

ASPECTS OF LIVING CORAL ASSOCIATES IN JAMAICA

ASPECTS DE LA MACRO-FAUNE ASSOCIEE AUX CORAUX VIVANTS A LA JAMAIQUE

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ABSTRACT

Qualitative and quantitative surveys of macro-infaunal associates of living corals in Jamaica revealed a number of previously unreported associations, including a new species of Lithophaga.

The mud shrimp, Upogebia operculata was found boring in Porites astreoides where mated pairs excavate ramifying chambers similar to their better-known mud burrows.

Two coral crabs, Pseudocryptochirus corallicola and P. hypostegus live in different, non-overlapping hosts. Although a single coral species (or even a single colony) may contain a number of associates of different taxa, no coral species was inhabited by both crabs. Similarly, two barnacle species, Ceratoconcha quarta and Boscia madreporarum inhabit different host species.

Lithophaga madracensis, a new, small mytilid bivalve inhabits Madracis mirabilis and M. decactis below approximately 10 m in both fore and back reef environments at Discovery Bay.

The more generalized borer, L. bisulcata has been found in 10 coral species belonging to 6 families. However, it is most common in only two corals, Stephanocoenia michelini and Siderastrea siderea. It also bores into dead bases of colonies and in coral rock. Fitness of this bivalve species in living and dead coral was examined to determine the relative advantages of the two micro-habitats. Results indicate that bivalves in living coral are more successful. Larval stages display different behaviour patterns on the two substrate types and observations of larval behaviour provide the first clues to how larvae of living coral associates handle the surface tissue layer when settling.

RESUME

Des études qualitatives et quantitatives de la macro-faune associée aux coraux vivants en Jamaïque a montré plusieurs associations non encore décrites, incluant une nouvelle espèce de Lithophaga.

La crevette de vase, Upogebia operculata perfore Porites astreoides dans lesquels les couples creusent des chambres ramifiées semblables à celles mieux connues dans la vase.

Deux crabes de coraux, Pseudocryptochirus corallicola et P. hypostegus, vivent dans des hôtes différents, non embriqués. Bien qu'une seule espèce de corail (ou même une seule colonie) puisse contenir plusieurs associés de différents taxa, il n'existe pas une espèce de corail où habitent les deux crabes. De même, deux espèces de barnacle, Ceratoconcha quarta et Boscia madreporarum habitent des espèces hôtes différentes.

Lithophaga madracensis, une nouvelle petite moule habite Madracis mirabilis et M. decactis, en dessous de 10m de profondeur environ dans les environnements d'avant et d'arrière récif à Discovery Bay.

Le perforant le plus fréquent, L. bisulcata a été trouvé dans 10 espèces de corail appartenant à 6 familles. Cependant, il est réellement commun dans seulement deux espèces, Stephanocoenia michelini et Siderastrea siderea. Il perfore aussi les bases de colonies mortes et les blocs coralliens. L'aptitude de cette espèce de bivalve à vivre dans le corail vivant et dans le corail mort est examinée pour déterminer les avantages relatifs de ces deux microhabitats. Les résultats indiquent que les bivalves dans les coraux vivants sont plus favorisés. Les stades larvaires montrent différents modes de comportement sur les deux types de substrats et les observations du comportement larvaire fournissent les premiers indices prouvant que les larves associées aux coraux vivants présentent une modification de la couche superficielle de leur tissu en s'installant.

INTRODUCTION

Fauna inhabiting live coral colonies on Caribbean reefs have been little studied. Usually only single species or taxonomic groups have been described (eg. Patton, 1967; Bacon, 1976; Shaw and Hopkins, 1977). No community studies have been detailed, like those which are available for several locations in the Indo-Pacific (Austin et al. 1980; Gotelli and Abele, 1983, etc.). In most cases it is not clear from the available literature what corals contain which associates or what type of association exists (eg. amensalism, commensalism, parasitism, etc. For an exception see Glynn, 1983). This basic information is required for an understanding of the dynamics of coral reef communities in the Caribbean and for comparison of the Caribbean with the better-known Indo-Pacific reef communities. The present study will examine some aspects of these variables of coral-associate ecology and will provide a preliminary comparison of these two reef provinces.

MATERIALS AND METHODS

Macro-infaunal associates of living corals at and near Discovery Bay, Jamaica (18° 28' N, 77° 24' W) were surveyed between December, 1982 and December, 1984 by three methods: a destructive survey, a visual survey of coral borers using quadrats and a reef-wide search for all hermatypic coral species for *in situ* examination of associates. While all macrofaunal associates in living coral were recorded these surveys are quantitative only for the crustaceans and bivalves because of the sampling methods employed. Polychaetes other than *Spirobranchus giganteus* may have been too small to be sampled without dissolving the coral skeleton (Hutchings, 1978). For a quantitative comparison of borers in living and dead coral, dead coral was also sampled for all *Lithophaga* species and *Upogebia operculata*. A living coral infaunal associate is defined as one which lives in the coral skeleton and whose aperture opens onto the living coral tissue.

Shallow East Back Reef Destructive Survey. A 120 m transect line was laid on a bearing perpendicular to the reef crest. Three living colonies, if present, of all common coral species were collected around the 20 m interval markers of the transect, at depths from 1 m to 5.6 m. At the Discovery Bay Marine Lab they were broken into small pieces with a hammer and chisel to extract the macrofaunal associates. All colonies were weighed and length and width measured. Surface area was calculated using the appropriate formula for a rectangle, circle or hemisphere, depending on colony shape.

Visual Survey of Borers. Borers were surveyed visually at 8 sites in and around Discovery Bay by laying a 1 m² quadrat end to end 30 times perpendicular to the reef slope to make a horizontal transect of 30 m². This transect was repeated at several depth intervals at the sites. In all, 26 transects of 30 m² or a total of 780 m² of reef were examined between

3 and 30 m depth. All *Lithophaga bisulcata* and *Upogebia operculata* and their hosts were recorded. The total number of borers in living coral on the reef determined by this visual census was adjusted by a correction factor to allow for holes missed during the survey. This correction factor (1.143) was calculated as a ratio of borers extracted in the East Back Reef Survey to holes counted *in situ* while collecting the colonies.

Survey of corals. The reef was exhaustively surveyed for a representative sample (minimum of 10 colonies, except for very rare species) of all hermatypic corals recorded from Jamaica by Wells and Lang (1973). Forty-two of the 49 hermatypic species, plus *Madracis formosa* were censused. Deep reef species were collected with the aid of PC-8, a two-man submersible maintained at the marine lab; all others were examined *in situ* by SCUBA diving.

Percent cover of corals was determined at 4 sites, known locally as Gorgo Heights, Arena, Columbus Park and East Back Reef, by the point transect method (Dodge, et al., 1982). A 1.5 m line marked at 10 cm intervals was thrown repeatedly over the reef and all coral species and other substrate types were recorded under approximately 4500 points. In addition, percent cover for Rio Bueno was generously supplied by Terry Hughes.

Aggression rank was determined from Lang's (1973) aggression hierarchy (1 = most dominant species). Corals with equal numbers of subordinate species were ranked equally.

Polyp diameter was estimated by measuring the distance between polyp centres. Data were taken from Zlatarski and Estalera (1982), Wells (1973) or direct measurement.

Larvae from *Lithophaga bisulata* boring into *Stephanocoenia michelini* were reared by the basic methods of Loosanoff and Davis (1963) and R. Mann (pers. comm.). They were fed *Isochrysis galbana* (Tahitian strain) for 24 days to the pediveliger stage (shell diameter approximately 350 µm). They were then offered a variety of coral species and calcium carbonate as settlement substrates. Their subsequent behaviour was observed under a dissecting microscope.

Data were analysed using regression, correlation and multiple regression analysis (Zar, 1984). All data were tested for violations of the assumptions of these procedures. Where violations occurred (usually of normality) non-parametric regressions were performed on the ranked data. Pearson Correlation Coefficient (PCC) and Spearman Correlation Coefficient (SCC) were used for parametric and non-parametric data, respectively.

RESULTS

Survey results. A list of associates and their host corals was compiled from all surveys

Table 1. List of coral associated infauna in Jamaica and their % infestation of coral hosts.

ASSOCIATE	% INFESTATION
PORIFERA	
<u>Cliona mucronata</u>	
<u>Madracis formosa</u>	?
<u>Cliona langae</u>	
<u>Porites astreoides</u>	?
<u>Cliona vermifera</u>	
<u>Montastrea annularis</u>	?
<u>Cliona laticavicola</u>	
<u>Montastrea annularis</u>	?
<u>Agaricia agaricites</u>	?
<u>Cliona janatrix</u>	
<u>Montastrea annularis</u>	?
<u>Agaricia agaricites</u>	?
<u>Siphonodictyon sp.</u>	
<u>Montastrea annularis</u>	?
sp. X	
<u>Montastrea annularis</u>	?
<u>Agaricia agaricites</u>	?
SIPUNCULA	
<u>Lithacrosiphon alticonus</u>	
<u>Por. es astreoides</u>	4
<u>Phascolosoma perlucens</u>	
<u>Porites branneri</u>	20
sp. ?	
<u>Porites furcata</u>	4
sp. ?	
<u>Agaricia agaricites</u>	3
POLYCHAETA	
<u>Spirobranchus giganteus</u>	
<u>Acropora palmata</u>	9
<u>Siderastrea siderea</u>	5
<u>Porites astreoides</u>	16
<u>Porites branneri</u>	20
<u>Porites furcata</u>	4
<u>Diploria strigosa</u>	14
<u>Montastrea annularis</u>	4
BIVALVIA	
<u>Lithophaga bisulata</u>	
<u>Stephanocoenia michelini</u>	20
<u>Agaricia agaricites</u>	13
<u>Siderastrea siderea</u>	43
<u>Siderastrea radians</u>	9
<u>Diploria strigosa</u>	7
<u>Lithophaga sp.</u>	
<u>Madracis decactis</u>	80
<u>Madracis mirabilis</u>	80
<u>Madracis formosa</u>	?
CIRRIPEDIA	
<u>Ceratoconcha quarta</u>	
<u>Siderastrea siderea</u>	62
<u>Siderastrea radians</u>	64
<u>Porites astreoides</u>	56
<u>Porites branneri</u>	40
<u>Porites furcata</u>	9
<u>Montastrea annularis</u>	12
<u>Boscia madreporarum</u>	
<u>Stephanocoenia michelini</u>	10
<u>Madracis formosa</u>	?
<u>Agaricia agaricites</u>	77
<u>Agaricia grahamae</u>	?
<u>Helloseris cucullata</u>	10
<u>Dichocoenia stokesi</u>	9

DECAPODA

<u>Pseudocryptochirus corallicola</u>	
<u>Stephanocoenia michelini</u>	10
<u>Diploria clivosa</u>	56
<u>Diploria strigosa</u>	7
<u>Manicina areolata</u>	50
<u>Montastrea annularis</u>	38
<u>Isophyllia sinuosa</u>	50
<u>Pseudocryptochirus hypostegus</u>	
<u>Agaricia agaricites</u>	20
<u>Agaricia lamarcki</u>	70
<u>Agaricia grahamae</u>	?
<u>Siderastrea siderea</u>	10
<u>Domecia acanthophora</u>	
<u>Acropora palmata</u>	73
<u>Upogebia operculata</u>	
<u>Porites astreoides</u>	12

(Table 1). It includes some new and interesting additions to the coral-associated faunal assemblage.

An undescribed species of Lithophaga (Scott, submitted) is common in Madracis decactis and M. mirabilis. It also occurred in submarine collections of M. formosa from 49 m depth.

Upogebia operculata, of the normally mud-burrowing family Upogebidae, was found boring almost exclusively in Porites astreoides. Mated pairs lived in ramifying tunnels. Boring appeared to be mechanical or mainly mechanical with reinforced chelae. Boreholes are lined with fine organic mud and CaCO₃ particles.

Sipunculans were found boring in living corals, especially species of Porites. Although common in dead corals and rubble, this is the first record of the group in association with living coral species.

Two species of barnacle, Ceratoconcha quarta and Boscia madreporarum, were common at Discovery Bay. They were never found together in the same host (species or even family). C. quarta was most common in Porites astreoides; B. madreporarum in Agaricia agaricites. Similarly, two gall crab species, Pseudocryptochirus corallicola and P. hypostegus did not have overlapping host species or families. P. corallicola primarily inhabited faviids; P. hypostegus was more abundant in agariciids. A third crab, Domecia acanthophora, lived in Acropora palmata.

The total number of associates was not correlated with the size of colony determined by surface area or weight for 3 of the 4 common corals in the East Back Reef, P. astreoides, Siderastrea siderea and Montastrea annularis. The exception was A. agaricites ($P = 0.043$ and 0.039 , $r^2 = 0.22$ and 0.23 for surface area and weight, respectively). The number of associates/cm² was also unrelated to surface area of colony at $P < 0.05$, except for A. agaricites, with which associate abundance was negatively correlated ($P = 0.03$, $r^2 = 0.25$). The number of associates per kg was similarly unrelated to colony size, except again with A. agaricites, in which number/kg decreased with

increase in coral weight ($P = 0.02$, $r^2 = 0.29$). Although they are significant, only a small amount of variance is explained by these relationships between size of Agaricia agaricites colony and abundance of associates.

There was no statistically discernible relationship between abundance of associates and depth in any of the surveys. The percent of corals containing all associates decreased insignificantly with depth for all groups combined ($P = 0.24$, $r^2 = 0.41$) as well as for barnacles ($P = 0.11$, $r^2 = 0.62$), crabs ($P = 0.49$, $r^2 = 0.17$) and bivalves ($P = 0.98$, $r^2 = 0.00$) alone. The second survey (of borers) also indicated their abundance was not related to depth in the 3 to 30 m range studied ($P = 0.21$, $r^2 = 0.36$, slope positive).

Associates occurred more frequently in the more common, less aggressive corals with smaller polyps. The percent of corals containing associates was statistically correlated with coral abundance ($SCC = 0.432$, $P = 0.005$, $n = 41$) and inversely correlated with coral aggression rank ($SCC = -0.458$, $P = 0.004$, $n = 38$) and polyp size ($SCC = -0.463$, $P = 0.003$, $n = 38$). Non-parametric multiple regression of associate abundance vs. the three variables (with interaction effects) was also significant ($P = 0.04$, $r^2 = 0.670$).

Larval experiments. Competent pediveligers of approximately 350 μm showed no reaction to contact with tissues of the most frequent hosts Stephanocoenia michelini and Siderastrea siderea. Once on the living coral surface the pediveligers extended the foot for short periods of exploration (approx. 30 s to 1 min) followed by somewhat longer inactive periods. However, the pediveliger retracted the foot violently when exposed to other coral species, eg. Scolymia lacerata, Agaricia agaricites and Favia fragum. When closed, or nearly closed, the bivalves were moved along the coral surface by coral ciliary currents and/or by its own velum. With the valves tightly shut the larvae were undamaged by contact with any coral species, although Artemia nauplii offered to the same colonies were quickly paralysed and ingested.

In the case of most of the corals offered as substrate, the larvae either swam away from contact with the living surface or, with their valves tightly closed, they were caught up in mucus strands and sloughed off the edge of the colony. However, on S. michelini, approximately 78% of the time the bivalves were ingested. These corals did not ingest empty valves or tightly closed living larvae. The veligers which were ingested retained the valves slightly agape, with occasional foot contact with the tissue. Veligers less than 300 μm , not yet competent to settle were digested by the coral and the valves ejected within 24 - 48 hours. Pediveligers of other bivalve species were also digested and ejected within approximately 48 - 72 hours. Lithophaga bisulcata pediveligers were not eaten, but survived digestion and over a period of 52 days grew inside the coral polyp. During this period

the presence of the larvae could not be detected by inspection of the coral surface. The bivalve lay wedged between sclero-septa, creating no lump in the flattened oral disc, even when the coral was fully retracted. After 52 days the bivalve had not yet begun to bore into the skeleton of S. michelini.

DISCUSSION

It has often been supposed, although never tested, (eg. Newman and Ladd, 1974; Castro, 1976) that living coral associates have larval stages adapted to settling on living coral tissue. It has never been suggested how they might accomplish this. It is now clear that, at least in the case of Lithophaga bisulcata they are ingested by the polyps and survive coelenteric digestion much as a parasite does. Such a finding is not completely surprising since it is known that Fungiacava eilatensis lives its entire life with the siphons opening into the coelenteron of its host (Goreau et al., 1970). S. michelini was often observed with its mouth slightly open; such a posture would allow the intracoelenteric bivalve to pump water from the external environment.

Behaviour of the pediveliger on the host appeared to indicate a recognition of nematocysts and/or the host tissue. Almost all corals were explored, however briefly, usually with the foot but occasionally also with the mantle. Corals generally ingested the bivalve when the valves were open slightly but rejected it when they were tightly shut. Once ingested the bivalve disappeared from surface view and seemed to remain in that position for the 52 days of the experiment. Since it did not begin to dissolve the skeleton, it may have been waiting for the coral to secrete skeleton over it. Alternatively, the bivalve may have been still too small at 400 μm to require enlarging the hole and would have begun to bore if the experiment had run for a longer period.

The mode of larval settlement may also explain the correlations of associates with some characteristics of the host. Large polyped corals surveyed did not contain associates. The distance from the oral disc to base of the polyp may be unfavourable for sufficient water exchange, and the sclero-septa may be too widely spaced for the settling larva to gain a purchase. A histogram of % coral species containing associates vs. polyp size (Figure 1) shows that the spectrum of corals containing barnacles have a smaller mean size (2.91) than those containing crabs (4.50); this may be directly related to differences in sizes of the settlement stages of the two groups. Bivalves are intermediate (3.16), but the much larger L. bisulcata live in hosts with larger polyps (3.70) than the tiny L. sp. (2.25), which presumably has smaller eggs and larvae.

The causes, if any, of an inverse correlation between aggression rank and % corals with associates are unclear. It is not yet understood how the aggression hierarchy is maintained among corals. Polyp size may be

involved, as there is a strong correlation between aggression rank and polyp size (SCC = 0.788, P = 0.0001, n = 35). Examination of size of mesenterial filaments and nematocyst type, size and concentration of all coral species may provide clues. Although scleractinians have a reduced number of nematocyst types compared with other cnidarian groups, marked differences were noted in the reaction of bivalve larvae to living tissue of different coral species.

Only two associates were host specific. *Domecia acanthophora* occurred only in *Acropora palmata*. However, it also occurs epifaunally in other coral species (Patton, 1967; Bak et al., 1982). *Upogebia operculata* was found only in *Porites astreoides* although it apparently occurs in other species at other Caribbean localities (Kleemann, 1984). It is not an obligate associate since *U. operculata* also lives in coral rubble and rock. Other associates tend to live in the locally most abundant species within their potential host assemblage. This may be the result of simple statistical probability of finding a given species during the settlement period. Comparison with other Caribbean localities could be used to test this hypothesis.

Lack of overlap of host species between closely related associates appears to be unique to the Caribbean. Indo-Pacific shrimps, crabs and barnacles, in contrast, frequently have overlapping hosts (Bruce, 1976; Castro, 1976; Newman, et al., 1976). The greater age of the Indo-Pacific reef community has permitted extensive speciation of reef associates with specializations for coral inhabitation which apparently do not include host segregation (eg. trophic resource allocation). The Caribbean associates are less specialized. The barnacles, for example, are plesiomorphic; there are no derived forms and no species are modified to feed on coral tissue or mucus (Ross and Newman, 1969; Newman and Ladd, 1974; Newman et al., 1976). Among the decapods, no shrimps and only 3 of 63 obligate coral commensal crab species live in the tropical Atlantic and, of these, the two hapalocarcinids are less host specific than their Pacific counterparts (Bruce, 1976; Castro, 1976).

The families of corals most commonly inhabited by associates differ in the Pacific and the Caribbean (Table 2). Siderastreidae and Agariciidae, two relatively unimportant Indo-Pacific families, contain the most associates in Jamaica. Pocilloporids are important in both regions but faviids, which are extremely important Indo-Pacific hosts, contain relatively few associates in the present Caribbean survey.

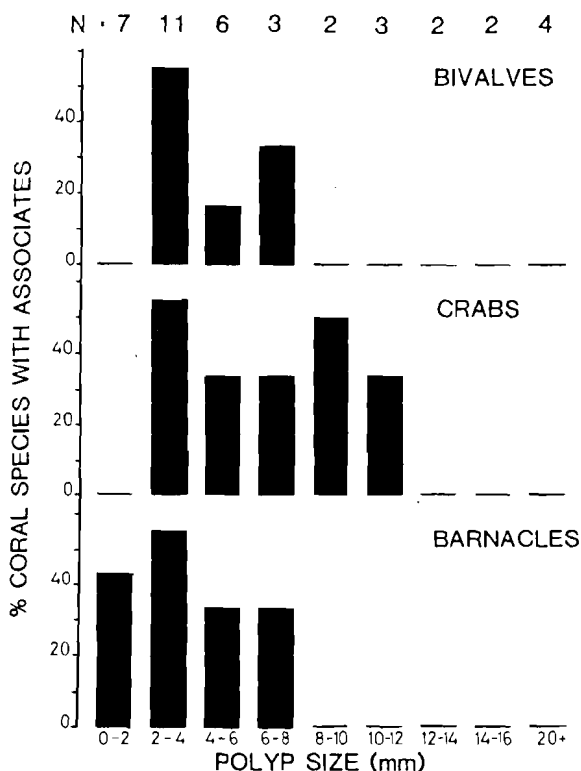


Figure 1. Per cent of coral species containing each of the three most common associate groups vs. polyp size. N = number of coral species surveyed with polyps in the size range indicated below.

Table 2. List of Caribbean coral families and the percent of those corals inhabited by associates.

FAMILY	BARNACLES	CRABS	UPOGEBIA	LITHOPHAGA	ALL ASSOC.
SIDERASTREIDAE	63	6	0	31	69
AGARICIIDAE	44	24	0	7	62
POCILLOPORIDAE	0	0	0	53	53
ASTROCOENIIDAE	10	10	0	40	50
ACROPORIDAE	0	38	0	0	38
PORITIDAE	26	0	4	0	27
FAVIDAE	3	16	0	1	18
MUSSIDAE	0	8	0	0	8
MEANDRINIDAE	3	0	0	0	3

CONCLUSION

Macro-infaunal associates of corals in Jamaica include seven species of sponges; at least two sipunculans; the polychaete, Spirobranchus giganteus; two species of Lithophaga; two barnacles; three crabs and one thalassinid. Distribution of the associates was correlated with coral abundance and inversely correlated with aggression rank and polyp size, all of which may affect the settlement success of larval stages. Distribution was not strongly related to depth or coral colony size. It has been demonstrated that L. bisulcata larvae do land and settle on the living coral tissue where they are ingested but not digested.

Associate species which are unspecialized and endemic to the Caribbean; differences in the families of coral which are important hosts; and in host specificity of the associates indicate large differences in the evolutionary history of associations in the two reef provinces.

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