of the lagoon and seaward reefs are illustrated in Fig. 4. Species counts are based on all mollusks except for triphorids and some small rissoids which were lumped together in each of those categories respectively because of difficulties in identification.

Several techniques were utilized to gain a quantitative insight into the distribution of individual species. Relative abundance values, or percentage composition of the assemblages; frequency, the number of occurrences of a species in a habitat type; and standing crop, the number of shells per cm^3 of sediment, were computed. Trophic structure was determined by counting the number of individuals associated with a particular feeding habit and dividing by the total number of individuals in the sample. Species diversity was calculated using the function

$$H = -\Sigma p_i \log_2 p_i,$$

where p_i equals the fraction of the total number of individuals represented by each species (Pielou 1969).

Samples from 29 stations were utilized in sediment analysis. A representative portion of each sample was sorted through a series of sieves, each 20 cm in diameter. Table 2 shows the phi (ϕ) and mesh sizes of the sieves used. Each fraction obtained was weighed and its percentage of the sample calculated. Cumulative dry-weight percentages were plotted on probability paper. The graphic mean, M_z, was plotted, the mean defined as $M_z = \phi16+\phi50+\phi84/3$ (Folk 1968). The formula $\sigma = \phi84-\phi16/2$ was used to determine graphic standard deviation.

LAGOON TOPOGRAPHY

The lagoon molluscan assemblages are conveniently described in terms of three general topographical areas: the lagoon reef flat, the patch reefs of the lagoon basin, and the lagoon floor. Details of topography, salinity, nutrient concentrations, etc. are found in Maragos *a* and *b*, Smith and Pesret, and Stroup and Meyer (all, this issue).

The lagoon reef flat is a predominantly sandy flat extending from 50 to 300 meters in width around the lagoon shore. Most of the reef flat is exposed at zero tides. Patches of turf-forming algae such as *Hypnea*, *Polysiphonia*, and *Schizothrix* occur on the flat, as do occasional patches of rubble and exposed sections of fossil reef studded with *Tridacna* valves *in situ*. The lagoonward edge is marked by the occasional occurrences of colonies of *Acropora* and/or *Porites* and clumps of the brown alga *Turbinaria*. Two types of discontinuity interrupt the otherwise continuous reef flat: passes between the islands of the atoll and brackish water inlets. Three passes dissect the lagoon reef flat, a single deep pass (ca. 8 m in depth) at English Harbor and two shallow passes (or intertidal reef flats ca. 1 m in depth) at North Pass and Rapa Pass. The reef flat in the shallow passes is paved with coralline algae and mats of *Hypnea* and *Polysiphonia* (Doty and Russell 1973). The lagoon shore is dissected by inlets which effect changes in salinity in the surrounding lagoon (Guinther 1971, this issue). The lagoon reef flat north of English Harbor is distinguished by a short stretch of rubble and shingle shoreline.

The lagoon basin is divisible into a clear-water

TABLE 1

MOLLUSKS RECORDED FROM FANNING ISLAND, JULY–AUGUST 1972[1]

AMPHINEURA

CHITONIDAE

Ischnochiton sp.

GASTROPODA

SCISSURELLIDAE

Scissurella coronata Watson, 1886
Scissurella sp.

FISSURELLIDAE

Diodora granifera (Pease, 1861)
Emarginula bicancellata Montrouzier, 1860
E. dilecta A. Adams, 1851[2]
Hemitoma sp.

PATELLIDAE

Patella flexuosa Quoy & Gaimard, 1834[3]

TROCHIDAE

Euchelus angulatus Pease, 1867
Monilea nucleus (Philippi, 1849)
Monilea sp.
Trochus histrio Reeve, 1848

STOMATELLIDAE

Stomatella rosacea (Pease, 1867)
Synaptocochlea concinna (Gould, 1845)

TURBINIDAE

Astraea calcar (Linnaeus, 1758)[4]
Leptothyra sp. cf. *wellsi* Ladd, 1966
Turbo argyrostomus Linnaeus, 1758

PHASIANELLIDAE

Tricolia variabilis (Pease, 1860)

NERITOPSIDAE

Neritopsis radula (Linnaeus, 1758)

NERITIDAE

Nerita albicilla Linnaeus, 1758
N. plicata Linnaeus, 1758
N. polita Linnaeus, 1758
Puperita bensoni (Recluz, 1850)[5]

PHENACOLEPADIDAE

Phenacolepas sp.

LITTORINIDAE

Littorina coccinea (Gmelin, 1791)
L. scabra (Linnaeus, 1758)
L. undulata Gray, 1839

RISSOIDAE

Alvania sp. cf. *kenneyi* Ladd, 1966
Alvania sp.
Merelina (two spp.)
Parashiela beetsi Ladd, 1966
Pyramidelloides sp. cf. *miranda* (A. Adams, 1861)
Rissoina ambigua Gould, 1849
R. exasperata Souverbie, 1866
Rissoina sp. cf. *incisa* (Laseron, 1956)
R. miltozona Tomlin, 1915
R. plicata A. Adams, 1851
R. tenuistriata Pease, 1867
R. turricula Pease, 1860
Zebina semiplicata (Pease, 1863)
Z. tridentata (Michaud, 1830)

ASSIMINEIDAE

Assiminea nitida Pease, 1864

VITRINELLIDAE

Teinostoma (two spp.)

ORBITESTELLIDAE (= Vitrinellids of Kay 1971) (two spp.)

SKENEIDAE

Parviturbo minutissimus (Pilsbry, 1921)[6]

RISOELLIDAE

Risoella sp.

TRUNCATELLIDAE

Truncatella sp.

OMALOGYRIDAE

Omalogyra japonica (Habe, 1972)[7]

ARCHITECTONICIDAE

Heliacus sp.
Philippia sp.

VERMETIDAE

Dendropoma (two or three spp.)
Serpulorbis alii Hadfield & Kay, 1972

CAECIDAE

Elephantenellum sp.
Meioceras sp. cf. *sandwichensis* de Folin, 1879

PLANAXIDAE

Planaxis lineatus (Da Costa, 1776)[8]

[1] Rehder (personal communication) indicated that an additional 14 species probably should be added to the list, the specimens collected by Dr. Charles Staseck in 1963 and now in the California Academy of Science.

[2] As *Emarginula peasei* Thiele, 1918 (Kay 1971).

[3] As *Patella stellaeformis* Reeve, 1842 (Kay 1971).

[4] As *Astraea helicina* (Gmelin, 1791) (Kay 1971). Rehder (personal communication) suggested that *A. confragosa plicatospinosa* Pilsbry may be a more appropriate name.

[5] As *Neritina bensoni* (Kay 1971).

[6] As a vitrinellid, *Lophocochlias* (Kay 1971).

[7] This is the first record of this minute shell described as *Ammonicera* outside of Japan.

[8] Rehder (personal communication) has suggested that the Indo-Pacific species is separable as *P. zonatus* A. Adams, 1853.

TABLE 1 (*cont.*)

DIASTOMIDAE
Alaba goniochila (A. Adams, 1860)
Diala flammea (Pease, 1867)
Obtortio diplax (Watson, 1886)
O. pupoides (A. Adams, 1860)[9]
O. sulcifera (A. Adams, 1862)
Obtortio sp.

CERITHIIDAE
Bittium impendens (Hedley, 1899)
B. zebrum (Kiener, 1841)
Bittium (two spp.)
Cerithium articulatum Adams & Reeve, 1850
C. atromarginatum Dautzenberg & Bouge, 1933
C. bavayi Vignal, 1902
C. columna Sowerby, 1834
C. echinatum (Lamarck, 1822)
C. nesioticum Pilsbry & Vanatta, 1906
C. sculptum Pease, 1869
Clypeomorus brevis (Quoy & Gaimard, 1834)
Plesiotrochus sp.
Rhinoclavis asper (Linnaeus, 1758)
R. procera (Kiener, 1841)
R. sinensis (Gmelin, 1791)
Seila sp.

CERITHIOPSIDAE
Cerithiopsis turrita (Laseron, 1956)
Cerithiopsis (five spp.)

TRIPHORIDAE
Triphora cancellata Hinds, 1843
T. cingulifera Pease, 1861
Triphora sp. cf. *decorata* (Laseron, 1958)
T. incisa Pease, 1861
Triphora sp. cf. *minuta* (Laseron, 1958)
T. regalis Jousseaume, 1884
T. rubra Hinds, 1843
Triphora sp. cf. *tessellata* (Kosuge, 1963)[10]
T. triticea Pease, 1861
T. violacea Quoy & Gaimard, 1833
Triphora (four spp.)

EPITONIIDAE
Epitonium sp. cf. *symmetrica* Pease, 1867
Epitonium (four spp.)

EULIMIDAE
Balcis (four spp.)
Leiostraca sp.

STILIFERIDAE
Stilifer sp.

STROMBIDAE
Lambis chiragra chiragra (Linnaeus, 1758)
L. truncata sebae (Kiener, 1843)
Strombus gibberulus gibbosus (Röding, 1798)
S. lentiginosus Linnaeus, 1758
S. luhuanus Linnaeus, 1758
S. maculatus Sowerby, 1842
S. mutabilis mutabilis Swainson, 1821

HIPPONICIDAE
Capulus tricarinata (Linnaeus, 1758)
Hipponix conicus (Schumacher, 1817)

FOSSARIDAE
Fossarus cumingii (A. Adams, 1853)
Fossarus sp.

VANIKORIDAE
Vanikoro gueriniana (Recluz, 1843)

CALYPTRAEIDAE
Cheilea equestris (Linnaeus, 1758)

CYPRAEIDAE
Cypraea annulus Linnaeus, 1758
C. arabica Linnaeus, 1758
C. argus Linnaeus, 1758
C. asellus Linnaeus, 1758
C. caputserpentis Linnaeus, 1758
C. carneola Linnaeus, 1758
C. childreni (Gray, 1825)
C. clandestina Linnaeus, 1767
C. cribraria Linnaeus, 1758
C. depressa Gray, 1824
C. erosa Linnaeus, 1758
C. fimbriata Gmelin, 1791
C. goodalli Sowerby, 1832
C. helvola Linnaeus, 1758
C. isabella Linnaeus, 1758
C. lynx Linnaeus, 1758
C. maculifera Schilder, 1932
C. mauritiana Linnaeus, 1758
C. moneta Linnaeus, 1758
C. nucleus Linnaeus, 1758
C. poraria Linnaeus, 1758
C. schilderorum Iredale, 1939
C. scurra Gmelin, 1791
C. talpa Linnaeus, 1758
C. teres Gmelin, 1791
C. testudinaria Linnaeus, 1758
C. tigris Linnaeus, 1758
C. vitellus Linnaeus, 1758

OVULIDAE
Ovula ovum (Linnaeus, 1758)

ERATOIDAE
Pedicularia pacifica Pease, 1865
Proterato sulcifera schmeltziana (Crosse, 1867)
Trivirostra pellucidula (Gaskoin, 1846)
Trivia sp.

NATICIDAE
Natica gualteriana Recluz, 1844[11]
Natica robillardi Sowerby, 1893
Polinices melanostomus (Gmelin, 1791)
P. tumidus (Swainson, 1840)[12]

CASSIDIDAE
Casmaria ponderosa ponderosa (Gmelin, 1791)

[9] As *Obtortio pyrrhacme* (Melvill & Standen, 1896)(Kay 1971).
[10] As *Triphora dolicha* Watson, 1886 (Kay 1971).
[11] As *Natica marochiensis* (Kay 1971).
[12] As *Polinices mamilla* (Kay 1971).

TABLE 1 (*cont.*)

CYMATIIDAE

Charonia tritonis (Linnaeus, 1758)
Cymatium gemmatum (Reeve, 1844)
C. muricinum (Röding, 1798)
C. nicobaricum (Röding, 1798)
C. pileare (Linnaeus, 1758)

BURSIDAE

Bursa bufonia (Gmelin, 1791)
B. granularis (Röding, 1798)
Bursa sp.[13]

TONNIDAE

Malea pomum (Linnaeus, 1758)
Tonna perdix (Linnaeus, 1758)

MURICIDAE

Chicoreus sp.
Murex sp.

THAISIDAE

Drupa morum Röding, 1798
D. ricina (Linnaeus, 1758)
Drupella elata (Blainville, 1832)[14]
Drupina grossularia (Röding, 1798)
Maculotriton digitalis (Reeve, 1844)
Morula anaxeres (Kiener, 1835)
M. granulata (Duclos, 1832)
M. margariticola (Broderip, 1832)
M. uva (Röding, 1798)
Nassa serta (Bruguière, 1799)
Thais aculeata (Deshayes in Milne-Edwards, 1844)
T. armigera (Link, 1807)
T. intermedia (Kiener, 1836)

CORALLIOPHILIDAE

Coralliophila violacea (Kiener, 1836)
Coralliophila (two spp.)
Magilus fimbriatus (A. Adams, 1852)
Quoyula madreporarum (Sowerby, 1832)

COLUMBELLIDAE

Anarithma metula (Hinds, 1843)
Euplica palumbina (Gould, 1845)
E. varians (Sowerby, 1832)
Mitrella rorida (Reeve, 1859)
Seminella varia (Pease, 1861)

BUCCINIDAE

Cantharus undosus (Linnaeus, 1758)
Engina maculata (Pease, 1869)
E. mendicaria (Linnaeus, 1758)
E. tuberculosa Pease, 1863
Pisania ignea (Gmelin, 1791)
P. truncatus (Hinds, 1844)[15]

NASSARIIDAE

Nassarius gaudiosus (Hinds, 1844)
N. graniferus (Kiener, 1834)
N. ravidus (A. Adams, 1851)

FASCIOLARIIDAE

Latirus amplustris Dillwyn, 1817
L. iris (Lightfoot, 1786)
Peristernia gemmata Reeve, 1847
P. nassatula (Lamarck, 1822)

VASIDAE

Vasum armatum (Broderip, 1833)

HARPIDAE

Harpa amouretta Röding, 1798

MARGINELLIDAE

Granula sandwicensis (Pease, 1860)
Hyalina elliptica (Redfield, 1870)
Marginellids (four spp.)

MITRIDAE

Imbricaria conovula (Quoy & Gaimard, 1833)
I. punctata (Swainson, 1821)
Mitra acuminatus Swainson, 1824
M. coffea Schubert & Wagner, 1829
M. cucumerina Lamarck, 1811
M. ferruginea Lamarck, 1811
M. litterata Lamarck, 1811
M. mitra (Linnaeus, 1758)
M. paupercula (Linnaeus, 1758)
M. saltata Pease, 1865
M. stictica Link, 1807
Pterygia crenulata (Gmelin, 1791)
Vexillum lautum (Reeve, 1845)
V. rubrum (Broderip, 1836)

CONIDAE

Conus catus Hwass in Bruguière, 1792
C. chaldaeus (Röding, 1798)
C. ebraeus Linnaeus, 1758
C. flavidus Lamarck, 1810
C. lividus Hwass in Bruguière, 1792
C. miles Linnaeus, 1758
C. miliaris Hwass in Bruguière, 1792
C. pulicarius Hwass in Bruguière, 1792
C. rattus Hwass in Bruguière, 1792
C. retifer Menke, 1829
C. sponsalis Hwass in Bruguière, 1792
C. tulipa Linnaeus, 1758
C. virgo Linnaeus, 1758

TEREBRIDAE

Hastula penicillata (Hinds, 1844)
Terebra affinis Gray, 1834
T. argus Hinds, 1844
T. crenulata (Linnaeus, 1758)
T. dimidiata (Linnaeus, 1758)
T. flavofasciata Pilsbry, 1921
T. maculata (Linnaeus, 1758)
T. subulata (Linnaeus, 1767)

[13] As *Bursa cruentata* (Sowerby, 1835) (Kay 1971).
[14] As *Drupella cornus* (Röding, 1798) (Kay 1971).
[15] As *Caducifer truncatus* (Hinds, 1844) (Kay 1971).

TABLE 1 (*cont.*)

TURRIDAE

Carinapex minutissima (Garrett, 1873)
Daphnella interrupta Pease, 1860
Etrema sp. cf. *scalarina* (Deshayes, 1863)
Eucithara angiostoma (Pease, 1868)
Iredalea (two spp.)
Kermia pumila (Mighels, 1845)
Macteola sp. cf. *thiasotes* (Melvill & Standen, 1897)
Microdaphne sp.
Tritonoturris sp.
Turrids (seven spp.)

PYRAMIDELLIDAE

Chemnitzia (two spp.)
Herviera gliriella (Melvill & Standen, 1896)
Odostomia sp. cf. *oodes* Watson, 1886
Odostomia sp. cf. *scopulorum* Watson, 1886
Odostomia (three spp.)
Otopleura mitralis (A. Adams, 1855)
Pyramidella sp.
Turbonilla sp. A.
Turbonilla (two spp.)

ACETEONIDAE

Pupa sulcata (Gmelin, 1791)
Pupa sp.

HYDATINIDAE

Haminea sp.

SCAPHANDRIDAE

Acteocina sp. cf. *sandwicensis* (Pease, 1860)

AGALIIDAE

Chelidonura sp.

AEOLIDS (two spp.)

ATYIDAE

Atys cylindricus (Helbling, 1779)
Cylichna pusilla (Pease, 1860)
Diniatys dentifer (A. Adams, 1850)

ELLOBIIDAE

Melampus flavus (Gmelin, 1791)
Melampus sp.

ELYSIIDAE

Elysia ornata (Pease, 1860)
E. rufescens (Pease, 1870)

OXYNOIDAE

Lobiger sp.

APLYSIIDAE

Dolabrifera dolabrifera (Rang, 1828)
Stylocheilus longicaudus (Quoy & Gaimard, 1824)

DORIDIDAE

Dendrodoris nigra (Stimpson, 1856)
Jorunna tomentosa (Cuvier, 1804)

BIVALVIA

LIMOPSIDAE

Cosa sp.

ARCIDAE

Acar plicata (Dillwyn, 1817)
Arca ventricosa Lamarck, 1819
Barbatia decussata (Sowerby, 1833)
B. parva (Sowerby, 1833)

MYTILIDAE

Lithophaga nasuta (Philippi, 1846)
Modiolus metcalfei Reeve, 1858
Septifer (two spp.)

ISOGNOMONIDAE

Isognomon isognomon (Linnaeus, 1758)
I. perna (Linnaeus, 1767)

PTERIIDAE

Electroma sp.
Pinctada margaritifera (Linnaeus, 1758)

PINNIDAE

Atrina vexillum (Born, 1778)
Pinna muricata Linnaeus, 1758

PECTINIDAE

Chlamys sp.
Gloripallium pallium (Linnaeus, 1758)

SPONDYLIDAE

Spondylus ducalis Röding, 1798
Spondylus (two spp.)

LIMIDAE

Lima fragilis (Gmelin, 1791)

OSTREIDAE

Ostrea hanleyana Sowerby, 1871
O. sandvichensis Sowerby, 1871

CHAMIDAE

Chama imbricata Broderip, 1834

LUCINIDAE

Codakia bella (Conrad, 1837)
C. punctata (Linnaeus, 1758)
"*Lucina*" *edentula* (Linnaeus, 1758)
Wallucina sp. cf. *gordoni* (E. A. Smith, 1886)

ERYCINIDAE

Kellia sp.
Neobornia sp.

CARDITIDAE

Cardita variegata (Bruguière, 1792)

CARDIIDAE

Cardium sp.
Fragum fragum (Linnaeus, 1758)

MESODESMATIDAE

Rochefortina sandwichensis Smith, 1885

TRIDACNIDAE

Tridacna maxima (Röding, 1798)

TABLE 1 (*cont.*)

TRAPEZIIDAE

Trapezium oblongum (Linnaeus, 1758)

TELLINIDAE

Arcopagia scobinata (Linnaeus, 1758)
Macoma dispar (Conrad, 1837)
Quidnipagus palatam Iredale, 1929
Tellina robusta (Hanley, 1844)
T. tongana (Quoy & Gaimard, 1833)
T. virgata Linnaeus, 1758
Tellinids (four spp.)

SEMELIDAE

Semelangulus crebrimaculatus Sowerby, 1835

VENERIDAE

Gafrarium pectinatum (Linnaeus, 1758)[16]
Periglypta reticulata (Linnaeus, 1758)
Periglypta sp.
Pitar prora (Conrad, 1837)

SPORTELLIDAE

Anisodonta sp. cf. *lutea* Dall, Bartsch, & Rehder, 1933

DIPONDONTIDAE

Diplodonta sp.

[16] As *Asaphis violascens* (Kay 1971).

TABLE 2

ϕ SCALES, MESH OPENINGS, AND SIZE CLASSES OF SIEVES USED IN SEDIMENT ANALYSES

ϕ SCALE	MESH OPENING (mm)	SIZE CLASS
−2.0	4.00	Granule
−1.0	2.00	Very coarse sand
0.0	1.00	Very coarse sand
1.0	0.50	Coarse sand
2.0	0.25	Medium sand
3.0	0.125	Fine sand
4.0	0.0625	Very fine sand
< 4.0	pan	Silt

sector in the vicinity of English Harbor (Fig. 1) where visibility is from 10 to 15 m, and into turbid water sectors in the north and south basins where visibility is less than 2 m (Roy and Smith 1971). In the turbid lagoon, patch reefs are predominantly fringed by ramose *Acropora* (Roy and Smith 1971; Maragos 1974*a*—this issue). The lagoon floor, 10 to 15 m deep in the clear water area and 4 to 8 m deep in the turbid lagoon, comprises living corals and carbonate mud sediments. Live corals cover 62 percent of the clear water area and 31 percent of the turbid lagoon floor (Roy and Smith 1971).

RESULTS

Lagoon Reef Flat Assemblages

Approximately 100 species were recorded from the lagoon reef flat, of which 33 were large mollusks and 65 micromollusks. Of the large mollusks, 16 were recorded alive and the remaining 17 consisted of juveniles and/or fragments in the sediments. The most frequently occurring of the living mollusks were two cerithids, *Rhinoclavis asper* and *Clypeomorus brevis*; two opisthobranchs, *Pupa sulcata* and *Pyramidella* sp.; and two bivalves, *Fragum fragum* and *Tellina robusta*. All are sand-dwellers and, except for *Clypeomorus* which occurs on the surface of the substrate, were found buried or partially buried in sand. The distribution of *Rhinoclavis*, *Clypeomorus*, and *Pupa* is shown in Fig. 2. *Pupa* is the most frequently occurring of these mollusks, recorded from 47 percent of the stations. It is most frequent (33 percent) on the northeast near Vai Tepu. *Fragum* and *Tellina* occurred at 25 percent of the stations, with *Fragum* most frequent (30 percent) on the northeast and *Tellina* most frequent (37 percent) on the southwestern perimeter. *Pyramidella* is most frequent (40 percent) on the reef flat of the northwestern perimeter. *Rhinoclavis* is most frequent (37 percent) on the eastern shore near

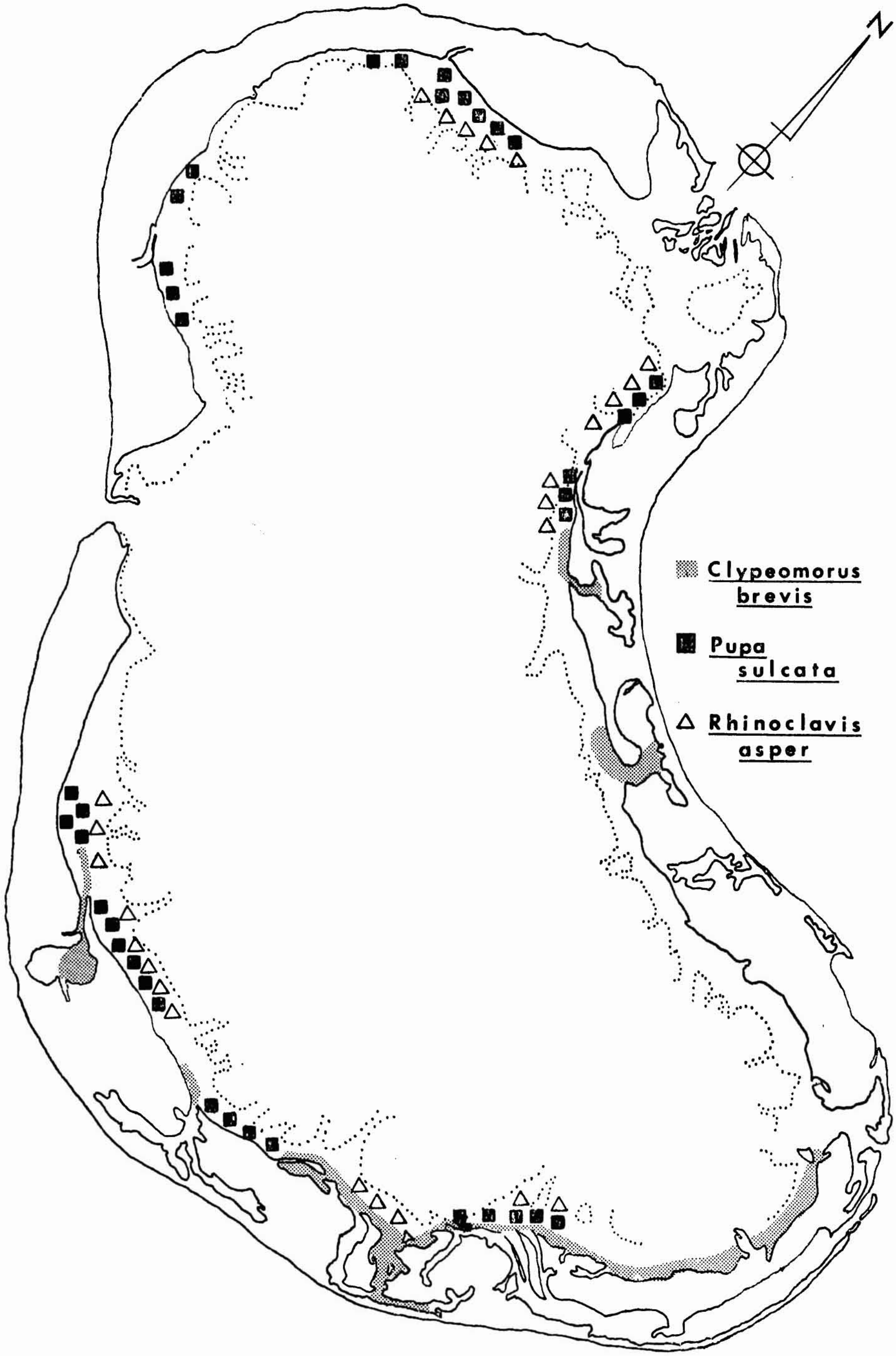

FIG. 2. Distribution of *Clypeomorus*, *Pupa*, and *Rhinoclavis* in Fanning Lagoon.

TABLE 3

STATIONS (SHOWN IN FIG. 1) ACCORDING TO MEAN GRAIN SIZE, STANDARD DEVIATIONS, AND PRESENCE OR ABSENCE OF THE SIX MOST COMMONLY ENCOUNTERED LARGE MOLLUSKS, FANNING LAGOON

STATION	M_z (ϕ)	g (ϕ)	*Clypeomorus*	*Fragum*	*Pupa*	*Pyramidella*	*Rhinoclavis*	*Tellina*
P6	−0.52	1.78						
F1	−0.43	0.80						
P3	−0.33	1.98			×			
V8	−0.32	1.53						
CS4	0.00	1.47		×				
P5	0.05	1.55			×			×
V5	0.07	1.45	×	×			×	
V4	0.08	1.58	×	×	×			
CS3	0.18	1.77			×			
P8	0.27	1.20	×					
R2	0.32	1.30		×				×
V5	0.42	1.75		×	×			
CS6	0.43	1.45				×		
P7	0.43	1.40	×					
V1	0.60	1.75			×	×		
R3	0.63	1.15		×				
R1	0.67	0.98		×				×
P1	0.68	1.30		×	×	×		×
P2	0.68	1.43		×	×			×
V3	0.73	1.20						
CS2	0.90	1.10		×	×	×		
CS5	0.90	1.35			×			
V7	0.90	1.40					×	
V6	1.03	1.05		×			×	
F2	1.18	1.18						
CS1	1.31	0.95			×	×		
V2	1.40	1.43						
P4	1.50	1.15					×	
V9	1.58	2.03						

Vai Tepu, noticeable on the south shore, and relatively infrequent on the western shore (3 percent). *Clypeomorus* is restricted to the southern, southwestern, and eastern lagoon reef flat.

In addition to the dominant macromollusks of the reef flat, six localized assemblages were recorded: a complex *Cypraea moneta*/*C. annulus* assemblage on the rubble shoreline near English Harbor (Kay 1971); three colonies of *Cypraea moneta* in the infrequent rubble patches along the shore, two north of Cable Station and one at Vai Tepu; three colonies of *Macoma dispar*, one near Cable Station and two on the southern perimeter; two colonies of *Conus pulicarius*, one near English Harbor and the other near Rapa Pass; a single assemblage of *Strombus gibberulus* and *Natica gualteriana* off the village north of Cable Station; and occasional specimens of *Gafrarium pectinatum* near brackish water inlets at Vai Tepu and Napu Naiaroa.

The distribution of the most frequently occurring of the sand-dwelling mollusks is, at least in part, associated with sediment grain size and salinity. Table 3 lists several stations (shown in Fig. 1) according to mean grain size, the standard deviations, and presence or absence of the six most commonly occurring large mollusks. Mean grain size ranges from -0.52ϕ to $+1.58\phi$ (0.76 to 0.35 mm). *Pupa* inhabited the widest range of grain size habitats. *Clypeomorus* was restricted to a smaller range of larger grain size (0.07ϕ to 0.43ϕ). Subjective observations that *Rhinoclavis* was usually located in areas of fine sand were substantiated in the analysis with the species found in samples of mean grain size of $+0.13\phi$ to $+1.50\phi$.

The distribution of *Clypeomorus* is also associ-

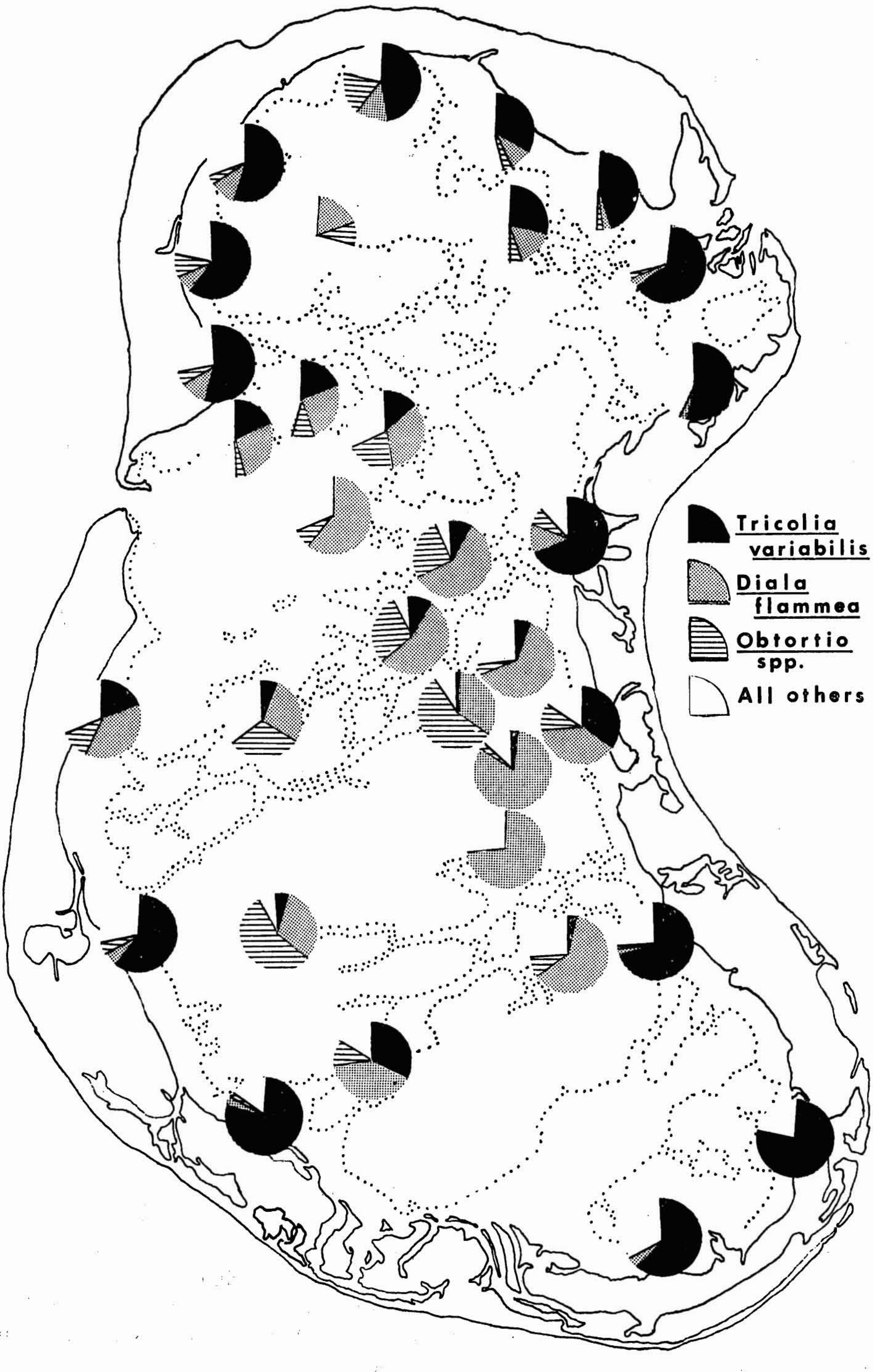

FIG. 3. Molluscan species composition in terms of relative abundance in Fanning Lagoon.

TABLE 4

STANDING CROP, SPECIES DIVERSITY, RELATIVE ABUNDANCE, AND TROPHIC STRUCTURE OF THE MOST COMMON MICROMOLLUSKS IN FANNING LAGOON

	LAGOON REEF FLAT*					PATCH REEFS		LAGOON FLOOR	
	CABLE STATION ISLAND	PUTA TUTAE	VAI TEPU	RAPA PASS	NORTH PASS	CLEAR	TURBID	CLEAR	TURBID
Average No./cm³	4.5	8.4	17.5	11.5	5.9	6.2	4.5	9.5	12.3
Species Diversity (H′)	3.0	2.4	2.1	1.5	1.9	2.6	2.8	2.8	1.8
Species or Species Groups									
Leptothyra	7	4	4	7	9	1	7	–	–
Tricolia	46	55	57	77	64	9	12	4	–
Parviturbo	3	1	3	2	5	1	+	+	–
Orbitestellidae (two spp.)†	2	2	2	2	+	+	+	+	–
Merelina sp. A	4	2	3	2	2	2.5	3	–	–
Diala	10	12	13	–	3	48	41	58	52
Obtortio pupoides	2	4	2	–	1	4	4	4	31
O. sulcifera	5	1	2	–	+	16	13	+	+
Triphoridae (six spp.)	+	+	+	+	+	–	1	+	+
Acteocina	6	6	4	1	6	4*	3	+	+
Pyramidellids (five spp.)	4	2	+	+	2	4	8	10	9
Trophic Structure‡									
Herbivores	87	91	92	97	89	89	93	72	88
Suspension/Deposit Feeders	+	+	+	+	2	5	1	11	+
Faunal Grazers	2	2	+	+	2	+	+	+	+
Predators/Scavengers	6	5	4	1	5	4	3	6	+
Parasitic	4	2	+	+	2	†	2	10	9

NOTE: Species composition and trophic structure are given as percent composition. + signifies less than 1 percent of the assemblage.

* Reef flat stations refer to those in Fig. 1.

† "Vitrinellids" of Kay 1971.

‡ Herbivores include archaeogastropods (*Tricolia* and *Leptothyra*), rissoids, cerithids, diastomids, etc.; suspension or deposit feeders are represented by bivalves; faunal grazers include triphorids, cerithiopsids, and marginellids that feed on sponges, etc.; predators/scavengers are columbellids, turrids, and others of the neogastropods and some opisthobranchs; the pyramidellids are considered parasitic.

ated with salinity: this gastropod was exclusively confined to areas where brackish water inlets open to the reef flat on the southern, southwestern, and eastern perimeter of the lagoon (Fig. 2). No specimens were encountered in our sampling on the northwestern lagoon reef flat where similar conditions were present, although occasional shells were found there in 1970 (Guinther 1971). *Clypeomorus* withstands salinities as great as 55‰, but becomes inactive at salinities less than 27‰, and its occurrence on the lagoon shore may be associated with a migration from the brackish water inlets of the interior of the islands (Guinther, personal communication).

We did not attempt to estimate standing crops of large mollusks in terms of biomass, and, because of variations in the sizes of these mollusks (*Rhinoclavis* averaged 32 mm in length, and *Tellina* and *Pupa* 14 mm and 18 mm, respectively), estimates of standing crop would be meaningless without further analysis. Estimates of density, however, suggest that *Clypeomorus* occurs in the greatest numbers per unit area of substrate, with densities of more than 70 per m². Greatest densities were recorded on the southern perimeter of the lagoon where *Clypeomorus* predominated, and on the eastern (windward) shore where *Rhinoclavis* was dominant.

Trophic structure of the large mollusks is a mixture of grazing herbivores, suspension

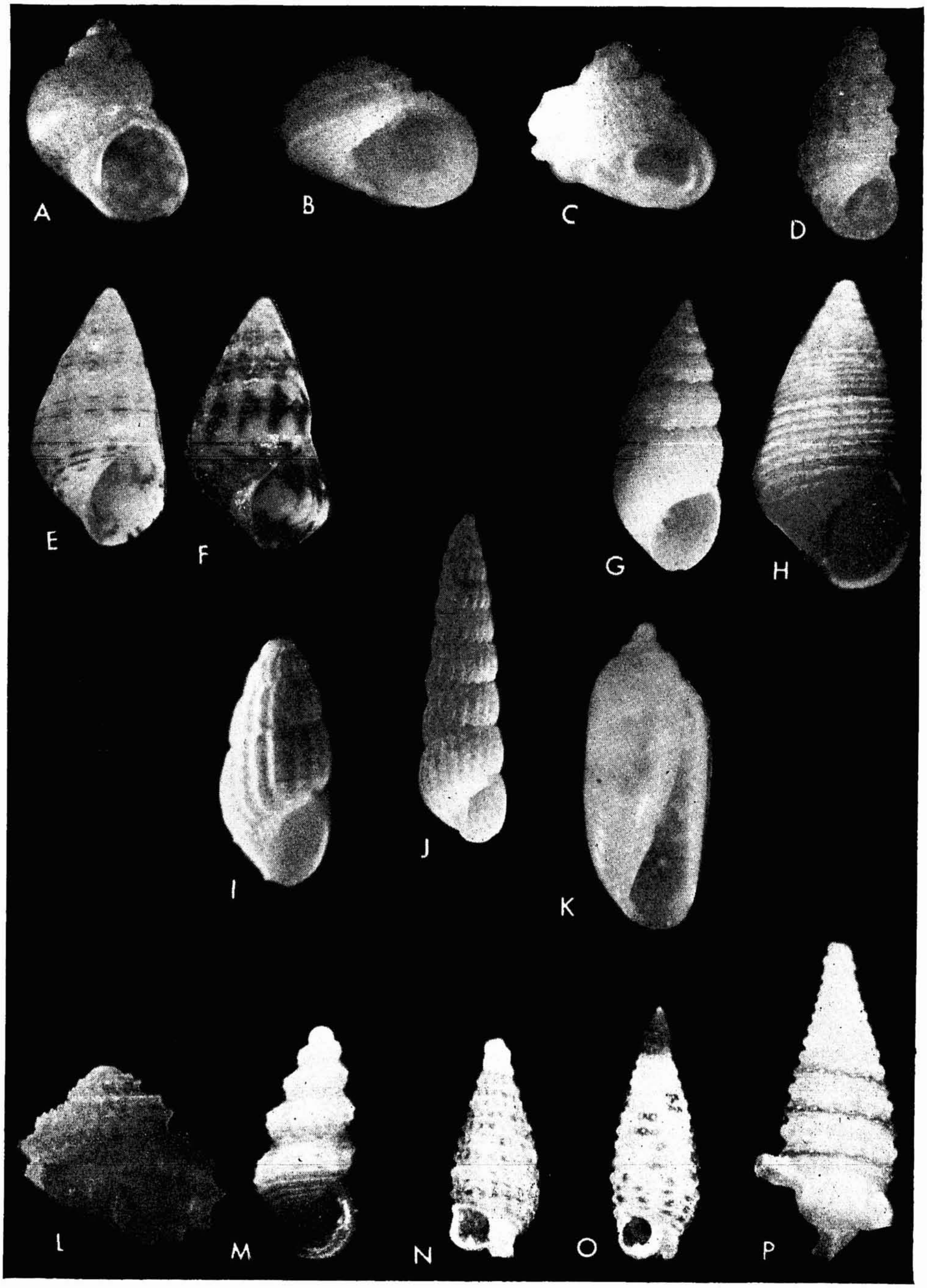

FIG. 4. Micromollusks common in the lagoon and on the seaward reefs at Fanning Island. A, *Tricolia variabilis*, length 1 mm; B, *Leptothyra* sp. cf. *wellsi*, height 1 mm; C, *Parviturbo minutissimus*, height 0.5 mm; D, *Merelina* sp. A, length, 0.75 mm; E–F, *Diala flammea*, two color variations, 3 mm; G, *Obtortio pupoides*, length 4 mm; H, *O. sulcifera*, length 4 mm; I, *Odostomia* sp. cf. *oodes*, length 0.75 mm; J, *Turbonilla* sp. A, length 2.5 mm; K, *Acteocina sandwicensis*, length, 3 mm; L, *Euchelus angulatus*, height 3 mm; M, *Merelina* sp. B, length 1.5 mm; N, *Triphora* sp. cf. *minuta*, length, 2 mm; O, *Triphora* sp. cf. *tessellata*, length 2.5 mm; P, *Triphora* sp. cf. *decorata*, length 2.5 mm.

feeders, and infaunal carnivores, with the grazing herbivores (or detritus feeders) *Rhinoclavis* and *Clypeomorus* being predominant.

The micromolluscan assemblages of the lagoon reef flat are marked by the inordinate abundance of the small (ca. 1 mm in length) phasianellid *Tricolia variabilis*, which comprises 46 to 77 percent of the assemblages (Fig. 3 and Table 4). *Tricolia* is most abundant on the reef flat of the northwestern and southwestern perimeters (Fig. 3). Other small mollusks which form dominant components of the assemblage are three diastomids, *Diala flammea*, *Obtortio pupoides*, and *O. sulcifera*; a rissoid, *Merelina* sp. A; a turbinid, *Leptothyra* sp. cf. *wellsi*; and the opisthobranch *Acteocina* sp. cf. *sandwicensis* (Fig. 3, Table 4). Shells illustrating these species are shown in Fig. 4. The skeneid *Parviturbo minutissimus* and two minute "orbitestellids" were found in lesser abundance (Table 4).

The occurrence of the dominant forms was remarkably consistent at all stations except in the passes where *Tricolia* was relatively more abundant and *Diala* and the two species of *Obtortio* less abundant or absent (Fig. 3, Table 4). *Diala* was the only species which was more abundant than *Tricolia* at any of the stations; on the two sections of the reef flat where it dominated (Fig. 3), grain sizes approximate those of the patch reefs. All the micromolluscan species encountered are epifaunal except for *Acteocina*, which is infaunal. Although time did not permit detailed studies of the habitats of micromollusks, we noted living *Tricolia* and *Diala* in mats of the red algae *Hypnea* and *Polysiphonia* in the passes, and we found *Diala* on the brown alga *Turbinaria* floating in the lagoon, on *Hypnea* associated with rubble on the lagoon reef flat, and on *Polysiphonia* on the patch reefs.

Standing crops of micromollusks were greatest on the eastern periphery of the reef flat from Vai Tepu south and at Rapa Pass (Fig. 5). Trophic structure of the micromolluscan assemblages is predominantly grazing herbivore (Table 4). Species diversity values are highest north of the cable station (CS, Fig. 1), one of the few areas where there was rubble on the reef flat; lowest values were recorded in the passes and in the northeastern sector of the lagoon.

Patch Reefs

Thirty-two species of large mollusks and 44 species of micromollusks were recorded from the patch reefs. Of the macrofauna, 15 species occurred with frequencies of more than 10 percent. The habits of the macromollusks are divisible into three categories, epifaunal species associated with rubble and coral, sessile bivalves attached to coral, and those which are infaunal in sand.

Cypraea moneta is the most ubiquitous of the epifaunal mollusks, found at 52 percent of the stations. *Trochus histrio* (30 percent) and *Cymatium pyrum* (26 percent) were found on both living coral and rubble but were more frequent on the former than the latter. Three bivalves were associated with living coral and two with living and dead coral. *Electroma* sp. was found most frequently on *Acropora*; *Ostrea sandvichensis* occurred more frequently on *Stylophora* than on *Acropora*; and *Barbatia decussata* was found only in massive heads of *Porites*. *Tridacna maxima* and *Cardita variegata* were found in *Porites* and *Acropora* but were not limited to living coral. Large numbers of small vermetids were also associated with corals, especially those encrusted with coralline algae. The sand dwellers *Rhinoclavis* and *Cerithium sculptum* were found more frequently in sand under living coral than in sand under rubble, but the bivalves *Gafrarium*, *Pitar*, and *Trapezium* were found more frequently in sand under rubble than under living coral.

The distribution of the large mollusks reflects the division of the lagoon into clear and turbid water sectors: *Tridacna* and *Barbatia* were limited in their distribution to the massive corals of the clear lagoon (Fig. 6). *Gafrarium*, *Pitar*, and *Trapezium* occur in greater numbers on the rubble-covered reefs of the southern turbid lagoon than in other sectors, and we noted that the boring mytilid *Lithophaga* is more common in corals of the turbid lagoon than in the clear lagoon. *Electroma* and *Ostrea* are distributed throughout the lagoon, but densities of *Electroma* appeared greater in the turbid lagoon than in the clear lagoon. Other mollusks such as *Cymatium* and *Nassarius* that were reported as being characteristic of the lagoon (Kay 1971) were found to be restricted almost entirely to the patch reefs of the clear lagoon.

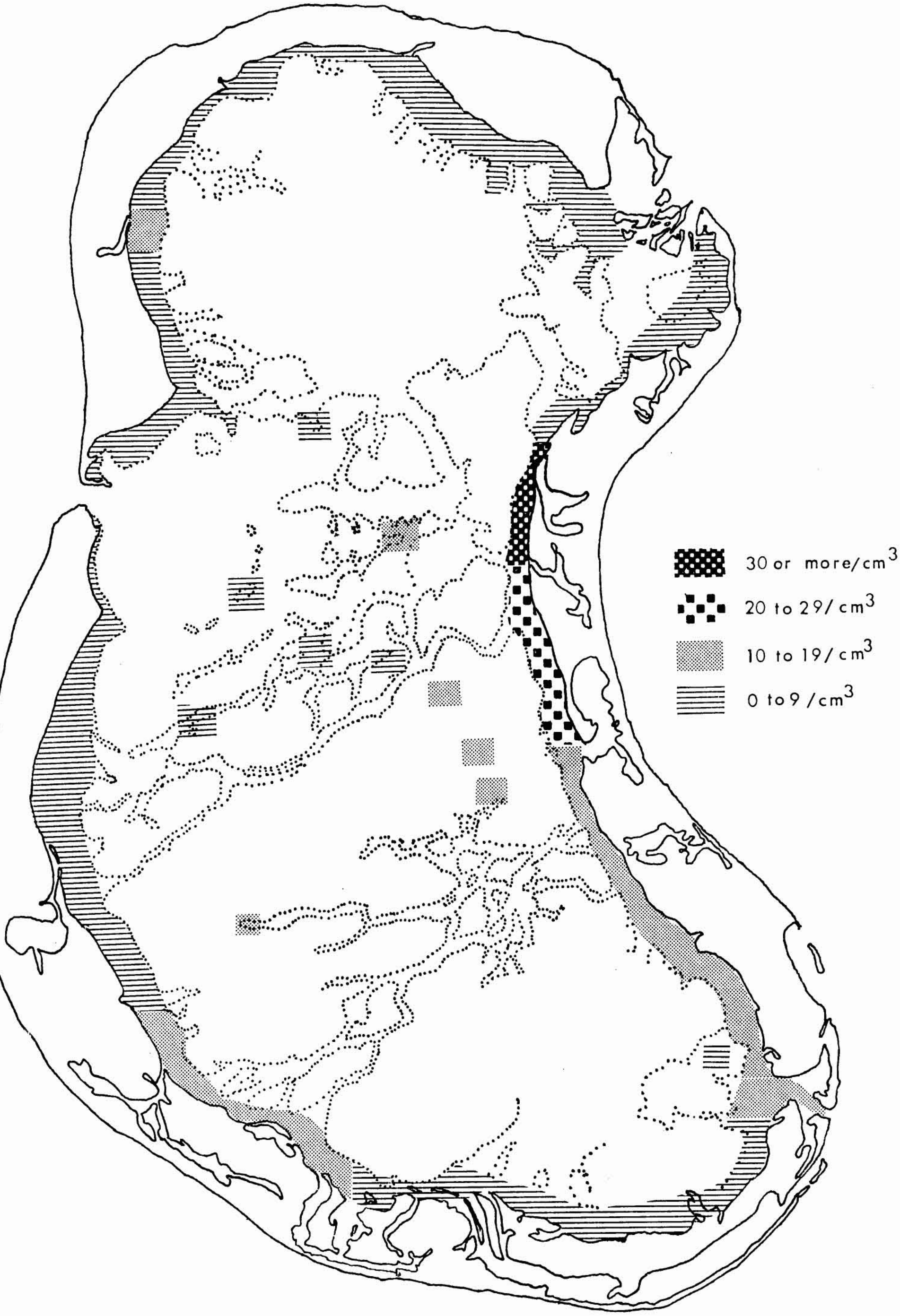

FIG. 5. Distribution of the standing crop of micromollusks in Fanning Lagoon.

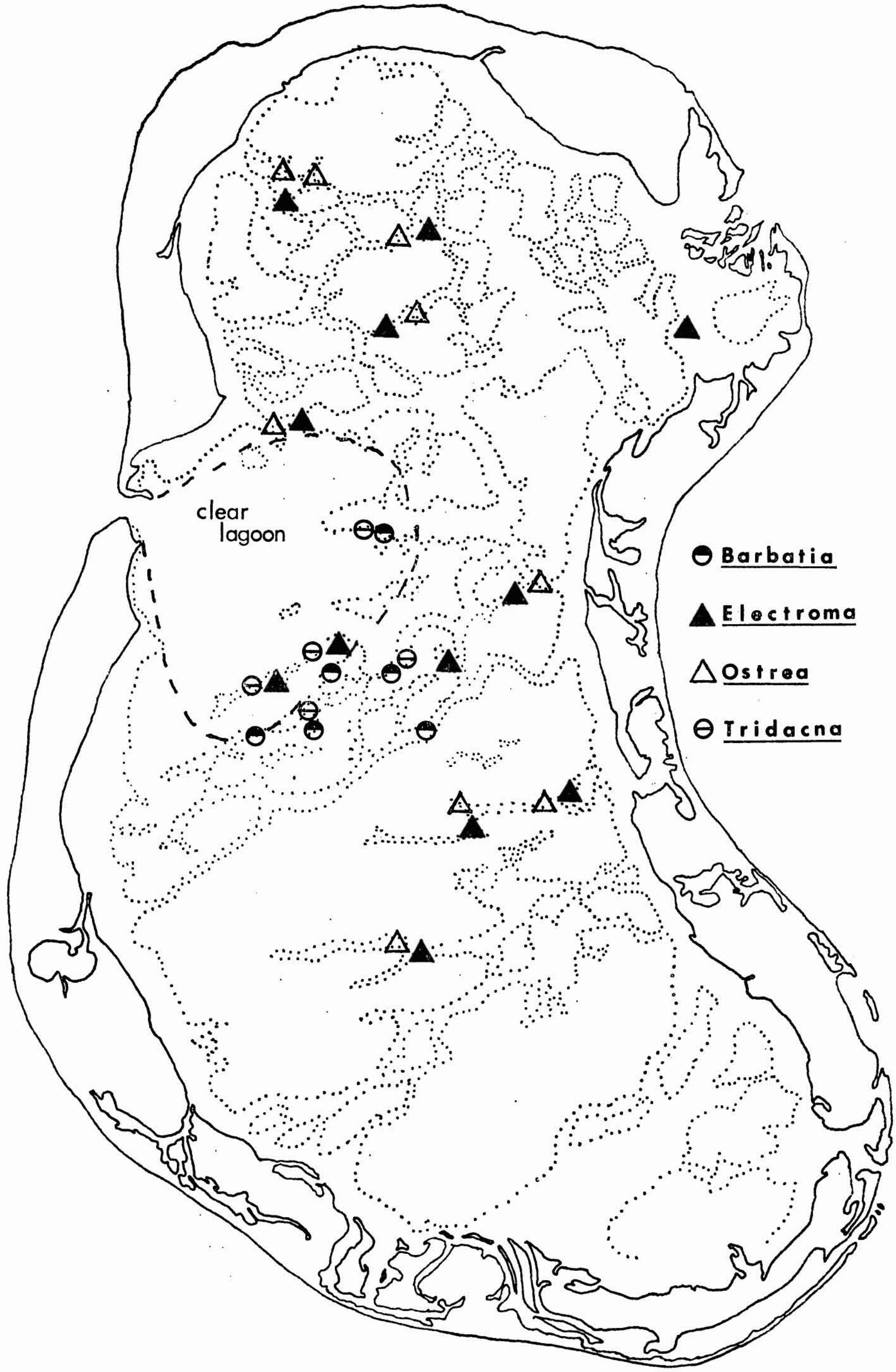

FIG. 6. Distribution of *Barbatia*, *Electroma*, *Ostrea*, and *Tridacna* in Fanning Lagoon.

The mollusks associated with living coral and the infaunal forms of the patch reefs are predominantly suspension feeders because of the preponderance of bivalves and vermetids. The rubble-associated mollusks are largely grazing herbivores.

The dominant component of the micromolluscan assemblages of the patch reefs is *Diala flammea* (Fig. 3, Table 4). *Obtortio sulcifera* and *Tricolia* are found in lesser abundance, and *Merelina*, *Leptothyra*, and *Acteocina* are least abundant (Table 4). There is some indication of a distinction between the micromolluscan assemblages of the clear lagoon and those of the turbid lagoon, although it is not so striking as with the large mollusks. *Diala* and *O. sulcifera* are more abundant in the clear lagoon than in the turbid lagoon, and *Leptothyra*, *Tricolia*, and pyramidellids are more abundant in the turbid lagoon than in the clear lagoon (Table 4). The clear lagoon sediments are also characterized by a greater proportion of small tellinids (comprising 64 percent of the bivalves [suspension feeders, Table 4]) than occurs in the turbid lagoon (29 percent of the bivalves).

Lagoon Floor

Relatively few large mollusks were recorded from the lagoon floor. In the clear lagoon, *Terebra maculata*, *Atrina vexillum*, and two or three species each of *Mitra* and *Conus* were recorded, while only *Cerithium sculptum* and *Codakia divergens* were recorded from the calcareous mud sediments of the turbid lagoon.

Fifty-three species of micromollusks were recorded from the sediments of the lagoon floor, with 31 species found only in the clear lagoon and 8 species recorded only in the turbid lagoon. *Diala* is the dominant species in both the clear and turbid sectors, comprising more than 50 percent of the assemblages (Table 4). *Obtortio pupoides* is second in abundance and is clearly predominant in the turbid lagoon (Table 4). *Leptothyra* and *Merelina* were not recorded from the sediments of either the clear or the turbid lagoon, nor were *Tricolia*, *Parviturbo*, or the "orbitestellids" found in the turbid lagoon sediments. Pyramidellids comprise about 10 percent of the gastropod assemblages in both areas (Table 4), with *Odostomia* sp. cf. *oodes* forming 53 percent of the pyramidellids of the turbid lagoon and *Turbonilla* sp. A making up 81 percent of the pyramidellids in the clear lagoon versus 36 percent in the sediments of the turbid lagoon. The clear lagoon is also distinguished from the turbid lagoon by a higher proportion of bivalves (suspension feeders, Table 4), and small tellinids comprise 71 percent of the bivalves in the clear sector.

Dead Shells and Fossils

The occurrence of several accumulations of dead shells on shoreward areas of the lagoon reef flat, on the patch reefs, and in mounds and flats of fossil shells is also noteworthy. We found accumulations of large shells of *Fragum* and *Gafrarium* both on the lagoon reef flat and on the patch reefs and of *Rhinoclavis* at North Pass. Fossil *Tridacna* valves *in situ* on sand-free areas of the reef flat were noted above. In addition we recorded several species as fossils in mounds on Cable Station Island and at Vai Tepu; these included specimens of *Strombus lentiginosus*, *Philippia*, and *Terebra* which have not been recorded alive at Fanning.

Seaward Reefs

The molluscan assemblages of the seaward reefs have been described (Kay 1971). The dominant mollusks of the seaward reef flats are the herbivores *Turbo*, *Astrea*, *Patella*, and *Cypraea moneta*, and carnivorous thaisids, fasciolarids, *Vasum*, cones, and miters. Of the 20 macromollusks that can be considered common on the seaward reef flats, only *Cypraea moneta* is also dominant and widespread in the lagoon. *Vasum*, *Maculotriton*, and *Cymatium pyrum* were also recorded in the lagoon but were found only in the clear water sectors or near English Harbor.

For purposes of comparison of the microfauna of the seaward reefs and the lagoon, samples from the leeward seaward reef flat, moats near English Harbor, and from depths of 10, 21, and 36 m off the reef slope were analyzed. Sixty-six species of micromollusks were recorded in these samples. Only the Triphoridae and *Merelina* sp. A, the latter also common in the lagoon, are consistently present at all the stations. Each of the three shallow

TABLE 5

STANDING CROP, SPECIES DIVERSITY, RELATIVE ABUNDANCE, AND TROPHIC STRUCTURE OF THE MOST COMMON MICROMOLLUSKS OF THE LEEWARD SEAWARD REEFS

	REEF FLAT*	MOAT†	10 m‡	21 m†	36 m†
Average No./cm³	–	1.25	2.2	4.3	5.0
Species Diversity (H′)			3.9	3.6	4.4
Species or Species Groups					
Euchelus	2	8	–	+	+
Leptothyra	–	–	2	–	–
Tricolia	3	–	–	–	2
Parviturbo	5	–	10	–	2
Orbitestellidae (one sp.)§	8	–	–	–	–
Merelina sp. A	6	10	24	+	3
Merelina sp. B	–	–	–	6	8
Bittium zebrum	13	6	–	–	–
Diala	–	–	4	+	–
Obtortio pupoides	–	–	–	–	+
Triphoridae (eight spp.)	3	12	8	39	30
Mitrella rorida	1	15	–	9	2
Euplica varians	26	3	4	–	+
Acteocina	1	–	2	–	–
Pyramidellids (three spp.)	–	–	6	–	2
Trophic Structure¶					
Herbivores	46	38	60	31	41
Suspension/Deposit Feeders	+	10	10	3	5
Faunal Grazers	16	34	14	58	43
Predators/Scavengers	37	18	10	8	7
Parasitic	–	–	6	–	2

NOTE: Species composition and trophic structure are given as percent composition. + signifies less than 1 percent of the assemblages.

* Data from coral/algal washings in 1970.

† Shallow tidepools described by Chave and Eckert (this issue) and stations on the seaward reef transect described by Maragos (1974*b*—this issue).

‡ From one station on the reef slope off the cable station.

§ "Vitrinellid" of Kay 1971.

¶ Categories described in Table 4.

stations shows a different species as being dominant: on the reef flat, *Euplica varians*; in the moats, *Mitrella rorida*; and at the 10 m station, *Merelina* sp. A. The two deep stations resemble each other in the high proportion of triphorids present. Trophic structure is predominantly faunal grazer at all of the stations; standing crops are less than those recorded in the lagoon and the species diversity index is higher (Table 5).

DISCUSSION AND CONCLUSIONS

Approximately 350 species of mollusks have now been recorded from Fanning Island. In this report we describe the distribution of the lagoon mollusks, attempt to relate distribution patterns to various parameters within the lagoon, and compare species composition, abundance, and diversity with those of the seaward reefs. Three characteristics of the assemblages exhibit empirical patterns: mode of life, species composition, and species diversity. In addition, we find a striking contrast between the community structure of the macrofauna and that of the microfauna on the same grounds.

The three habitat types initially distinguished —lagoon reef flat, patch reef, and lagoon floor— subsume three major types of substrates—sand, rubble, and living coral. These substrate types at once serve to define some of the distributional patterns observed for the large mollusks. Sand-dwelling mollusks are found in all three habitat types, that is, on the lagoon reef flat, on patch reefs, and on the lagoon floor. Coral-associated forms are restricted to the occurrence of living corals, most of which are found on the patch reefs and particular types of which are associated with the turbid and clear water areas of the lagoon respectively. Rubble-associated mollusks occur where there is rubble, primarily on the patch reefs and to a lesser extent on the reef flat.

The dominant sand-dwelling mollusks are cerithids, opisthobranchs, and the bivalves *Fragum*, *Gafrarium*, *Pitar*, *Tellina*, and *Trapezium*. The coral-associated mollusks are predominantly sessile bivalves: *Barbatia*, *Cardita*, *Electroma*, and *Tridacna*; and the epifaunal mollusks comprise primarily *Cypraea moneta* on rubble and *Trochus* on coral.

Within each of the major substrate types there are subsidiary distribution patterns which we associate with salinity, turbidity, and sediment grain size. *Clypeomorus* appears to be associated with the brackish water inlets that dissect the lagoon shore; *Barbatia* and *Tridacna* are found only in clear-water areas of the lagoon; and the distribution of *Rhinoclavis*, *Pupa*, *Pyramidella*, and *Tellina* is associated with sediment grain size. The sand-dwellers also appear to be influenced by the presence or absence of rubble: three species (*Pupa*, *Pyramidella*, and *Tellina*) occur almost exclusively on the reef flat where there is little rubble; *Rhinoclavis* is more frequent on the lagoon reef flat than on the rubble-covered patch reefs; and *Cerithium sculptum*, *Gafrarium*, *Trapezium*, and *Pitar* are almost entirely confined to rubble-covered sand on the patch reefs.

The habitat types of the macrofauna parallel those reported by Salvat (1972) for the lagoon mollusks at Réao, Tuamotu Islands. Salvat reported only 28 species of mollusks in the lagoon at Réao; and species composition there is somewhat different from that at Fanning, a fact consistent both with Salvat's (1967) suggestion that it is species composition of lagoons which distinguishes the biota of atolls in the Pacific, and with the location of Fanning at the eastern periphery of the central Pacific faunal region. Of the infaunal species reported for Réao (Salvat 1972), only *Tellina robusta* is also dominant in Fanning Lagoon. *Macoma dispar* and *Codakia divergens* are present but not in the apparent numbers reported for Réao. Three of the Réao species are represented by ecological equivalents at Fanning: *Cerithium fasciatum* appears to be replaced at Fanning by *Rhinoclavis*; *Solidula solidula* is replaced by *Pupa*; and *Cerithium salebrosum*, which occurs in the fine sediments of the Réao lagoon, may be replaced by *Cerithium sculptum* at Fanning. Of the species of the Réao coral assemblage (*Acropora facies* of Salvat 1972), *Tridacna* and *Cypraea moneta* are also dominant at Fanning, but *Pinctada maxima* and *Astralium petrosum* appear to be replaced by *Electroma* and *Trochus* respectively. Both dominant species of the massive corals at Réao, *Arca ventricosa* and *Chama imbricata*, are present in Fanning Lagoon, but the dominant species of massive corals at Fanning is a third species, *Barbatia decussata*, which was not recorded from Réao.

In contrast to the obvious division of the macrofauna into groups associated with substrate types and differences in trophic structure among the major habitats, the micromollusks exhibit somewhat different patterns. The micromollusks are predominantly epifaunal and herbivorous throughout the lagoon, but each habitat type is distinguished in terms of species composition. Although we know little of the specific habits of the micromollusks encountered, it is tempting to relate differences in species composition to patterns of algal distribution reported by Tsuda (1973), who noted that "functional groups" of algae are distributed in recognizable patterns throughout the lagoon, with a *Schizothrix–Microcoleus* community along the shore where water movement is minimal, a *Polysiphonia–Enteromorpha–Hypnea* community near the passes where there is considerable water movement, and a *Polysiphonia–Gelidiella* community on the patch reefs. The distribution of micromollusks may also be associated with water clarity: tellinids predominate among the bivalves in the clear water areas of the lagoon, both on the patch reefs and on the lagoon floor, and different species of the diastomid genus *Obtortio* and pyramidellids characterize clear and turbid water areas respectively. It is of perhaps some interest that we have also recorded *Obtortio pupoides* (or a closely related species) in Hawaii in areas similar to those on the lagoon floor at

Fanning, that is, where there is little water movement and where sediments are silt or fine sand (Kay, unpublished). Standing crops are, in general, greater on the reef flat where there is relatively little topographical diversity than they are on the patch reefs or lagoon floor, and species diversity is in general higher in the clear water areas of the lagoon. Whatever the factors responsible for the distribution of micromollusks, it is clear from the patterns reported there is little sediment transport among lagoon reef flat, patch reef, and lagoon floor at Fanning. If, in future studies, we are able to define more clearly the factors affecting the distribution of micro mollusks, we should be able to use these animals as useful indicator organisms in reconstructing the history of lagoons.

The lagoon mollusks are distinguished from the seaward reef assemblages in both species composition and feeding types. On the seaward reefs the macrofauna is predominantly epifaunal, and is carnivorous or herbivorous; in the lagoon there is a high proportion of sessile bivalves and, hence, suspension feeders. The microfauna of the seaward reefs is predominantly faunal grazer, that of the lagoon is grazing herbivore. These differences reflect major differences in substrate and water chemistry between lagoon and seaward reefs. On the seaward reefs, extreme water clarity, wave action, and a predominantly solid substrate prevail; in the lagoon, sand and rubble predominate, water movement is minimal, and the waters of the lagoon have both higher nutrient concentrations and variable salinity (Gordon 1971; Smith and Pesret, this issue). Standing crops of micromollusks on the seaward reefs are noticeably less than in the lagoon, and species diversity is higher.

Several features of the lagoon mollusks suggest both contemporaneous fluctuations in molluscan populations and changes that have occurred in the past. The accumulations of dead shells we noted are similar to those reported by Salvat (1972) at Réao, which were attributed to a local "epidemic." We suggest that the accumulations of dead shells at Fanning were caused by local fluctuations in salinity and/or turbidity in the lagoon. The occurrence of fossil *Tridacna in situ* on various sectors of the lagoon reef flat where no living *Tridacna* now occur, and the presence of *Strombus lentiginosus*, *Philippia*, *Terebra*, etc. in fossil beds on the lagoon shore, indicate past changes in the lagoon. These changes may be associated with the closure of former passes into the lagoon and consequent changes in water clarity, coral growth, and/or changes in sea level.

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