

Relative roles of bioerosion and typhoon-induced disturbance on the dynamics of a high latitude scleractinian coral community

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Located at 22°N on the northern shore of the South China Sea, Hong Kong experiences a seasonal, monsoonal climate and its resident scleractinian corals, comprising some 50 species, live here at the limit of their ranges. Summers are hot and wet, winters cold and dry and this study was initiated to determine the effects of bioerosion and periodic episodes of strong wave action on coral death and beaching. Coral rubble washed up on Telecom Bay Beach in the Cape d'Aguilar Marine Reserve was collected every month from January 1996 until December 1997, inclusive. Quantities were greatest after typhoons and storms, with the average monthly weight of recently-living corals accounting for approximately 0.007%, by weight, of the total live coral in the bay. Seventeen species of Mollusca were recorded from within the skeletons of this rubble and included a new record for Hong Kong, *Anchromasa yoshimurai* (Pholadidae). Species of *Lithophaga* dominated, with highest mean abundances recorded from within *Goniastrea aspera*, the most abundant living coral in the bay and from within the heaviest fragments. The overall incidence of borers was, however, low although it appears that dead coral borers, notably the basally boring *Lithophaga lima*, act to weaken coral attachment resulting in dislodgement and beaching during and after storms. At this relatively unperturbed site, therefore, the significance of borers in weakening coral attachment with subsequent detachment and beaching during and after storms, respectively, is low, a situation also seen elsewhere.

INTRODUCTION

Biological destruction of coral reefs is caused by three main groups of organisms, i.e. grazers, etchers and borers (Hutchings, 1986). Infaunal borers comprise sponges, sipunculans, polychaetes, barnacles and molluscs. Representatives of all five groups have been observed to bore into the corals in the Cape d'Aguilar Marine Reserve, Hong Kong, but the most obvious taxa identified in this study were the bivalves. The advantage of studying this group is the ability to be able to identify their boreholes (Mokady et al., 1997) and, often, the species of borer involved in any washed up pieces of coral rubble, not only by the shape of their burrows (Bromley, 1978) but also by the presence of empty shells or, sometimes, living individuals. This is not so with polychaetes and cirripedes, for example. Six bivalve families have representatives which are coral borers, i.e. Mytilidae (Lithophaginae), Gastrochaenidae, Petricolidae, Pholadidae, Clavagellidae and Tridacnidae. Species of the Lithophaginae and Gastrochaenidae are particularly important agents in the ecology and bioerosion of reefs (Morton, 1990). Most boring bivalves inhabit inert substrata, including the dead parts of corals, but some, especially members of the Lithophaginae, have the ability to penetrate living coral tissue (Scott, 1980) and some species are restricted to this habitat (Kleeman, 1980).

The ability to bore live corals is rare within the Bivalvia and Kleeman (1980) considered that with the exception of species of *Fungiacava*, all such borers, as far as

is known, belong to the genus *Lithophaga*. Studies of the Lithophaginae, Pholadidae and Tridacnidae have suggested an intimate relationship with living corals (Morton, 1990) and this has recently been substantiated by Mokady et al. (1997). Boring bivalves have mainly been studied qualitatively (Otter, 1937; Yonge, 1963; Kleeman, 1980). Highsmith (1980a), however, showed much geographic variation in bivalve densities in museum collection corals and ranked them in the sequence: eastern Pacific > western Atlantic > Indian Ocean > western Pacific, suggesting that this could be correlated with global patterns of primary productivity. The validity of these data was, however, questioned by Loya (1982) for the Gulf of Eilat where field densities were much higher than those recorded from museum specimens. Correlations between productivity and bioerosion have also been documented in the field by Bergman (1983), Glynn & Wellington (1983), Rose & Risk (1985) and Hallock et al. (1988).

Studies by Stearn & Scoffin (1977), Davies (1983), Hubbard et al. (1985) and Hutchings (1986) described the importance of bioerosion to sediment production and the physical growth of reef environments. Scoffin et al. (1980), Hallock & Schlager (1986) and Hutchings (1986) describe bioerosion as one of the important factors controlling rates of reef accretion. Coral reef structure, both ancient and modern, is a result of the interaction between growth and destruction. Along with physical erosion, bioerosion creates newly available substrata for colonisation by sedentary species such as corals

(Sammarco, 1980, 1982) and the burrows create habitats for non-boring species (Morton et al., 1991) which may be major contributors to the recycling of nutrients on reefs (Hutchings, 1983). Connell (1978) postulated that such disturbances are important in maintaining species diversity on reefs. Conversely, if bioerosion consistently exceeds growth, then the reef and its framework will be destroyed (Stearns & Scoffin, 1977; Ginsburg, 1983).

The extent of internal bioerosion in corals has been shown to be a prime control of a colony's ability to resist wave shock (Hein & Risk, 1975; Highsmith, 1980b, 1981a, 1982; Highsmith et al., 1983; Tunnicliffe, 1981, 1983; Sammarco & Risk, 1990).

It was suggested by Choi (1982) that the entire crypto-biotic coral community, including both borers and nestlers, can serve as sensitive indicators of environmental stress and that cores through such communities can provide information on environmental conditions operating over time. Rates of bioerosion, both internal and external, vary in space and time in association with a number of biotic and abiotic factors. These include events such as crown-of-thorns starfish predation (Endean et al., 1988), coral bleaching (Glynn, 1988), organic pollution/eutrophication (Rose & Risk, 1985; Cuet et al., 1988; Hallock et al., 1988), fish grazing (White, 1980; Risk & Sammarco, 1982; Sammarco et al., 1986, 1987) and turbidity and rates of sedimentation (Tudhope & Risk, 1985; Acevedo & Morelock, 1988). These have all been described as threats to reefs and which kill corals and enhance rates of bioerosion. An understanding of the processes of bioerosion on dead coral has, according to Kiene & Hutchings (1994), become more important recently with the increasing number of reports of corals killed by disturbances in reef environments. Coral reef substrata do not generally become heavily bored until the veneer of living tissue dies (McCloskey, 1970). Studies documenting rates of boring and grazing in a variety of reef environments are crucial to predictions regarding the consequences of widespread mortality on their biological and geological structure (Kiene & Hutchings, 1994).

It is well known that wave energy is one of the most important factors that controls coral growth, reef development and coral island formation (Yonge, 1940; Adey, 1978; Dollar, 1982), both directly and through its influence on biological interactions. Coral reefs are reported to be affected by physical forces, such as storm surges and tsunami's, which dislodge pieces of reef framework of various sizes (Sammarco, 1996). Coral reefs are also influenced by the processes of bioerosion, which often weaken the skeletal substratum and make it more susceptible to chemical erosion and physical disturbance, with, as noted earlier, the reverse also being true (Sammarco, 1996).

The effects of tropical storm and hurricane-generated waves on the geomorphology of reefs have been documented (Maragos et al., 1973; Stoddart, 1974; Hernandez-Avila et al., 1977; Bradbury & Young, 1981; Woodley et al., 1981; Fenner, 1991; Rogers et al., 1991; Blair et al., 1994). Dollar (1982) described physical disturbance from waves as the most significant factor determining the structure of coral reef communities in Hawaii, with severe, infrequent, storms causing massive mortality to all coral species, thus obliterating the former pattern of community structure. Few quantitative studies of hurri-

cane-produced coral damage have, however, been reported upon (Woodley et al., 1981; Rogers et al., 1982; Mah & Stearn, 1986; Blair et al., 1994). Hurricanes, depending on their intensity and proximity to a reef, have been shown to inflict a wide range of damage to coral communities. Relatively minor damage to reef populations has been recorded, with coral damage being patchy after the strongest hurricane on record in the western hemisphere, Hurricane Gilbert, passed over Cozumel, Mexico (Fenner, 1991). Minor damage was also recorded for Hurricanes David and Frederic (1979) and Hugo (1989) by Rodgers et al. (1982, 1991). Severe damage has, however, also been recorded (Highsmith et al., 1980; Woodley et al., 1981; Harmelin-Vivien & Laborute, 1986). Woodley et al. (1981) reported that waves produced by Hurricane Allen, and the dislodged material that they carried, devastated the shallow reefs in Discovery Bay, Jamaica. Stoddart (1974) studied the effects of Hurricane Hattie in Belize and Blair et al. (1994) studied Hurricane Andrew's effects in Florida. Both showed that damage was patchy, being severe in some areas and moderate to mild in others. Glynn et al. (1964) and Woodley et al., (1981) reported that wave surge during hurricanes was greater in shallow than deep water, thus, generally, producing greater damage in the former, with branching coral species tending to suffer more destruction than both encrusting and massive species (Woodley et al. 1981).

This study, therefore, examined beached coral heads and pieces on a beach adjoining a coral community within the Cape d'Aguilar Marine Reserve in Hong Kong which was established in July 1996 (Morton, 1998). It attempts to estimate the effect of borers, mainly species of *Lithophaga*, and storm events upon the resident corals. We also wished to determine the degree of congruence between these biological and physical processes and, thereby, to establish a baseline figure for such impacts on what is considered to be a generally locally unperturbed habitat and, finally, therefore, permit comparisons with locally perturbed communities.

MATERIALS AND METHODS

Survey site

The inner, north-east, end of Telecom Bay, within the Cape d'Aguilar Marine Reserve, consists of a 380 m² cobble and sand beach, derived from local rock formations (Figure 1). Telecom Bay is approximately 9000 m² and relatively shallow, with a maximum depth of ~9 m chart datum (CD) at its southerly end before shelving down to ~22 m CD outside the bay area. Although wave heights are on average, one metre higher in winter than in summer in Hong Kong, typhoons can occur during the latter months, i.e. between June and September (Morton, 1982), and produce waves 7% of which have heights of between 3 and 7 m above normal (Li & Li, 1992). It is these waves that have the potential to impact any corals within the otherwise protected marine reserve. Telecom Bay is generally sheltered by the island of Kau Pei Chau and it is thus affected only by strong wave action from the south-west and which occurs in summer when the prevailing wind direction is from this quadrant (Morton & Harper, 1995) and, especially, during storm and

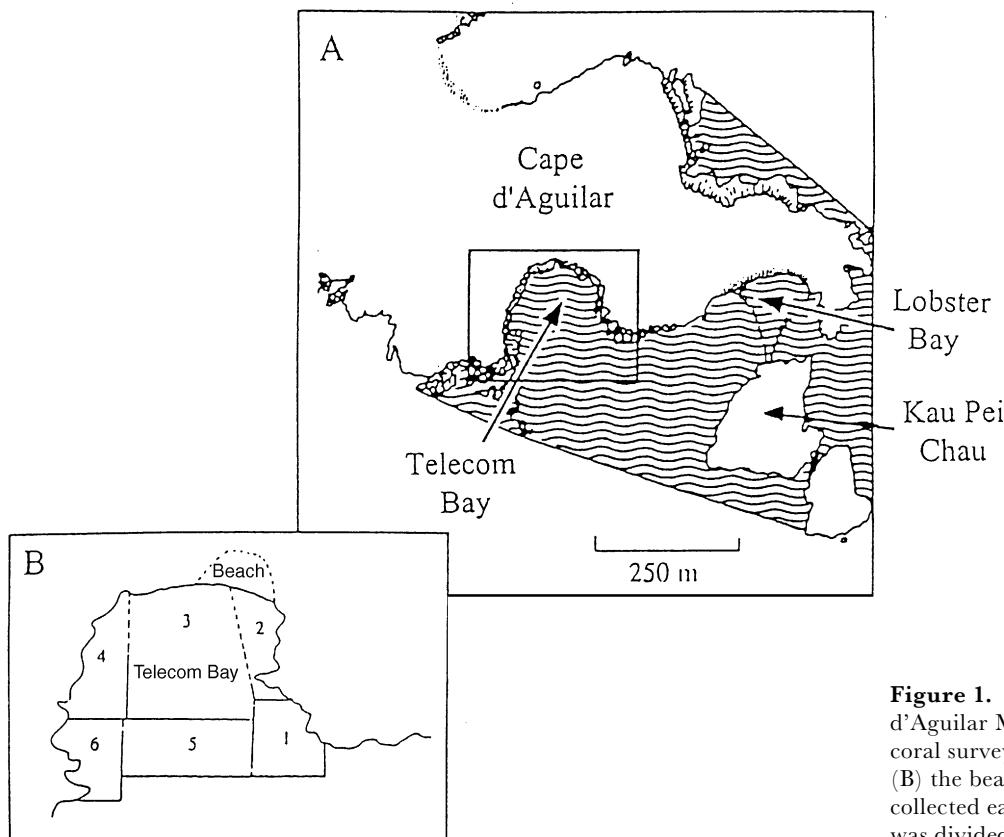


Figure 1. (A) A map of the Cape d'Aguilar Marine Reserve showing the coral survey site in Telecom Bay; and (B) the beach where the corals were collected each month and how the bay was divided into six survey areas.

typhoon events (Royal Observatory 1996, 1997). It is highly unlikely that coral rubble could be transplanted to the bay from elsewhere and, accordingly, that washed up on Telecom Bay Beach is thus assumed to be representative of those species which once lived within it. The Cape d'Aguilar Marine Reserve is described in greater detail by Morton & Harper (1995).

Quantification of live coral cover in Telecom Bay

An optimized, stratified-random, sampling technique was adopted to survey the bay (McCormick & Choat, 1987). The abundance of corals within the present study area was influenced by habitat structure (Clark, 1997, 1998) and, thus, a stratification technique was used to sample each area independently and remove, as much as possible, the variation due to differences among habitats. In Telecom Bay, within the Cape d'Aguilar Marine Reserve, six discrete units were decided on for surveying due to their physical and biological characteristics. Section 1 was the south-easterly component of the bay which consisted of a steep bedrock slope; section 2 in the north-east part of the bay was a shallow bedrock and boulder slope; section 3 was the northerly mid-section with a shallow sandy substratum covered with numerous boulders; section 4 was the north-west side of the bay which was a shallow bedrock and boulder slope; section 5 to the south of the middle area of Telecom Bay consisted of a deeper area of sand with fewer boulders; section 6 was a steep bedrock slope in the south-western part of the bay (Figure 1).

The area of each, approximately rectangular, section was measured using a fibreglass tape-measure. The

optimum transect length and the number of transects were determined from cumulative species curves for each area (Figure 2). The boundaries chosen for each section were tested for large differences in densities between areas and small variances within populations. This gives an indication of accuracy of choice with regard to the different areas of habitat. In each section (1-6), three replicate 3×20 m transect tapes were laid and the coral colonies within 1 m of each side of these lines were recorded to species level and their maximum diameters (a) and diameters perpendicular to this (b) measured. These results were used to calculate the surface area of each colony and, hence, to estimate the total coral cover of each species within Telecom Bay.

Collection and treatment of coral rubble

Collections of all the, visible, pieces of coral rubble, deposited on Telecom Bay Beach, were carried out monthly, always around the 24th day, at low tide from January 1996 to December 1997, inclusive. A 30-min search time was allocated for each survey. Additional collections were made on 8 September 1996 and 3 August 1997, immediately after a near miss by Typhoon Sally and a direct hit on Hong Kong by Typhoon Victor, in these, respective, years. In the laboratory, the corals were sorted to the most detailed taxonomic category, i.e. to genus or species, using Swire Institute of Marine Science museum specimens for reference. Each coral was weighed on a KCI 38–50 counting scale to the nearest 10 g and examined for the presence of molluscan boreholes. The coral pieces were later divided into six weight groupings, to make the identification of trends easier. Such groupings

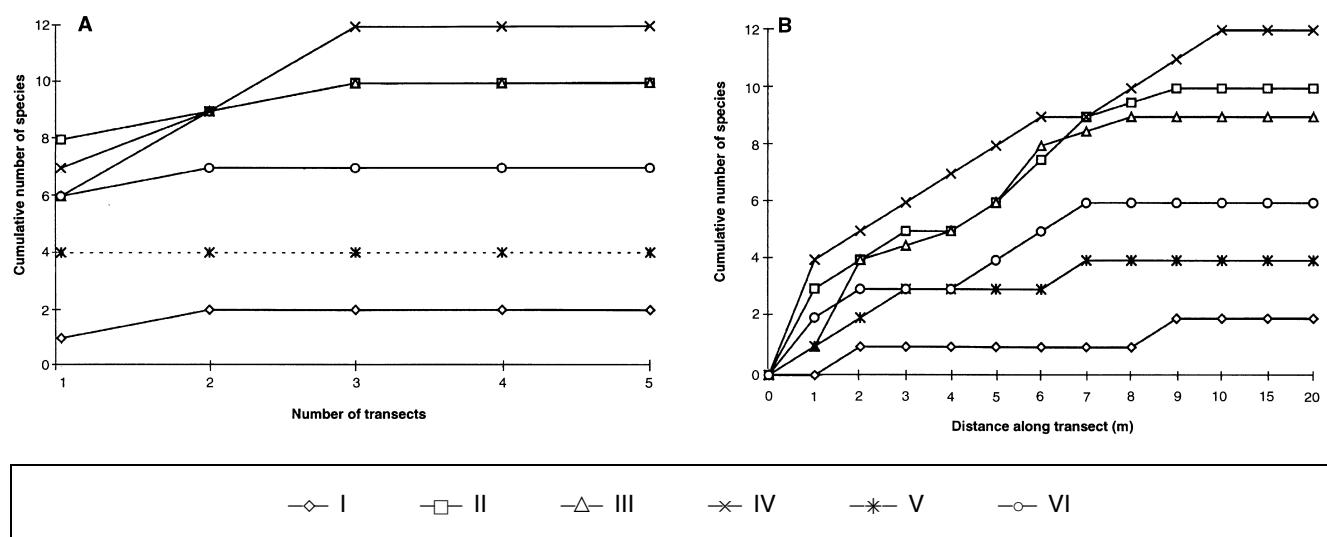


Figure 2. Cumulative species curves for six areas within Telecom Bay, in the Cape d'Aguilar Marine Reserve (I–VI). (A) Cumulative number of species recorded with respect to distance along a transect (m); and (B) cumulative number of species recorded with respect to number of transects surveyed. Data were obtained in March 1997.

were 10–49, 50–99, 100–199, 200–499, 500–999 and >1000 g. The numbers of boreholes in each fragment were recorded and the coral pieces broken open using a hammer and chisel to remove any borers from the skeleton. These molluscs were then identified using taxonomic literature (Morton, 1977; 1985, 1990; Scott, 1980; Morton & Scott, 1980; Kleeman, 1980, 1984; Lui, 1988) and measured with SPI calipers along either their greatest lengths (bivalves) or heights (gastropods), to the nearest 1 mm.

The surface area of each piece of dead coral rubble was calculated from measurements taken of the longest diameter (a) and the diameter perpendicular to this (b), using the equation:

$$\pi(\frac{1}{2}(a + b)/2)^2 \quad (1)$$

Plots were then made for each coral species of the weight of the piece of coral rubble against the surface area (Figure 4). This allowed estimates to be made as to the percentage of coral washed up on the beach compared with the amount of live coral cover in the bay, also calculated using surface areas.

Statistics

Data analyses were performed using SPSS software for Windows (SPSS Inc., 1996). Data were tested for normality using the Kolmogorov–Smirnov test (Zar, 1996) and for homogeneity of variances by Bartlett's test (Bartlett, 1937), both at the 0.05 level of significance. To test the null hypothesis that there were no differences between both seasons and coral species for the weights of coral washed up on Telecom Bay Beach, a two-way ANOVA was conducted on the log transformed data. To test the null hypothesis that there were no differences between wind direction and speed on the weights of coral rubble washed up on Telecom Bay beach, a two-way ANOVA was conducted on the log transformed data. A χ^2 -test was performed on mollusc species counts to test

the null hypothesis that there were no differences in species distribution between coral species. Where differences were detected, SNK tests and Duncan's tests were performed to identify where the differences lay (Sokal & Rohlf, 1969; Zar, 1996).

RESULTS

Telecom Bay live coral cover

Fourteen genera of live corals belonging to seven families, the Poritidae, Agariciidae, Acroporidae, Thamnasteriidae, Faviidae, Dendrophylliidae and Astrocoeniidae were recorded from within Telecom Bay during this research. Their ranking, in terms of surface area (cm^2), is illustrated in Figure 3A. *Platygyra* spp. was recorded to have the greatest surface area ($2,383,482 \text{ cm}^2$) followed, in decreasing order, by *Favites* spp. ($1,107,420 \text{ cm}^2$), *Favia* spp. ($395,430 \text{ cm}^2$), *Porites* spp. ($355,507 \text{ cm}^2$), *Goniastrea* spp. ($186,148 \text{ cm}^2$), *Psammocora* spp. ($182,855 \text{ cm}^2$), *Turbinaria* spp. ($169,570 \text{ cm}^2$), *Plesiastrea* sp. ($139,544 \text{ cm}^2$), *Montipora* sp. ($84,852 \text{ cm}^2$), *Cyphastrea* spp. ($84,384 \text{ cm}^2$), *Hydnophora* sp. ($68,584 \text{ cm}^2$), *Stylocoeniella* sp. ($15,276 \text{ cm}^2$), *Pavona* sp. (6135 cm^2) and, finally, *Acropora* spp. (412 cm^2).

Table 1A shows the results used to estimate live coral cover as reported in Figure 3A, including the actual area of each of the six sections surveyed within Telecom Bay (Figure 1) along with a description of each of the areas and the totals for Telecom Bay as a whole. The total area surveyed within Telecom Bay was $88,200,000 \text{ cm}^2$. This contained 470 colonies of coral belonging to 14 species. The mean coral cover in each 120 m^2 was recorded as $617,787 \pm 92,573 \text{ cm}^2$, the percentage cover was 0.417% and the species diversity (H') was calculated as 2.897.

The area with the least mean coral cover 120 m^{-2} ($2763 \pm 1071 \text{ cm}^2$), number of colonies (2), number of species (2) and percentage cover (0.0863%) was section 1 which was also the smallest ($3,200,000 \text{ cm}^2$). The second smallest area ($7,000,000 \text{ cm}^2$), section 6, had the second lowest mean coral cover 120 m^{-2} ($9896 \pm 986 \text{ cm}^2$) and

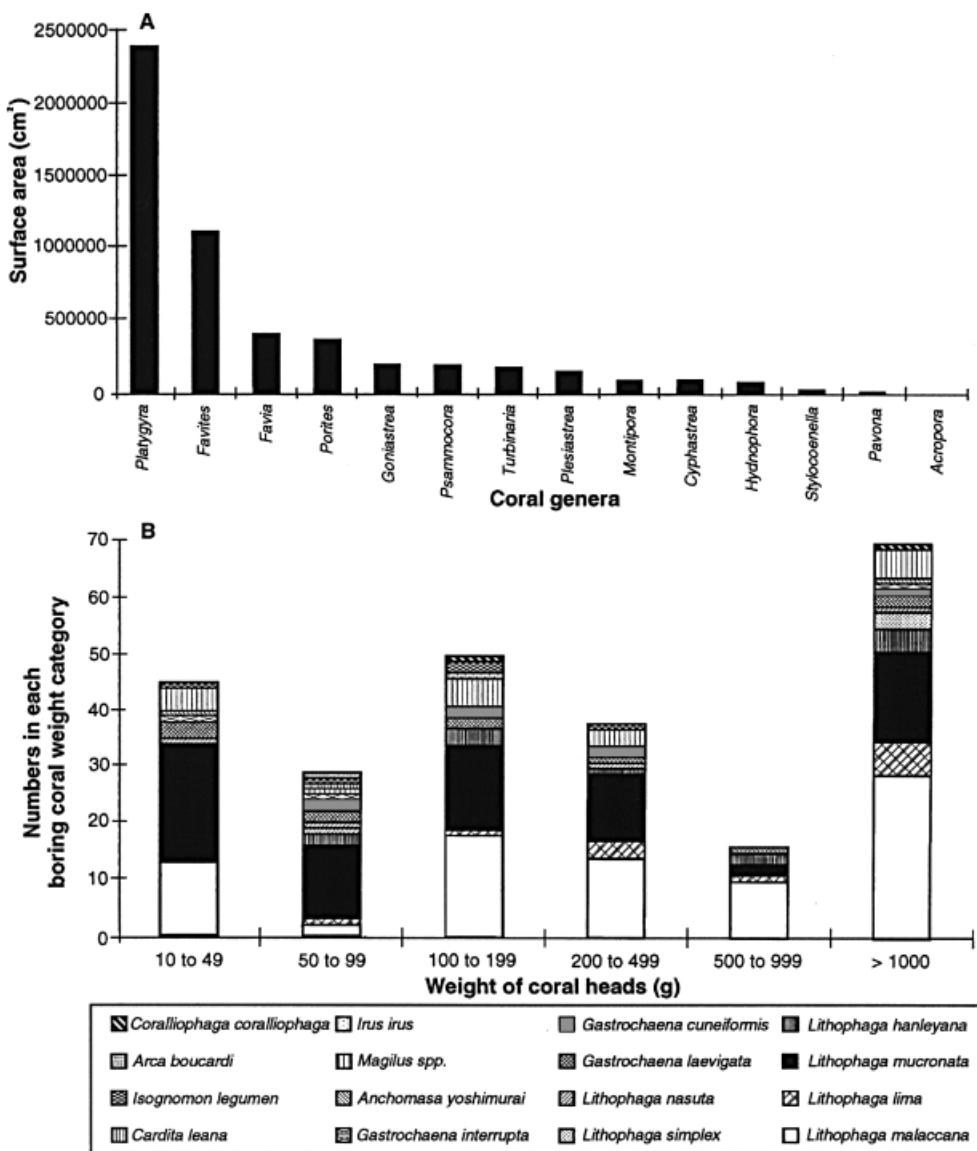


Figure 3. (A) Estimation of total surface area of live coral recorded from within Telecom Bay; and (B) number of molluscs recorded from different weight categories of the pieces of dead coral collected. Dead coral pieces were collected from Telecom Bay Beach between January 1996 and December 1997, inclusive. Estimates of live coral cover were calculated by recording coral cover along nine transects, (length=20 m, width=2 m), in each of six areas within the bay and extrapolating the results to the actual area of each of the six sections. Data for estimates of live coral cover were collected between March and May 1997.

number of colonies (27), a low species count (7) and percentage cover (0.141%). Sections 2, 4 and 5 were similar in size (15,000,000, 15,000,000 and 18,000,000, respectively), with the largest area being section 3 (30,000,000 cm²). The greatest mean coral cover 120 m⁻² was recorded from section 2 (247,564 ± 923 cm²), followed by section 3 (48,741 ± 892 cm²), section 4 (37,124 ± 1867 cm²) and section 5 (24,632 ± 1218 cm²). Species numbers were maximum in section 4 (12) followed by sections 2 and 3 (both with 10) and section 5 (4). Colony abundance was greatest in section 2 (171), with 103 colonies recorded from section 3, 92 colonies from section 5 and 75 colonies from section 4. Percentage cover was again highest in section 2 (1.650%), with low cover recorded from the other sections, i.e. 0.248% in section 4, 0.163% in section 3 and 0.137% in section 5. Species diversity (H') was lowest in sections 3, 5 and 1 (0.383, 0.329 and 0.680, respectively),

and highest in sections 2 and 4 (3.800 and 3.129, respectively) with an intermediate figure result recorded from section 6 (2.595).

Table 1B shows the total weight of live coral in Telecom Bay estimated by extrapolating the data for weight and surface area measurements of coral rubble washed up on Telecom Bay Beach as recorded in Figure 4. *Goniastrea* spp. rubble accounted for the largest percentage, approximately 14.04%, by weight of the total live coral in the bay, followed by *Cyphastrea/Plesiastrea* spp. (4.92%), *Turbinaria* spp. (1.80%), *Favia* sp. (1.57%), *Favites* spp. (0.37%), *Porites* spp. (0.26%), *Psammocora* spp. (0.18%) and, finally, *Platygyra* sp. (0.03%), making a total of 23.07%. The average monthly quantity of coral rubble washed up as a percentage (and range) of the total live coral in the bay was 0.585 ± 0.94%, (range 0.01–3.68%) for *Goniastrea* spp., 0.21 ± 0.38% (0–1.43%) for *Cyphastrea/Plesiastrea* spp.,

Table 1. A, descriptions of the six sections (1–6) in Telecom Bay, Cape d'Aguilar, surveyed between March and May 1997; and B, estimations of the weights of live coral recorded from within Telecom Bay and the weight of all the coral rubble and of the recently living coral rubble, washed up on Telecom Bay Beach as a percentage of the total live coral. Data were collected monthly from Telecom Bay Beach between January 1996 and December 1997, inclusive. Recently living coral rubble was identified by the presence of tissue on the coral skeleton.

A							
Area	1	2	3	4	5	6	Total
Size (cm ²)	3200000	15000000	30000000	15000000	18000000	7000000	88200000
Mean coral cover 120 m ² (cm ²) (n=3)	2763 ± 1071	247564 ± 923	48741 ± 892	37124 ± 1867	24632 ± 1218	9896 ± 986	61787 ± 92573
Number of species	2	10	10	12	4	7	14
Number of colonies	2	171	103	75	92	27	470
% cover	0.0863	1.6504	0.1625	0.2475	0.1368	0.1414	0.4172
H'	0.6797	3.8003	0.3830	3.1287	0.3290	2.5947	2.8967

B					
Coral species	Estimated total weight (g) of live coral in Telecom Bay	Total weight of coral rubble (from 24 months) as a percentage of live coral (%)	Average monthly weight of all coral rubble as a percentage of live coral (%)	Range of monthly weight of all coral rubble as a percentage of live coral (%)	Average monthly weight of coral rubble, recently alive, as a percentage of live coral (%)
<i>Goniastrea</i>	1085863	14.04	0.585 ± 0.936	0.01–3.68	0.0070
<i>Favia</i>	1581720	1.57	0.070 ± 0.096	0–0.323	0.0003
<i>Cyphastrea/Plesiastrea</i>	506080	4.92	0.205 ± 0.377	0–1.43	0
<i>Psammocora</i>	8777040	0.18	0.007 ± 0.013	0–0.04	0
<i>Favites</i>	5891474	0.37	0.015 ± 0.032	0.001–0.14	0.0003
<i>Turbinaria</i>	356097	1.80	0.089 ± 0.129	0–0.48	0
<i>Platygyra</i>	6435401	0.03	0.001 ± 0.003	0.0002–0.014	0.0002
<i>Porites</i>	1651330	0.26	0.014 ± 0.018	0–0.07	0

0.09 ± 0.13% (0–0.48%) for *Turbinaria* spp., 0.07 ± 0.10% (0–0.32%) for *Favia* spp., 0.02 ± 0.03% (0.001–0.14%) for *Favites* spp., 0.01 ± 0.02% (0–0.07%) for *Porites* spp., 0.01 ± 0.01% (0–0.04%) for *Psammocora* spp. and 0.001 ± 0.003% (0.0002–0.014%) for *Platygyra* spp.

Of this coral rubble, only 19 pieces, usually whole colonies, with a total weight of 2030 g, possessed living tissue. These were represented by four genera, i.e. *Goniastrea* spp. (eight fragments and 1460 g), *Favites* spp. (eight fragments and 310 g), *Platygyra* spp. (one fragment and 170 g) and *Favia* spp. (two fragments and 90 g) and accounted for 0.13%, 0.005%, 0.003% and 0.006%, of the respective species, and a total of 0.15%, of the total weight of live coral in Telecom Bay. This equates to a monthly average of 0.007%, of the total weight of live coral within the bay, being deposited on the beach as newly-removed pieces.

Temporal distribution of coral rubble

Fifteen genera of coral, from six families, the Poritidae, Agariciidae, Siderastreidae, Thamnasteriidae, Faviidae and Dendrophylliidae, were recorded from Telecom Bay Beach (Figure 5). The Faviidae was dominant. Ten of these genera, i.e. *Favites* spp., *Favia* spp., *Goniastrea* spp., *Porites* spp., *Psammocora* spp., *Turbinaria* spp., *Platygyra* sp., *Plesiastrea* sp., *Cyphastrea* sp. and *Pavona* sp., were also recorded from the survey of live corals conducted within Telecom Bay (Figure 3) and four of the remaining five

genera, i.e. *Alveopora* spp., *Goniopora* spp., *Leptoseris* sp. and *Coscinaraea* sp., have been observed, though only rarely, during other dives within Telecom Bay and the Coral Pool (Clark, 1997, 1998). The only genus not observed live from this area was *Barabattoia* sp.

Due to the pronounced erosion of some of the pieces of coral rubble, difficulties occurred in separating some skeletons into individual genera. These were thus grouped as: *Alveopora* spp. with *Goniopora* spp.; *Leptoseris* sp. with *Coscinaraea* sp., and *Plesiastrea* sp. with *Cyphastrea* spp.

Figure 5A,B present the data for the number of fragments and the weights of different genera of dead coral, respectively, collected over a period of 24 months from Telecom Bay Beach. The total number of coral pieces collected was 3652 with a weight of 253,707 g which gave an average weight of 69.47 g per coral fragment. Initially, i.e. in January 1996, the abundance and weight of collected coral was high (~280 pieces and 38,500 g), this first collection being the result of years of deposition of such rubble, by wave action. The subsequent collections were of coral pieces re-exposed at the surface of the beach cobbles by variations in wave action and, sometimes, new pieces from intervening, major, storm events.

There was no significant difference between seasons for the weight of coral rubble washed ashore. There was, however, a significant difference between the weight of coral collected with regard to species which could be separated into two groups, as follows: group 1, *Barabattoia* sp.,

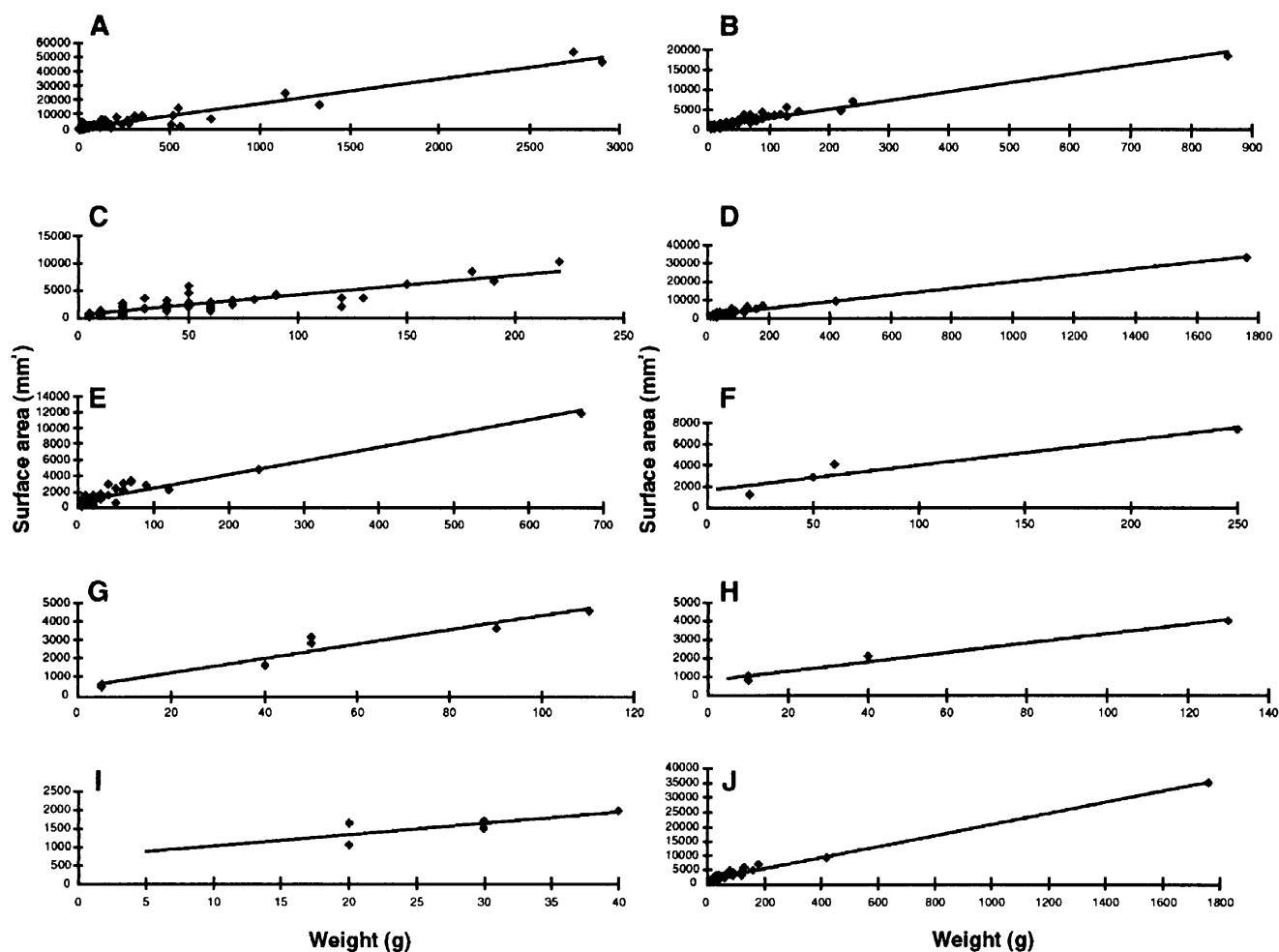


Figure 4. Surface areas (mm^2) of pieces of coral rubble of different weight (g), collected from Telecom Bay Beach, Cape d'Aguilar between January 1996 and December 1997, inclusive. (A) *Goniastrea* sp.; (B) *Favia* sp.; (C) *Cyphastrea*/*Plesiastrea* spp.; (D) *Psammocora* spp.; (E) *Favites* sp.; (F) *Alveopora*/*Goniopora* spp. (G) *Turbinaria* sp.; (H) *Platygryra* sp.; (I) *Lithophyllum*/*Coscinaria* spp.; (J) *Porites* sp. Black line represents line of best fit.

Pavona sp., *Plesiastrea*/*Cyphastrea* spp., *Platygryra* spp., *Turbinaria* spp., *Porites* spp., *Favia* spp., *Favites* spp., *Psammocora* spp., *Leptoseris*/*Coscinaraea* spp. and *Alveopora*/*Goniopora* spp.; and group 2, *Goniastrea* spp. (Table 2B). Overall, the largest quantity of coral washed ashore, both in terms of abundance and weight, was represented by *Goniastrea* sp. with 1145 pieces and a total of 152,504 g, followed by *Favia* spp. (675 pieces and 24,763 g, respectively), *Plesiastrea*/*Cyphastrea* spp. (662 pieces and 24,900 g, respectively), *Favites* spp. (591 pieces and 21,800 g, respectively), *Psammocora* spp. (222 pieces and 15,870 g, respectively) and *Porites* spp. (178 pieces and 4300 g, respectively). These seven genera provided counts of greater than 100 pieces of coral rubble each over the collection period and accounted for 95% of the total number and the 96% of the total weight of coral fragments collected, respectively. *Turbinaria* spp., were recorded from 78 pieces of rubble, less than *Porites* spp. (178), but the weight of 6410 g for the former was greater than that of the latter (4300 g).

There is a general trend towards a decrease in both the numbers of fragments (from 277 pieces to 36 pieces and from 119 pieces to 34 pieces) and the weight of collected coral rubble (from 38,560 g to 940 g and from 4330 g to 540 g), between January and July in both 1996 and 1997,

respectively. In August 1996 and 1997 there were dramatic increases in the numbers of coral pieces (211 pieces and 808 pieces, respectively) and the weights of coral heads (24,327 g and 60,930 g, respectively) washed up on Telecom Bay Beach, with another slight increase in September 1996 (225 pieces and 26,370 g, respectively). October 1996 showed a slight drop in the numbers of coral fragments recorded (197 pieces) with a disproportionately large decrease in the weight of coral collected (11,350 g) and a large decrease in the number and weight of fragments was recorded in September 1997 (153 and 5890 g, respectively), through to December 1997 (53 and 2640 g, respectively). Again, there was a large increase in the number of pieces of coral rubble recorded (299 pieces) in November 1996 with a corresponding increase in weight (18,900 g). In December 1996, a decrease was recorded for the abundance of coral rubble (186 pieces) whereas there was an increase in the weight of coral collected (22,670 g).

Apart from *Porites* spp. and *Psammocora* spp., the increase in the number of fragments corresponded to an increase in the total weight of collected coral. This indicated that the weights of the *Porites* spp. were all low. The opposite was true for *Psammocora* spp., i.e. the pieces

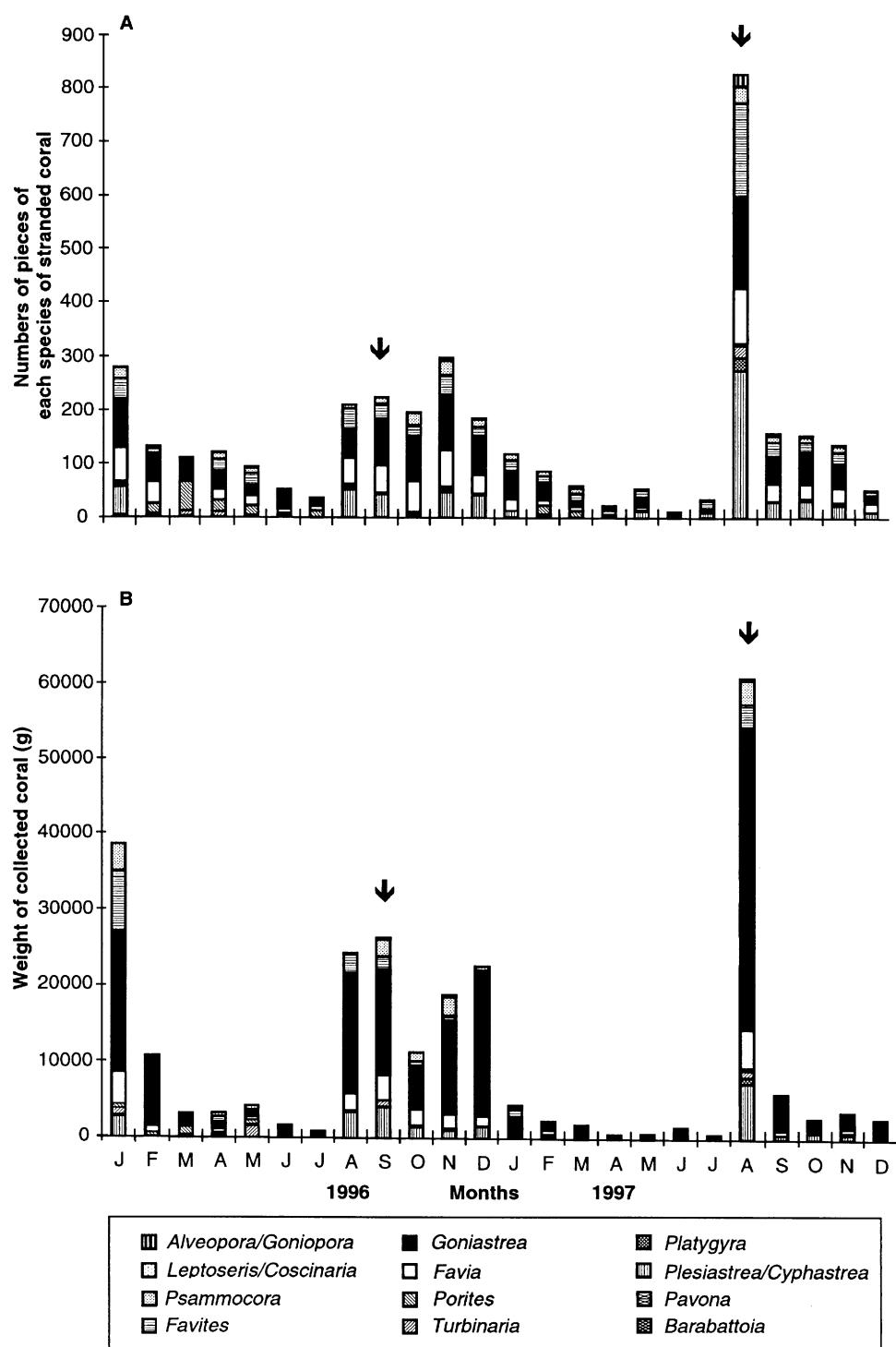


Figure 5. Dead corals collected from Telecom Bay Beach: (A) numbers of pieces of each species of dead coral; and (B) weights (g) of each species of dead coral. Collections were carried out monthly between January 1996 and December 1997, inclusive. Typhoon Sally passed close to Hong Kong on 8 September 1996 and Typhoon Victor hit Hong Kong on 2 August 1997 (arrows).

of coral collected for this genera were all comparatively heavy. Figure 5 shows that the collected *Porites* spp. fragments comprised a larger proportion of those which fell into the lowest weight category (10–49 g) than *Psammocora* spp. (151 and 142 pieces, respectively) although the latter did comprise a higher number of the heavier group corals (50 to >1000 g) than *Porites* spp. (75 and 23 fragments, respectively). The weight category 10–49 g comprised the

greatest abundance of coral rubble collected from Telecom Bay Beach in all months from January 1996 to December 1997 (Figure 6) and followed the same pattern as the total abundances and weights of all pieces collected, as described above for Figure 5. An exception to this pattern was shown for the data from September 1996 when the numbers of fragments of coral in the weight category 10–49 g decreased from 168–142 pieces (Figure 6), whereas Figure 5

Table 2. A, results of two-way ANOVA for the effect of season and species on the weight (g) of coral rubble recorded from Telecom Bay Beach; B, results of χ^2 analysis for effect of coral species and mollusc species on the number of molluscs collected from Telecom Bay Beach; C, results of a one-way ANOVA for the effect of coral species on the species of mollusc recorded from the coral rubble collected from Telecom Bay Beach; D, results of a two-way ANOVA for the effects of wind speed (km h^{-1}) and wind direction (degrees) on weight (g) of coral rubble recorded from Telecom Bay Beach. Data were collected between January 1996 and December 1997, inclusive. Data were log transformed so that all data then conformed to normality and homogeneity of variances at the 0.05 significance level.

A

Factor	df	F	P	Power of performed test ($\alpha=0.05$)	Remarks
Season	1	2.549	0.112	0.533	ns
Species	11	10.179	0.000	1.000	*
Season: Species	11	1.171	0.309	0.631	ns

Multiple comparisons using the SNK and Duncan's tests ($P=0.05$) groupings ($P>0.05$): species—(1) *Barabattoia*, *Pavona*, *Plesiastrea*/*Cyphastrea*, *Platygyra*, *Turbinaria*, *Porites*, *Favia*, *Favites*, *Psammocora*, *Leptoseris*/*Coscinaria*, *Alveopora*/*Goniopora*; (2) *Goniastrea*.

B

Factor	df	χ^2	Asymp. Sig.	Remarks
Coral species	11	0.157	1.000	ns
Mollusc species	18	0.000	1.000	*

Multiple comparisons using the SNK and Duncan's tests ($P=0.05$) Groupings: ($P>0.05$): Species—(1) *Lithophaga malaccana*, *L. mucronata*; (2) *L. hanleyana*, *L. lima*, *L. simplex*, *Gastrochaena laevigata*; *G. cuneiformis*; (3), *L. nasuta*, *G. interrupta*, *Anchomasa yoshimurai*, *Magilus* sp., *Irus irus*, *Cardita leana*, *Isognomon legumen*, *Arca boucardi*, *Coralliophaga coralliphaga*.

C

Factor	df	F	P	Mean square	Remarks
Mollusc species	16	0.942	0.465	31.053	ns

D

Factor	df	F	P	Mean square	Remarks
Wind direction	1	1.912	0.255	0.186	ns
Wind speed	5	3.731	1.000	0.000	*
Direction: Speed	1	3.606	0.760	0.76	ns

*, significant at $P<0.05$; ns, not significant.

indicates that there was an increase in both the total abundance and weight of coral collected. There was an increase in the abundance of coral fragments in the larger weight categories (50–99, 100–199, 200–499, 500–999 and >1000 g) between August and September 1996 (18 and 31 fragments, 12 and 25 fragments, 6 and 15 fragments, 2 and 6 fragments, and 4 and 5 fragments, respectively) and July and August 1997 (0 and 51 fragments, 0 and 36 fragments, 0 and 15 fragments, 0 and 9 fragments, and 1 and 4 fragments, respectively). There was an overall decrease in the abundance of coral fragments in the heavier weight categories 50 to >1000 g between September and October 1996 (82 and 62 pieces, respectively), but an increase between October and November 1996 (62 and 75 pieces, respectively) before decreasing from December 1996 (38 fragments) through to July 1997 (one fragment) then increasing again in August 1997 (115 fragments) before decreasing again in September 1997

(one fragment). Overall, with increasing coral fragment weight (10–49, 50–99, 100–199, 200–499, 500–999 and >1000 g), there was a decrease in the abundance of fragments (2870, 365, 194, 91, 38 and 28, respectively) (Figure 6A). Figure 6B shows that the majority of fragments in the weight category 10–49 g belonged to a few genera, i.e. *Goniastrea* spp. (846 fragments), *Plesiastrea*/*Cyphastrea* spp. (598 fragments), *Favites* spp. (454 fragments) and, to a lesser extent, *Porites* spp. (151 fragments) and *Psammocora* spp. (142 fragments), with the remaining six genera containing only about 5% of coral pieces in this weight category.

There was a significant difference in the weights of coral rubble washed up on Telecom Bay Beach in relation to wind speed ($P<0.05$) but not wind direction (Table 2D). The average monthly wind speeds and wind direction for Hong Kong over the period of coral rubble collection are shown in Figure 7. Wind direction was predominantly

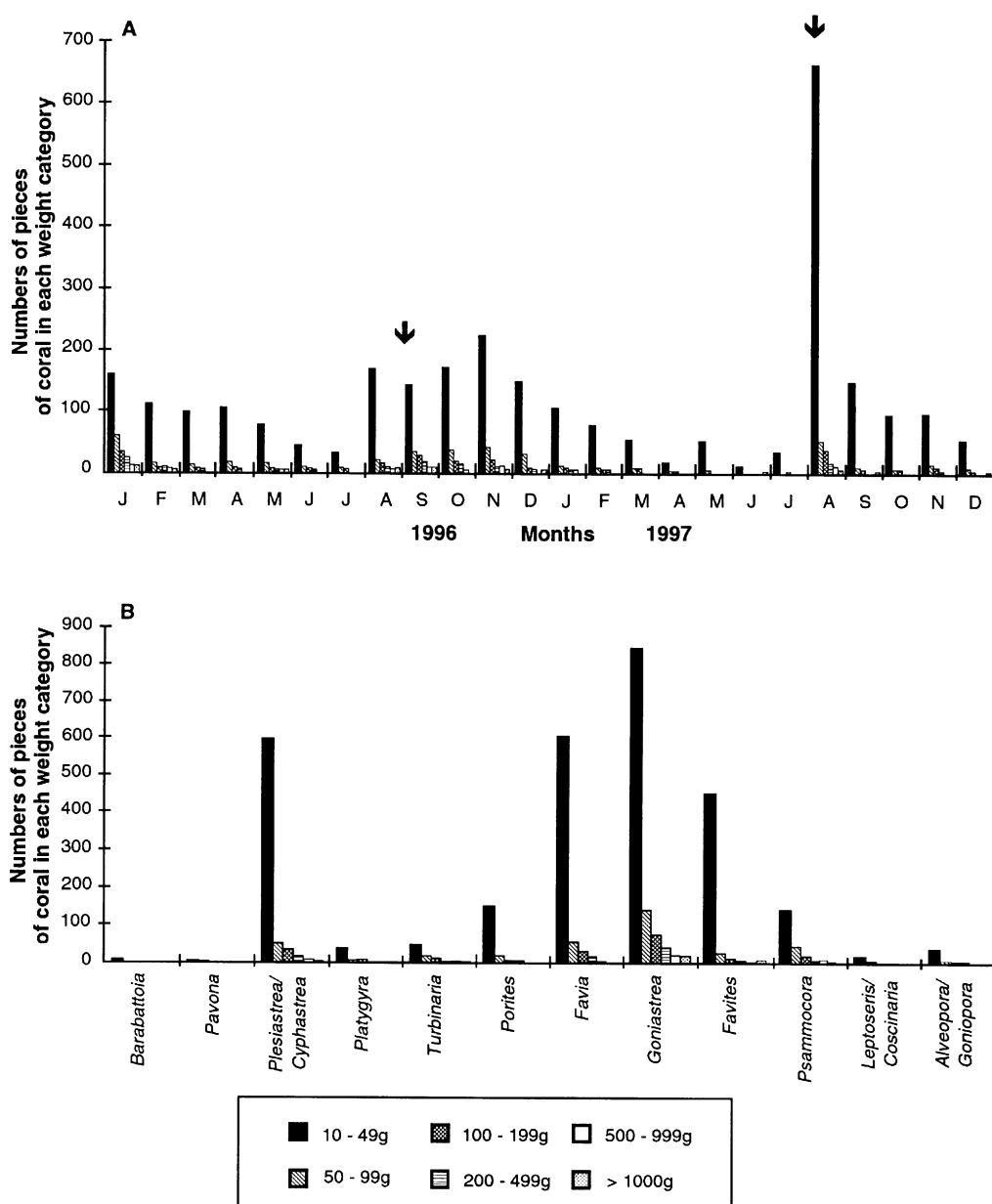


Figure 6. Dead corals collected from Telecom Bay Beach: (A) numbers of pieces of dead coral in each weight category (10–49, 50–99, 100–199, 200–499, 500–999, >1000 g) and; (B) abundance of each species of dead coral in each weight category (10–49, 50–99, 100–199, 200–499, 500–999, >1000 g). Collections were carried out monthly between January 1996 and December 1997, inclusive. Typhoon Sally passed close to Hong Kong on 8 September 1996 and Typhoon Victor hit Hong Kong on 2 August 1997 (arrows).

from the north-east, i.e. from January to May 1996, October 1996 to April 1997, and September to December 1997, spanning both summer and winter months. During June and July 1996 and 1997, however, wind direction was from the south-west and came increasingly from the west during August of both years. Wind speed was greatest in the winter months of November 1996 (31.6 km h^{-1}) and February 1996 and 1997 (28.5 and 30.7 km h^{-1} , respectively), and lowest during the months, mainly during the summer, from May to August 1996 (20.7–23.9 km h^{-1}), March to July 1997 (23.1–20.1 km h^{-1}) and September to December 1997 (20.1–23.5 km h^{-1}), with notable increases in September 1996 (26.4 km h^{-1}) and August 1997

(27.1 km h^{-1}), the two months experiencing local typhoon, Sally and Victor, events.

The molluscan borers

Seventeen species of Mollusca, belonging to nine genera, i.e. *Lithophaga*, *Gastrochaena*, *Anchomasa*, *Irus*, *Cardita*, *Isognomon*, *Arca* and *Trapezium* (Bivalvia) and *Magilus* (Gastropoda) (Figure 8) and nine families, i.e. *Gastrochaenidae*, *Malleidae*, *Arcticoidae*, *Pholadidae*, *Carditidae*, *Isognomonidae*, *Arcidae* and *Trapeziidae* (Bivalvia) and *Coralliophillidae* (Gastropoda), were recorded from within the skeletons of the coral rubble

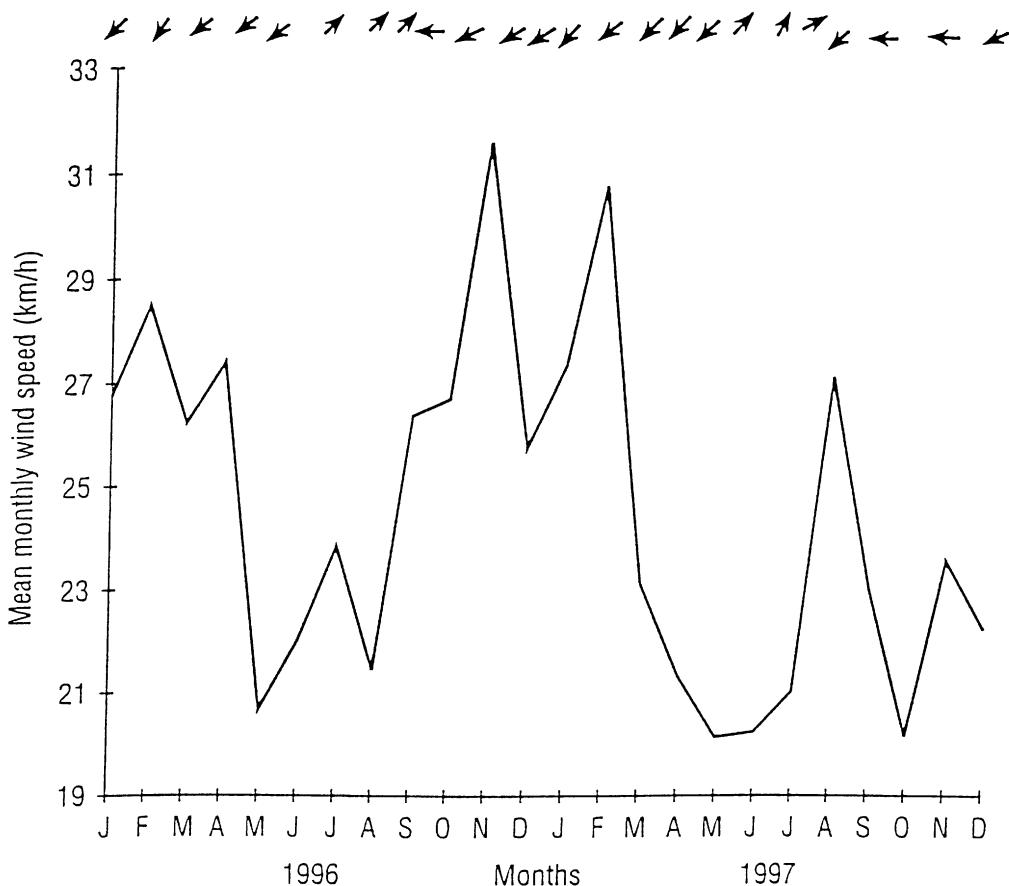


Figure 7. Mean monthly wind speeds (km h^{-1}) and wind direction ($^{\circ}$). Data recorded by the Royal Observatory, Hong Kong, Waglan Island (1966, 1997). Means of daily readings for each month. Arrows represent wind direction in degrees, \downarrow , 0° ; \leftarrow , 90° ; \uparrow , 180° ; \rightarrow , 270° .

collected from Telecom Bay Beach and included a new record for Hong Kong, *Anchomasa yoshimurai*. Species of *Lithophaga* dominated, with six of the 17 belonging to this genus. *Gastrochaena* ranked second, with three.

The numbers of mollusc shells collected which were intact enough to obtain length measurements were low, i.e. less than ten, apart from five of the six *Lithophaga* species and one *Gastrochaena* spp. *Lithophaga malaccana* had the maximum abundance (87) of measurable specimens recorded, followed by *L. mucronata* (81), *L. hanleyana* and *L. lima* (12 each), *L. simplex* (11) and *G. laevigata* (10). Collectively, these species accounted for approximately 89% of all the measurable specimens obtained. The largest specimens were *L. lima* with an average length of 47.18 ± 19.9 mm, *L. nasuta* being slightly smaller (41.25 ± 14.31 mm), followed by *Anchomasa yoshimurai* (26 ± 15.6 mm), *L. hanleyana* (24.9 ± 8.38 mm), *Coralliophaga coralliophaga* (24.8 ± 0 mm), *L. simplex* (24.5 ± 7.68 mm) and *L. malaccana* (21.5 ± 8.49 mm). The smallest species was *Gastrochaena interrupta* (10.23 ± 3.27 mm) with *G. cuneiformis* being slightly larger at (10.53 ± 2.53 mm) (Figure 8A).

There was a significant difference in the numbers of individuals of each species collected, with groupings shown to be: group 1, *Lithophaga malaccana* and *L. mucronata*; group 2, *L. lima*, *L. hanleyana*, *L. simplex*, *Gastrochaena laevigata* and *G. cuneiformis*; group 3, *L. nasuta*, *G. interrupta*, *Anchomasa yoshimurai*, *Magilus* spp., *Irus irus*, *Cardita leana*, *Isognomon legumen*, *Arca boucardi* and *Coralliophaga coralliophaga*. There was not, however, a significant difference

between the number of molluscs collected with regard to the different coral species (Table 2B) and no significant difference was recorded in the species of molluscs collected between the coral species (Table 2C).

Figure 8B shows that the greatest average numbers of molluscs coral fragment $^{-1}$ were recorded from *Turbinaria* spp. (0.56 ± 0.073). *Barabattoia* sp. had the next highest abundance (0.25 ± 0.063). This was, however, a result obtained from only four collected fragments of this species and is, thus, not reliable. The next highest mean abundance was recorded from *Goniastrea* spp. (0.16 ± 0.022 fragment $^{-1}$), each fragment having a mean weight of ~ 69.47 g. Only five genera, i.e. *Goniastrea* spp., *Psammocora* spp., *Favites* spp., *Porites* spp. and *Plesiastrea/Cyphastrea* spp. were responsible for almost 100% of the molluscs present, discounting *Barabattoia* sp. *Lithophaga mucronata* dominated the molluscan community with regard to overall average abundance coral fragment $^{-1}$ (0.556 ± 0.040), followed by *L. malaccana* (0.339 ± 0.018).

Lithophaga mucronata accounted for the largest average number of molluscs fragment $^{-1}$ recorded from *Goniastrea* spp. (0.087), *Porites* spp. (0.040), *Psammocora* spp. (0.028), *Favites* spp. (0.020) and *Favia* spp. (0.010). Species of *Plesiastrea/Cyphastrea* spp. were, however, dominated by *L. malaccana* with 0.019 ind coral fragment $^{-1}$ recorded; *Platygyra* spp. were dominated by *L. lima* (0.043) and *Turbinaria* spp. were dominated by *Magilus* spp. (0.161). *Alveopora/Goniopora* spp., *Leptoseris/Coscinarea* spp. and *Pavona* sp. were recorded to contain no borers. The nine

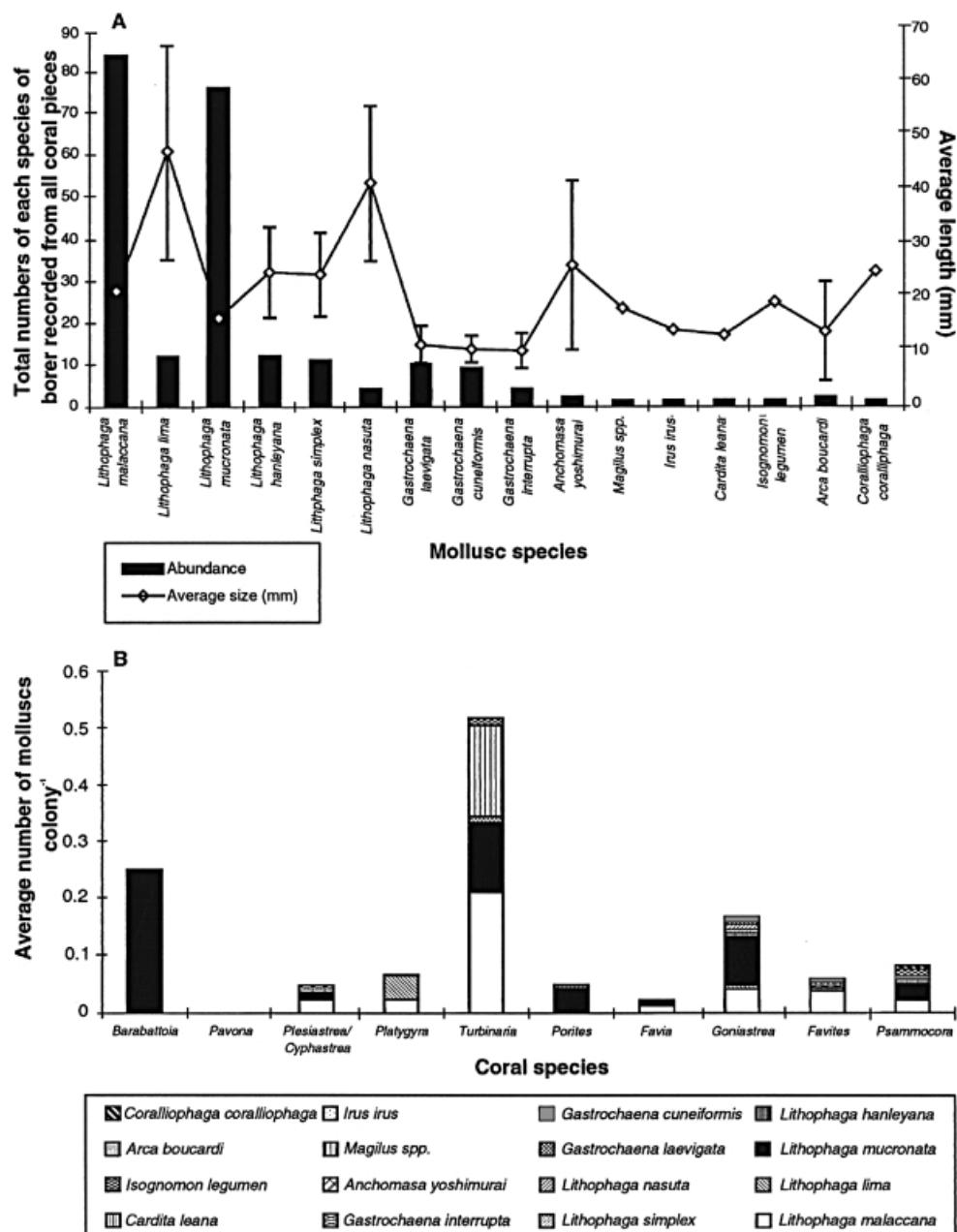


Figure 8. Molluscs recorded from dead pieces of coral washed up on Telecom Bay Beach, Cape d'Aguilar. (A) Shows the abundance and size of each species of borer recorded from dead pieces of coral, black bars represent abundance, black lines with white diamonds represent lengths of molluscs; and (B) shows the average number of molluscs recorded from different species of dead coral. The coral was collected between January 1996 and December 1997, inclusive.

genera represented in Figure 8B were almost exclusively occupied by one genus of mollusc, i.e. *Lithophaga* spp. *Turbinaria* spp. contained mainly *L. malaccana*, *L. mucronata*, *Gastrochaena laevigata*, *Magilus* spp. and *Isognomon legumen*. *Plesiastrea/Cyphastrea* spp. contained mainly *L. malaccana* and *L. mucronata*. *Porites* spp. provided a habitat for *L. mucronata* and *G. laevigata*. *Goniastrea* spp. was occupied mainly by *L. malaccana*, *L. lima*, *L. mucronata*, *L. hanleyana*, *L. simplex*, *L. nasuta*, *G. laevigata* and *G. cuneiformis*. *Favites* spp. was occupied by *L. malaccana*, *L. hanleyana*, *Coralliphaga coralliphaga* and *Isognomon legumen*. *Psammocora* spp. contained *L. mucronata*, *L. malaccana*, *L. hanleyana*, *G. cuneiformis*, *I. legumen* and *C. coralliphaga*. *Platygyra* spp. contained *L. malaccana* and *L. mucronata*. *Favia* spp. was

occupied by *L. mucronata*, *L. malaccana* and *I. legumen* while *Barabattoia* sp. contained only *L. mucronata*.

Data representing the abundance of molluscs for the different weight classes of coral rubble collected are presented in Figure 3B. The greatest abundance of molluscs (70 ind) was recorded from the largest weight category of coral fragments (>1000 g) with the next highest numbers (50 ind) recorded from the weight grouping 100–199 g, followed by the smallest weight category (10–49 g), with 44 specimens, and the weight categories 200–499 g (with 38 ind), 50–99 g (with 29 ind) and 500–999 g (with the lowest abundance of molluscs at 16 ind). *Lithophaga malaccana* was recorded mainly from the corals of >1000 g in weight (29 ind), followed by the

weight categories of between 100–199 g (with 18 ind), 200–499 g (with 14 ind), 500–999 g (with ten ind) and only two specimens being recorded from the weight category of 50 to 99 g. *Lithophaga mucronata* was also common throughout most weight categories, with the majority of this species (21 ind) recorded from the smallest weight grouping of 10–49 g, followed by 16 specimens from the >1000 g category, 15 individuals from the 100–199 g category, 13 from the 50–99 g category and 12 specimens recorded from the 200–499 g category, with only 2 individuals recorded from the 500–999 g grouping.

Coral fragments weighing between 10 and 49 g contained five other mollusc species (in addition to *L. malaccana* and *L. mucronata*), i.e. *L. nasuta* (1), *Gastrochaena laevigata* (3), *G. interrupta* (1), *Anchomasa yoshimurai* (1) and *Magilus* spp. (4), making a total of seven species. Eleven more species of mollusc were recorded from fragments of coral between 50 and 99 g, making a total of 12 in all, i.e. *L. hanleyana* (2), *L. simplex* (1), *L. nasuta* (1), *L. lima* (1), *G. interrupta* (1), *G. laevigata* (2), *G. cuneiformis* (2), *Magilus* spp. (1), *Cardita leana* (1), *Isognomon legumen* (1) and *Arca boucardi* (1). For pieces of coral between 100 and 199 g, a total of ten species of mollusc were recorded, the eight others being *L. lima* (1), *L. hanleyana* (3), *G. laevigata* (2), *G. cuneiformis* (2), *Magilus* spp. (5), *Irus irus* (1), *I. legumen* (2) and *Coralliphaga coralliphaga* (1). Seven other mollusc species were found within corals in the weight range 200–499 g, i.e. *L. lima* (3), *L. hanleyana* (1), *L. nasuta* (1), *G. laevigata* (1), *G. cuneiformis* (2), *Magilus* spp. (3) and *I. legumen* (1), bringing the total number of species to nine. Coral pieces weighing between 500 and 999 g had five species, the three additional ones being *L. lima* (1) and *L. hanleyana* (2) and *G. laevigata* (1), whereas, those weighing >1000 g contained ten other mollusc species bringing the total to 12, i.e. *L. lima* (6), *L. hanleyana* (4), *L. simplex* (3), *L. nasuta* (1), *G. laevigata* (2), *G. cuneiformis* (1), *G. interrupta* (1), *A. yoshimurai* (1), *Magilus* spp. (5) and *C. coralliphaga* (1).

DISCUSSION

Telecom Bay live coral cover

The survey of live corals in Telecom Bay showed similar species diversity values (H') (0.329–3.800) as those recorded for a survey of six sites (A–F) within the greater, 18 ha, area of the Cape d'Aguilar Marine Reserve (0.220–4.136) (Clark, 1997, 1998). Percentage cover was, however, much lower for the whole of Telecom Bay (0.417%), as compared with the six sites within the greater area of the marine reserve (<1–23.5%). This was due to the survey sites A–F having been chosen for their suitability for coral growth and the abundance of corals within each area, i.e. all sites were in the depth range 0 to –3 m CD with rock and boulder substrata, whereas Telecom Bay contains large areas of substratum unsuitable for coral survival, i.e. sand and small stones which move easily, as well as areas in waters of between –3 and –9 m CD, which appear to be below the optimal depth for coral survival locally.

Complete recovery of a damaged coral community would entail restoration of percentage cover, species diversity, species similarity and colony size distribution. This would be difficult to document and is a function of

the morphological and life history characteristics of the dominant species, the nature of the damage sustained and relative rates of bioerosion. Coral diversity has been seen to increase after moderate storms (Dollar, 1982) and after Hurricane Allen, Jamaica, in 1980 (Porter et al., 1981; Woodley et al., 1981) and in St John following Tropical Storm Klaus (1984) (Rogers & Zullo, 1985). Changes in mean percentage total coral cover provide more information on storm effects than measures of diversity (Rogers et al., 1991) and this study, therefore, provides such essential, basic, information for the Cape d'Aguilar Marine Reserve as well as identifying, for the first time in Hong Kong, typhoon-related impacts on its contained corals.

Temporal distribution of coral rubble

All but one genus of coral washed up on Telecom Bay Beach had been recorded previously from the survey carried out at six sites (A–F) within the Cape d'Aguilar Marine Reserve (Clark, 1997, 1998), with the dominant family, the Faviidae, being the same as for the live corals recorded from this area. The only genus not to have been observed live from this area was *Barabattoia*. Several coral species, such as *Montipora informis*, *Acropora pruinosa*, *Goniopora columnna*, *G. stutchburyi*, *Alveopora irregularis* and *Coscinaraea columnna*, have been recorded in low abundances of between two and four colonies and one species, *Leptoseris scabra*, has only been recorded as a single colony within the marine reserve. The fact, therefore, that *Barabattoia* sp. was recorded only as coral rubble and not alive, indicates that it is rare within Telecom Bay and may have existed, like *L. scabra*, as a solitary colony.

No significant difference was exhibited between the amount of rubble recorded from the beach between the summer, i.e. April–September and winter seasons, i.e. October–March, probably because the time of year when wind speeds and wave heights are high, i.e. when typhoons and storms are prevalent, is spread over both the summer and winter months, i.e. between July and December, respectively. Typhoons are most common between August and September and storms occur as the weather system in Hong Kong changes from summer to winter during October and November. During summer, the prevailing wind is from the south and typhoons at this time also cause higher waves to arrive from a more southerly direction, thus enabling them to enter Telecom Bay, which is otherwise generally protected from the more common wave direction from the north-east in autumn, winter and spring (Figure 7). Summer is, therefore, the time when either dead or weakened corals in the bay are most susceptible to being dislodged and deposited on the beach at the north end of Telecom Bay. Only during times of the strongest wave action, when wind direction was from the south-west, i.e. during typhoons Sally in September 1996 and Victor in August 1997 (Figure 7), was coral which still possessed some living tissue, washed up on the beach and no coral rubble was observed that appeared to have been healthy immediately prior to being deposited on the beach, i.e. with a high percentage cover of live, or recently living, tissue still present. If coral colonies are, therefore, removed from the substratum whilst still alive, they must remain in the bay for a time before they are washed up on the beach. It was

also during this summer time of locally highest wave action that the largest pieces, sometimes whole colonies, of coral were deposited on the beach and these were generally found at its rear, whereas the smaller, lighter, pieces were lower on the shore, indicating, further, stronger wave action at this time. Hence, during September 1996 and August 1997, greater numbers of large corals were recorded, accounting for the disproportionate weight of coral rubble to the number of fragments collected during these times. Many of the smaller pieces of coral were probably washed off the beach during these high energy events and then re-deposited later, when wave action was lower, to be recorded during the next routine collection of coral rubble.

The patterns of reef and coral community structure are the result, in part, of wave energy (Maxwell et al., 1964; Stoddart, 1969; Chappell, 1980), with damage resulting from the physical force of hurricane (or typhoon), or storm-induced, waves (Rogers et al., 1991) thus being more severe in shallow water (Endean, 1976; Porter et al., 1981; Woodley et al., 1981; Rogers et al., 1982). The amount and type of destruction which a reef sustains during a major storm will partly be a reflection of how much time has passed since a comparable event occurred (Woodley et al., 1981).

The most common live coral in Telecom Bay was *Platygyra* spp., both as recorded in this survey and for the sites within the greater area of the Cape d'Aguilar Marine Reserve, i.e. sites C and D (Clark, 1997, 1998). *Goniastrea* spp. was, however, the most abundant coral washed up on Telecom Bay Beach, with few pieces of *Platygyra* spp. being so recorded. This could be due to the relative degree of boring recorded from the different species and, thus, an increase in the weakening of the coral colony and the likelihood of it breaking away from the substratum, i.e. *Goniastrea* spp. had the greatest concentrations of borers within its skeleton while few were recorded from within those of *Platygyra* spp. Several authors (Highsmith 1981a; Sammarco & Risk 1990) have suggested that coral skeletal density is an important factor controlling bioerosion activity. Sammarco & Risk (1990) showed a negative correlation between increased skeletal density of *Porites lobata* and bioerosion data which, it was suggested, may be due to the increased difficulty of boring into the denser skeleton, whereas Highsmith (1981b) and Highsmith et al. (1983) showed a positive correlation between internal bioerosion and skeletal density and suggested that this may be due to the increased protection that the denser coral gives to the borer. The seven most bored coral species in this study, i.e. *Turbinaria* spp., *Goniastrea* spp., *Psammocora* spp., *Platygyra* spp., *Favites* sp., *Plesiastrea/Cyphastrea* spp. and *Porites* spp., appear to show no relationship between skeletal density and number of borers, as *Psammocora* spp. has the densest skeleton whereas *Platygyra* spp. and *Turbinaria* spp. have the lowest, with the other highly-bored corals having densities spanning the range exhibited by the species recorded from this survey.

Coral morphology has also been reported as a possibly important determining factor for total bioerosion levels. Species of *Lithophaga* have been shown to be a much more

important component of the bioeroding community in *Porites* than in *Acropora* and this was thought to be due to size constraints on *Lithophaga* living in branching corals (Risk et al., 1995).

The molluscan borers

It is known that species of *Lithophaga* are common borers of calcareous substrata (Dudgeon & Morton, 1982; Morton & Scott, 1980) in Hong Kong and have also been reported from natural limestone (Turner & Boss, 1962), large bivalve shells (Hodgkin, 1962) and dead coral skeletons (Otter, 1937; Yonge, 1974) elsewhere. The coral borers which occupy dead coral substrata include species of Petricolidae, Pholadidae and Clavagellidae, each represented by only a few species, with a more important family, the Gastrochaenidae, being the dominant coloniser of dead corals in both the Caribbean and the Indo-Pacific (Morton, 1990). It is now recognized that some tropical lithophagines also commonly inhabit live corals and are often host specific with *L. mucronata*, reportedly, being highly specific (Morton & Scott, 1980). This has recently been confirmed for coral-boring lithophagines in the Red Sea (Mokady et al., 1997). Representatives of the Lithophaginae are the most important living coral borers (Morton, 1990). In a study by Morton & Scott (1980), *L. malaccana* was collected from dead corals and *L. nasuta*, *L. lima*, *L. hanleyana*, *L. simplex* and *L. mucronata* were reported from live coral heads in Hong Kong. These species were also recorded from coral rubble during this study.

This study recorded 17 species of Mollusca associated with coral rubble, the greatest proportion being classified as 'live-coral' borers, whereas, a study of the coral-associated Mollusca of Tolo Harbour, Hong Kong (Dudgeon & Morton, 1982), recorded 92 species of molluscs most of which were associated with dead coral. Taylor (1968) suggested that the diversity of molluscs inhabiting coral areas which are alive and growing is, generally, less than on boulder zones at the edge of reef platforms. The species richness value recorded in this study compares with that obtained by Grassle (1976) who recorded 17 species of gastropods from live corals at Heron Island, Great Barrier Reef, and Taylor (1968) who recorded 24 species of bivalves from coral communities in Mahe, Seychelles. In the study by Dudgeon & Morton (1982), an increase in the numbers of molluscs was recorded from Inner to Outer Tolo Harbour and was thought to be due to increased salinity, water clarity and oxygenation at the latter stations, and an increase in the abundance of coral. It was noted, however, that a decline in species richness was also characteristic of environmentally stressed (polluted) communities. There was, surprisingly, a high incidence of live coral boring lithophagines at inner sites within Tolo Harbour and, it was further suggested, that this may be a result of the corals here being stressed by pollution and thus susceptible to borer attack (Dudgeon & Morton, 1982).

Some representatives of the dead coral boring Lithophaginae, i.e. *Lithophaga nigra*, *L. antillarum* and *L. malaccana*, the latter being recorded from this study, and the specialized coral nestler *Coralliophaga coralliophaga*, again recorded during this work, are common to the Atlantic and the Pacific, whereas the live coral-boring species of

Lithophaga are mutually distinct in the two reefal environments, as are the representatives of the dead coral-boring Gastrochaenidae (Morton, 1990).

Species of *Lithophaga* are one of only two chemically boring groups of bivalves that are restricted to live coral, with five species being recorded from the tropical areas of Lizard Island and three species reaching Heron Island in the subtropics, on the Great Barrier Reef. Another species, *L. purpurea*, was recorded from Aqaba, Red Sea (Kleeman, 1980).

Lithophagine host-specificity generally prevents competition for the same host, although overlapping occurs (Kleeman, 1980). *Lithophaga laevigata*, *L. lima* and *L. simplex* were recorded from a number of coral species in a study by Kleeman (1980) whereas another species, *L. kuehnelti*, was only identified from *Acropora palifera*. In the present work, only two species of *Magilus* (Gastropoda) were host specific with *Magilus* sp. recorded from *Turbinaria peltata* and *M. striata* from *Favia* spp., as also observed by Scott (1980). As numbers were low and it was impossible to determine whether the borers had first colonized either living or dead coral heads or a dead portion of a living (but also, later, dead) colony, however, no significant relationships between coral and mollusc species, either living or dead coral borers, could be identified from a statistical analysis of the present data.

Low numbers (<4) of a number of mollusc species were recorded during this study and included *Magilus* spp. (Gastropoda), *Irus irus*, *Cardita leana*, *Coralliophaga coralliophaga* and *Isognomon legumen* (Bivalvia). All the above bivalves, but not the gastropods, are generally regarded as nestlers (Morton, 1977, 1985, 1990; Dudgeon & Morton, 1982; Harper & Morton, 1994). *Isognomon legumen* was recorded from subtidal coral communities by Dudgeon & Morton (1982) and was seen to be present on both sheltered and exposed shores at Cape d'Aguilar, being common in Lobster Bay, in a study by Harper & Morton (1994). It was also reported to have a short lifespan of about two years. The specimens thus recorded in this study were probably slightly younger than 2-y old. *C. coralliophaga* was studied in Tolo Harbour, Hong Kong, by Morton (1977) and it was determined that this bivalve was a nestler inhabiting dead corals and which occur subtidally to a depth of -10.5 m CD. *I. irus* (Morton, 1985) is also a nestler and has been recorded from sublittoral dead coral crevices throughout Tolo Harbour (Dudgeon & Morton, 1982).

Most of the coral borers recorded to species level in this study were of *Lithophaga* and were live coral borers. This is probably because the intact borers were the ones which were contained protectively within the skeleton of the coral, i.e. the ones which had been grown around by the coral when it was alive (Morton & Scott, 1980). Any dead coral borers not so contained, would have been easily lost from their boreholes. The majority of the boreholes were, thus, empty, making it difficult to predict whether they were made either whilst the coral was alive or after it had died, either pre- or post-dislodgement and beaching. The large majority of the corals washed up on the beach were dead and were, presumably, broken away from the substratum due to a combination of water movement and weakened attachment to the basal rock as a consequence of boreholes, many of which were relatively

large and thus, probably, made by *L. lima* which was, as shown here, present in the bases of most of the whole, or almost whole, coral heads.

Levels of borer activity appeared to be relatively low at Cape d'Aguilar, a maximum value of 0.174 molluscs average coral fragment⁻¹ (=approximately 69.47 g) being recorded, although actual densities were not reported upon in this study. This agrees with the work of Highsmith (1980a) who suggested that there is a relationship between abundance of boring bivalves and plankton productivity, with low borer densities in the western Pacific and higher ones in the eastern Pacific, with a corresponding higher primary productivity occurring in the latter. Highsmith recorded lithophagine abundances at levels of several to hundreds of *Lithophaga* 0.01 m⁻² of living coral from Isla del Cano, in the eastern Pacific. High levels of boring bivalve infestations of up to 10.8% of coral area, were observed in a study by Sammarco & Risk (1990) and were reported to weaken the corals and cause them to become detached easily from the substratum. This was also recorded in the work of Highsmith (1980b) and Highsmith et al. (1980) where *Acropora* colonies were observed to be weakened by internal bioerosion and heavily bioeroded branches had low mechanical strength values. Colonies with more than between 20–30% bioerosion were broken quickly by wave action, particularly during storms (Tunnicliffe, 1981). According to the work of Woodley et al. (1981) and Johnson & Risk (1987), fragments of branching corals would be transported and redeposited during storms, as was the case for all the coral fragments, both branching and massive species, in this study. It was suggested by Sammarco & Risk (1990) that because of increased levels of bioerosion, *Porites lobata* populations on inshore reefs may be inherently more susceptible to damage from catastrophic high energy events such as storms and cyclones than their offshore counterparts which tend to have lower levels of bioerosion. *Porites lobata* was reported to have the lowest strength of corals measured in a study by Scott & Risk (1988) and this was seen to decline further when bored by *Lithophaga*, with all breaks occurring at boreholes. The coral–lithophagine relationship may, however, be more subtle than a simple one of borer/substratum and even the host/symbiont model proposed by Morton (1990), Mokady et al. (1997) showing that some 15% of the total ammonium consumption of the corals, mediated by the entrained zooxanthellae, being provided by the entombed bivalves.

It can be concluded that the boring molluscs recorded in this study do contribute to the weakening of the corals, whether alive or dead, especially the basally-boring *Lithophaga lima*, within the Cape d'Aguilar Marine Reserve and have aided in the bioerosion of these communities. The corals at Cape d'Aguilar, however, appear to be somewhat resistant, particularly *Platygyra* spp., as such a level of weakening seems low, the monthly percentage of coral pieces to have been alive recently, when removed from the substratum and dumped on the beach by wave action, being only about 0.007% of the total weight of live coral in the bay, probably due to the few borers recorded and the encrusting nature of the coral species occurring in the marine reserve. Such bioeroded corals are, however, particularly susceptible to being dislodged

during local storm and, especially, typhoon events, causing an increase in both the numbers of coral fragments and larger pieces, sometimes whole heads, being beached immediately following such natural perturbations, as shown here.

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