SOME ASPECTS OF THE BIOGEOGRAPHY AND ECOLOGY OF INTERTIDAL AND SHALLOW SUBTIDAL MARINE GAMMARIDEAN AMPHIPODS OF MAURITIUS (INDIAN OCEAN)

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by

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ABSTRACT

Sixty-nine species of marine gammaridean amphipods were reported from 34 sites (486 samples with 34,441 specimens) of varying exposure in the intertidal/shallow-subtidal zones of Mauritius (19^0 $59'$ E-$20^0 32'$ E; $57^0 18'$ S-$57^0 47'$ S, Indian Ocean) in April-July, 1995. Two sites, Souillac, a wave exposed site on the south coast, and Trou aux Biches, a sheltered site on the north-west coast were sampled most intensively.

Sand, coral rubble, debris, seagrass and algal substrates were sampled both qualitatively and quantitatively (10 cm x 10 cm quadrat). The occurrence and abundance of amphipods on algal substrates were studied in detail.

Forty-one of the 69 species are new records for the island and 19 of these are undescribed. One hundred and thirty species are now known from Mauritius and of these 32% appear to be endemic. Many Mauritian amphipod species are widely distributed in the Indo-Pacific. About 50% of the amphipod species are shared with Madagascar (the closest large land mass).

Amphipod species showed varying patterns of occurrence on sand, seagrass, coral rubble and algal substrates with some being specialists and others generalists. The frequency of occurrence of 35 amphipod species on 17 algal taxa showed that some species occurred on only a few, while others were more ubiquitous. Mean abundance of individuals per 10 cm x 10 cm quadrat was significantly different for 7 of the amphipod species on 12 algal taxa analysed at Souillac. At Souillac, only the mean number of individuals per quadrat for *Hyale grandicornis* was significantly different among algal morphological categories with the highest mean number occurring on foliose forms. Only mean numbers of individuals of *Hyale grandicornis* and *Mallacoota subcarinata* were significantly different among algal toughness categories.

The amphipod assemblages on algal substrates were compared in terms of total abundance and species diversity. The amphipod community on *Ulva lactuca* at an exposed and sheltered site were not significantly different in total numbers; species richness, however, was higher at the exposed location. Cluster analysis showed that exposed sites have different amphipod assemblages than protected/moderately exposed sites.

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Last but not least, I am grateful to my family especially my brother, Anand, my friends in Mauritius, especially Mala, Daya, Micheline and Jokhun for their love and constant moral support.

Dedication

To mum and dad

You have shown me the way to light

You have bestowed your love on me

You have guided me all through and though paths

were difficult, with your support nothing is impossible

A source of inspiration you have been and it is a gift of God to be your child.

This work is but a small token to show how grateful I am to both of you.

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1.0 INTRODUCTION

Amphipods are peracarid crustaceans that are grouped into four suborders, Gammaridea, Hyperiidea, Caprellidea and Ingolfiellidea. Recent classifications are given by Bousfield (1983) and Bousfield and Shih (1994). Amphipods like other peracarids have a lecithotrophic (nonplanktonic) development of eggs within a thoracic brood pouch of the female. One of the unique features of amphipods is the arrangement of the thoracic legs into two distinct groups: the first four pairs directed forward and the last three directed backwards. A second unique characteristic is the arrangement of abdominal limbs: the first three are biramous swimming legs (pleopods) and the last three are thrusting legs (uropods) (Bousfield and Shih, 1994). The gammarideans make up about 85% of the Amphipoda (Bousfield, 1973), of which more than 5700 species in about 1060 genera are known from freshwater and marine habitats (Barnard and Karaman, 1991). The hyperiids are specialized for a marine planktonic life, the caprellids are widespread on marine algae and hydroids, and some are ectoparasitic on marine mammals (Lincoln, 1979). The gammarideans, which are mostly free-living, occupy a wide variety of habitats; nestling in rocky crevices, on coral rubble, on algae and seagrasses, burrowing in sediments, living in fixed or mobile tubes and living in invertebrate hosts (Bousfield, 1973).

Indo-pacific regional faunistic studies on gammaridean amphipods include those of Walker (1909), and Chevreux (1901) in the Seychelles, Walker (1904) in Sri Lanka and Walker (1905) in the Maldives and Laccadives archipelagoes. More comprehensive studies in the Indo-pacific region include the work on the gammaridean fauna of the Bismarck archipelago (Bousfield, 1971), Hawaii (Barnard, 1970, 1971), India (Barnard, 1935; Nayar, 1950, 1959, 1966; Rabindranath, 1971a, 1971b, 1972a, 1972b,1972c, 1972d, 1974, 1975; Sivaprakasam, 1966, 1967a, 1967b, 1968a, 1968b, 1968c, 1969a, 1969b,1970a, 1970b), Micronesia (Barnard, 1965), Madagascar (Ledoyer, 1962, 1967, 1968, 1969a, 1969b, 1972, 1973a, 1973b, 1973c, 1976), Mozambique (Griffiths, 1973), the Philippines (Olerod, 1970). Barnard (1976) in a review of tropical Indo-pacific amphipods, emphasized the great taxonomic effort required to know the amphipods of the region. He pointed out that revisionary work is needed to clarify known species by improving descriptions and illustrations and by making further inter-regional comparisons of material. He suggested that taxonomic work in the form of keys and handbooks for the identification of amphipods and notes on their ecology in the region would stimulate studies in functional morphology and ecology. Since then detailed faunistic work on gammaridean amphipods has been done in the Cook Islands (Myers, 1990)*, the Fiji Islands (Myers, 1985), Madagascar (Ledoyer,1979b, 1982, 1986 (cited from Myers, 1997), Moluccas (Ledoyer, 1979a), Philippines and Indonesia (Lowry and Stoddart, 1993)*, New Guinea (Lowry and Stoddart, 1995; Myers, 1995), Sri Lanka (Karaman, 1984, 1985), the Society Islands (Myers, 1989)* and Tonga (Myers, 1986)*.

The Indo-pacific is the largest marine biogeographic region, extending from Hawaii and Easter Island to East Africa, covering a vast region with about 6570 000 km^2

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* : cited from Lowry and Stoddart, 1995

of continental shelf. It is also the most diverse region, having more than 6000 species of molluscs, 800 species of echinoderms, 500 species of hermatypic corals and 4000 species of fish (Briggs, 1995). A concentration of species is observed in the triangular region formed by the Philippines, the Malay peninsula and New Guinea, with a decrease in species diversity apparently correlated with distance away from the region (Briggs, 1995).

The island of Mauritius together with two other islands, Réunion and Rodrigues, form part of the Mascarene Islands located in the Western Indian Ocean (Figure 2.1). Michel (1974) pointed out that the marine fauna of Mauritius includes more than 600 species of fish, 244 species of crabs, 194 species of echinoderms, some 270 pelecypods and 1150 species of gastropods. The marine fauna of the island consists in part of widespread species found also on the east coast of Africa, Madagascar and as far as Hawaii. Peyrot-Clausade (1979), reported that about 58% of the marine polychaetes present in Mauritius are common to Madagascar and 77% of anomurans and brachyuran decapods found in Mauritius and Réunion are found in Madagascar. Although most of the marine organisms of the island are widely distributed in the tropical Indo-pacific, there is a significant endemic element (Hodgkin and Michel, 1962). For example, about 10% of the brachyurans are endemic to the island (Michel, 1964), as are a similar percentage of marine molluscs (Michel, 1974, 1985).

The marine fauna of Mauritius has been mostly studied from collections made by brief visits to the island. Michel (1974) compiled a bibliography on the faunistic work done on marine animals of Mauritius and a list of species, excluding fishes and crabs, recorded to that date. Studies on the crustacean fauna include the work of Michel (1964) who catalogued a list of brachyuran Crustacea recorded from Mauritius, and more recently that of Gherardi and McLaughlin (1994) who catalogued the shallow-water hermit crabs of the island. Studies on the gammaridean amphipod fauna of Mauritius are sparse, although studies on the marine amphipods of Mauritius date back to the 19th century when Templeton (1836) gave brief morphological descriptions of a few species. Barnard (1936) reported on three species of terrestrial amphipods and provided a brief identification key (Barnard, 1964). Recently one more terrestrial species has been described by Stock (1997). Michel (1974) listed marine amphipods reported from Mauritius including those by K.H. Barnard, through personal communications to the Mauritius Institute. To date the most extensive work on the marine amphipods of Mauritius is that by Ledoyer (1978). He analyzed samples of gammaridean amphipods collected at Balaclava and Trou aux Biches (areas in the north-west coast of the island), mostly from coral substrates at depths ranging from 0 to 25 metres, and recorded 89 species of which 24 were new. Ledoyer (1978) concluded that a high degree of endemism exists in Mauritius.

There is little ecological information available on the organisms of the marine littoral zone and lagoons of Mauritius. Work on the ecology of Mauritian rocky shores includes that of Hodgkin and Michel (1962), in which they describe aspects of the vertical zonation of the plants and animals. Baissac et al. (1962) described the fauna of the littoral zone and provided data similar to that of Hodgkin and Michel (1962). Pichon (1967) outlined the main benthic communities of coral reefs and lagoons with reference to the distribution of scleractinian corals. Peyrot-Clausade (1979) studied the distribution of polychaetes, and brachyuran and anomuran decapods in the cryptofauna associated with cavity substrates of reef flats. Henon (1979) studied the distribution of molluscs in the lagoon and on the reefs along a transect at Pointe D'Esny on the south-east coast of the island. Ledoyer's (1978) work is the only one which deals with gammaridean amphipods.

The intertidal zone of Mauritius is currently subject to disturbance due to industrialization and rapidly growing tourist development programmes. Fagoonee (1990) and Gendre et al. (1994) pointed out that untreated industrial waste, agricultural runoff, and sewage are polluting the lagoon ecosystems. The fauna and flora of the intertidal zone are likely to be affected from such anthropogenic changes in environmental conditions and there is a need for monitoring programmes which can help document environmental changes. Thomas (1993) stressed that gammarid amphipods are ideal candidates for such studies because they are ecologically and trophically important, numerically dominant, exhibit a high degree of niche specificity, have a documented sensitivity to a variety of pollutants and toxicants (Reish, 1993) and have relatively low dispersal capabilities. In his review he pointed out that amphipods also show altered behavioural responses to a variety of compounds besides toxicants and pollutants that can cause reduction and elimination of their populations (Thomas, 1993). Amphipods have also been documented to respond to activities like dredging, shoreline alteration, and fishing practices. However, the use of these organisms as bioindicators in the tropics is only possible if sound taxonomic and ecological information are available.

Moreover, amphipods form an important part of the food chain and are fed on by carnivorous fishes (Stoner, 1979). Knowing more about their biology will provide a baseline for futher investigations on feeding habits of nearshore fishes.

Ecological studies on marine invertebrates and their plant habitats have been the subject of various studies. Colman (1940) surveyed the invertebrate populations on intertidal seaweeds. Invertebrate fauna and phytal associations were studied by Dahl (1948), Ledoyer (1962), Hagerman (1966), and Sarma and Ganapathi (1970). Wieser (1952) studied the vertical distribution of the fauna inhabiting seaweeds pointing out that the substratum has a strong influence on the faunal distribution. A study by Sloane et al. (1961) also showed that some invertebrates show a clear preference for living on algae. The effects of physical variables such as currents (Ebling et al., 1948) and turbidity (Moore, 1972, 1973) have also been studied in relation to plant/animal interactions. In the past two decades studies on phytal and faunal associations have tried to determine if correlations exist between weight or biomass of plants and number of species and abundance of invertebrates (Heck and Wetstone, 1977; Gunnill, 1982; Norton and Benson, 1983; Lewis, 1984; Stoner, 1985). Plant/animal relationships in terms of habitat complexity (Stoner and Lewis, 1985), thallus width (Taylor and Cole, 1994) and surface area or degree of branching (Lewis, 1987), have also been investigated. Seasonal variations in the abundance of animals on different algal species (Edgar, 1983b) and seagrasses have also been studied (Mazzella et al., 1988).

Ecological studies on gammaridean amphipods have followed similar trends. Truchot (1963) found correlations between amphipod species and their abundance on different substrates. Selective preferences for substrates by amphipods have also been observed (Stoner, 1980a, 1980b). The relationship between amphipod abundance and habitat complexity in terms of biomass and blade surface of seagrass (Stoner, 1983), and shape, surface area, texture and architecture in algae (Russo, 1990; Hacker and Steneck, 1990) have been studied. Amphipods associate with plants because they use them as food and shelter (Zimmerman et al., 1979; Buschmann, 1990). Some algae produce secondary metabolites which deter predators (Hay et al., 1987; Duffy and Hay, 1994). Studies focusing on the use by amphipods of plants as shelter sites against predators, especially by fish, include those of Nelson (1979), Russo (1987) and Holmund et al. (1990). Other ecological work includes studies of how the abundance and distribution of amphipods are influenced by the vertical position of the plant substrate on the shore (Mcbane and Croker, 1983; Tararam et al., 1986). The influence of environmental variables such as wave-exposure (Krapp-Shickel and Krapp, 1975; Fenwick, 1976; Wakabara et al., 1983; Krapp-Shickel, 1993; Lancellotti and Trucco, 1993) and salinity (Skadsheim, 1983) have also formed part of ecological studies.

The present work has been undertaken to determine the amphipod species found in the intertidal/shallow subtidal zones at 34 sites on the island of Mauritius. In particular the study compares the amphipod fauna of two sites which differ in wave exposure in terms of their species abundance, dominance and diversity. It also investigates the occurrence of amphipod species on different substrates, with emphasis on algal substrates, and the relative abundance of amphipods on algal taxa with different structural morphologies. The work also aims at providing biogeographical information on the amphipods of Mauritius.

2.0 MATERIALS AND METHODS

2.1 Mauritius

2.1.1 Location

The island of Mauritius is located in the Western Indian Ocean at latitudes 19°59′S and 20°32′ S and longitudes 57°18′ E and 57°47′ E about 800 km east of Madagascar, the nearest large land mass (Figure 2.1). Mauritius together with Réunion (20°53′-21° 23′ S, 55°25′-55°50′ E) and Rodrigues (19°40′-19°48′S, 63°20′-63°30′ E) form the Mascarene archipelago.

2.1.2 Geology

Mauritius, the oldest of the three Mascarene islands, was formed by volcanic activity on the Mascarene plateau and the main shield was built between 7.8 and 6.8 million years ago in the early Pliocene (McDougall and Chamalaun, 1969). The island has an area of 1865 km^2 and a coastline 205 km in length. The northern part of the island is a plain while the centre is a plateau rising to a height of about 670 m. The island is surrounded by a large submarine platform (maximum width 25 km), allowing the development of extensive coral reefs covering an area of 300 km ^{2} (Montaggioni and Mahé, 1980). Coral reefs of the fringing type are discontinuous, delineating a series of lagoons, which are broader on the windward east coast (up to about 7.5 km), with an average depth of 1 to 2 m (Pichon, 1971). Coral reefs are absent off the basalt cliffs along the south and west coast and also in places like the mouth of rivers (Pichon, 1967). The shores in these areas are muddy or rocky. Rocky shores occur to a limited extent within lagoons, where much of the shore is sandy or, in the east coast, mangrove-covered (Hodgkin and Michel, 1962). Karisiddaiah et al. (1988) have studied the Mauritius

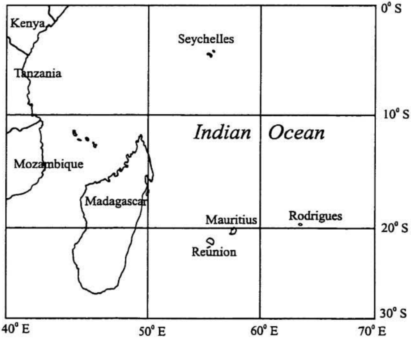


Figure 2.1 Location of the island of Mauritius in the Indian Ocean

beach sands, pointing out that they are mainly calcium carbonate and that the windward beaches along the southern shores of the island are composed of a relatively higher percentage of coarser sized particles as compared to the leeward beaches on the west coast.

About 200 km west of Mauritius is the island of Réunion, separated from it by oceanic depths of more than 4000 m. Réunion was built by two shield volcanoes during four important episodes of volcanic activity from the late Pliocene (about 2 million years ago) to the present period (McDougall, 1971). Réunion has an area of 2500 km^2 with coral reefs occupying an area of only 12 km^2. Rodrigues is situated about 600 km east of Mauritius, and is the youngest (1.5 to 1.3 million years old) (McDougall et al., 1965) and the smallest (110 km^2) of the Mascarene islands. It is surrounded by fringing reefs covering an area of 200 km^2 (Montaggioni, 1974; Faure, 1975).

2.1.3 Climate

The climate of Mauritius is determined by its oceanic position and its location at 20^0 S in the belt of south-east trade winds. These winds blow strongly throughout the winter months, April to September, but in summer they are weaker and veer to the east-south-east and east (Hodgkin and Michel, 1962). The rainfall is markedly seasonal, particularly in the coastal regions, and the wettest months are December to May. The annual rainfall varies from 1000 mm on the west coast to more than 1500 mm on the south-west coast. The central plateau receives about 5000 mm of rain annually. During summer (November to April) occasional cyclones bring strong winds and heavy rains.

The ocean swell is mainly from the south-east throughout the year. The eastern (windward) sector of the island therefore has much stronger wave action than the western (leeward) sector. Mean values for wave heights have been reported to range from 1.67 m in summer months to 2.86 m in winter months from measurements taken 500 m off the shore of Riambel on the south coast of Mauritius (Saha and Jugessur, 1983).

The mean winter (August to September) sea temperature is 22°C and the mean summer (January to April) temperature is 27°C (Michel, 1974). In the immediate vicinity of Mauritius (20°S), the surface sea temperature is lowest (23.3°C) in September and highest (27.9°C) in March (Fagoonee, 1989).

The tides are semidiurnal, with two high and two low tides in each lunar day. The neap tides have an amplitude of 0.5 m and the spring tides 0.7 m (Michel, 1974; Faure, 1975).

The salinity is 35 parts per thousand outside the reefs and slightly lower (33 to 34 parts per thousand) in the lagoons. However, the salinity can vary significantly in the immediate vicinity of river mouths (Michel, 1974).

2.2 Study Sites

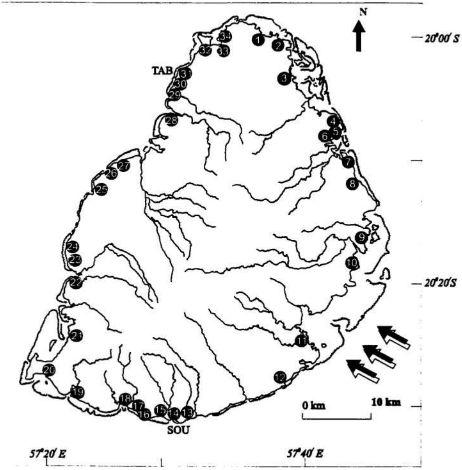
Two sites, namely Trou aux Biches (TAB) on the north-west coast and Souillac (SOU) on the south coast, were chosen for repeated sampling. These sites were selected because they represent sites with different wave exposure and algal substrates. Thirty-two other sites (Figure 2.2) representing a diversity of habitats of different exposures and substrates on nearly all parts of the coast were visited at least once.

Figure 2.2 Map of Mauritius showing the sites visited during the sampling programme

1 : Anse la Raie (ALR)
2 : Grand Gaube (GG)
3 : Pointe des Lascars (PDL)
4 : Roche Noires (RN)
5 : Poste la Fayette (PLF)
6 : Poste la Fayette(Fisheries post) (PLFF)
7 : Poste de Flacq (PDF)
8 : Belle Mare (BM)
9 : Beau Champ(BC)
10 : Quatre Soeurs (QS)
11 : Mahebourg (MAH)
12 : Le Bouchon (BOU)
13 : Gris Gris (GRI)
14 : Souillac (SOU)
15 : Riambel (RIAM)
16 : Pointe aux Roches (PAR)
17 : Saint Felix (STF)
18 : Rivière des Galets (RDG)
19 : M'ma Conde (MAC)
20 : Le Morne (MORN)
21 : Case Noyale (CN)
22 : Tamarin (TAM)
23 : Wolmar (WOL)
24 : Flic en Flac (FEF)
25 : Albion (ALB)
26 : Pointe aux Caves (PAC)
27 : Pointe aux Sables (PAS)
28 : Baie du Tombeau (BDT)
29 : Balaclava (BALA)
30 : Pointe aux Piments (PAP)
31 : Trou aux Biches (TAB)
32 : Mont Choisy (MCHOI)
33 : Grand Baie (GB)
34 : La Cuvette (CUV)

⇖⇖⇖ South-East Trade Winds

〰 Coral reefs


N
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20°20'S
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34
0 km
10 km
57°20' E
57°40' E

2.2.1 Souillac (SOU)

The study site is located at 20^0 31′ S and 57^0 31′ E on the south coast of the island (Figure 2.3A). The area consists of a rocky point with a basaltic cliff about 8 m high which drops to a platform about 15 m wide formed by erosion (Figure 2.3B, S1; Figure 2.4).

The rocky platform has two main tide pools, which together with the surrounding rocks contain a diversity of algae. East of the basaltic area there is a sandy beach (Figure 2.3A, SB; Figure 2 .5) with a few basaltic boulders. Coral reefs are approximately 100 m from shore. The point however is exposed to a high degree of wave action due to the ocean swell from the south and south-east. Northeast of the point the shore is protected and the substrate is a mixture of rocky, sandy, and muddy regions (Figure 2.3, S2; Figure 2.6, Figure 2.7). Terrestrial leaves, algal debris and pieces of wood accumulate as beach debris (Figure 2.3, S3; Figure 2.8). Further north the shore becomes sandy (Figure 2.3, S4; Figure 2.9) and the Savanne River flows into this end of the study area.

2.2.2 Trou aux Biches (TAB)

The study site is located at 20^0 02′ S and 57^0 32′ E in the north-west of the island (Figure 2.10A). The shore consists of a flat sandy substrate interspersed with loose basaltic boulders. The site is protected from waves by a reef about 200 m off shore. The algae are mostly restricted to the rocks and boulders (Figure 2.11). Figure 2.10B, T1, T2, T3, T4 and the corresponding figures 2.11, 2.12, 2.13, 2.14 show the areas where most of the samples were taken.

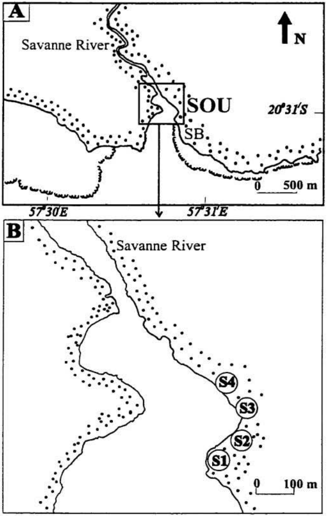

Figure 2.3 A: Part of the south coast of Mauritius showing the Souillac (SOU) study site and distribution of coral reefs

SB: sandy beach

B: The sampling areas (S1-S4) at Souillac

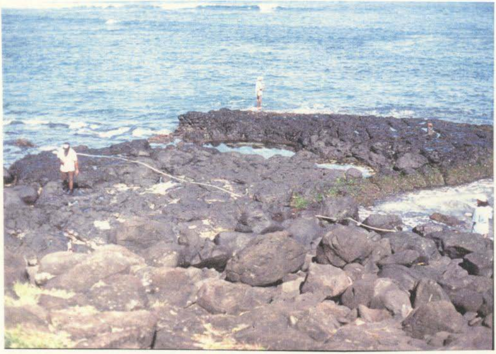

Figure 2.4 Rocky point at Souillac (SOU) showing the platform, two tide pools and basaltic boulders as observed at low tide.

Figure 2.5 Sandy shore with basaltic rocks immediately east of the point at Souillac (SOU). Coral reefs occur about 100 m off shore in the region where the waves are breaking.

Figure 2.6 Basaltic rocks with green and red algae attached, immediately to the west of the point at Souillac (SOU).

Figure 2.7 The most sheltered region at the Souillac (SOU) study site (region S2 and S3 in Figure 2.3B). The substrate consists of basaltic rocks covered with red and green algae.

Figure 2.8 **Terrestrial and algal debris occurring in the region S3 (Figure 2.3B) of the Souillac (SOU) site. The basaltic rocks are mostly covered with green algae and the shore is a mixture of soil and fine sand.**

Figure 2.9 The shore is a mixture of fine sand and soil in region S4 (Figure 2.3B) at Souillac (SOU). A few basaltic boulders covered with green algae are present. The Savanne River is located in the region further west (top right in photograph).

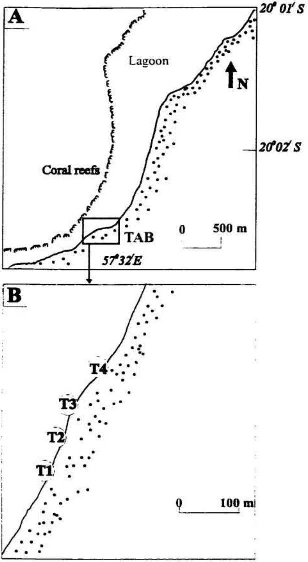

Figure 2.10 A: Part of the north-west coast of Mauritius showing the Trou aux Biches site (TAB) and the distribution of coral reefs.

B: The sampling areas (T1-T4) at Trou aux Biches

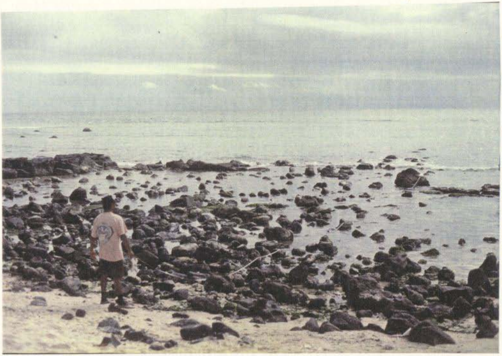

Figure 2.11 Sandy beach with basaltic rocks covered with a mixture of mostly red and green algae at the Trou aux Biches (TAB) study site (corresponds to the region T1 in Figure 2.10B) as observed at low tide. Coral reefs are about 200 m off shore.

Figure 2.12 **Basaltic rocks covered with a few patches of algae occur in the region T2 (Figure 2.10B) at Trou aux Biches (TAB) site.**

Figure 2.13 Basaltic rocks covered with mostly green algae are found in region T3 (Figure 2.10B) at the Trou aux Biches (TAB) site.

Figure 2.14 Basaltic rocks covered with green and red algae occur in the region T4 (Figure 2.10B) at the Trou aux Biches (TAB) site. Further to the north (top left in photograph) is the Trou aux Biches public beach.

2.2.3 Other sites

Summary descriptions of the 32 other sites are given in Appendix A. Representative photographs are given in Appendix B. These sites ranged from protected lagoons, for example, Anse la Raie (Appendix B, Figure B1) and La Cuvette (Appendix B, Figure B2) on the north coast to exposed rocky shores, for example, Pointe aux Roches on the south coast (Appendix B, Figure B3).

2.3 Sampling

The field sampling program was carried out from April to July 1995 with sites usually being visited at low tide.

At Souillac, samples were taken on April 15, May 19, June 5, and June 19 at the locations shown in Figure 2.3B, S1-S4. At Trou aux Biches samples were taken on April 19, 26, May 11, June 6 and June 20. At this site substrates were collected at the locations shown in Figure 2.10, T1-T4 along and perpendicular to the shore spanning a distance of 25 m from the high-water mark towards the lagoon. For all other sites samples were collected more or less randomly from the intertidal and shallow subtidal zones. Few samples were taken deeper than 0.5 m below low water.

2.3.1 Environmental Conditions

For most sites water temperature was recorded using a mercury-in-glass (0-100°C) thermometer held 8 - 10 cm below the surface of the sea, and salinity was recorded using a portable salinometer (refractometer model). The degree of wave exposure of the sites was assessed from observations of waves, and sites were classed into one of three categories :

protected, moderately exposed and exposed corresponding to observations on wave heights of < 0.2 m, 0.2-0.5 m, > 0.5 m respectively.

2.3.2 Algal substrates

Algal samples were collected by placing a 10 cm x 10 cm metal quadrat on the surface and removing all the algae by scraping the surface with a small hand shovel. The sample was quickly transferred to a labelled plastic bag and 5% buffered formalin was added to just submerge the sample. Formalin was used as an irritant and a poison causing the animals to release their hold on the substratum, swim for a few seconds and die (Barnard, 1976). The plastic bag was tied and samples transported to the laboratory. Most samples were sorted within three days of collection as the amphipods could be easily seen since they still retained their colour.

2.3.3 Beach debris substrates (dead algae, wood debris)

The amphipods in these substrates tended to move very fast so the samples of the substrate were collected by hand and quickly transferred to a plastic bag. A small amount of 5% formalin was added and the plastic bag was tied and transported to the laboratory.

2.3.4 Coral rubble and seagrass

Samples of coral rubble were collected from 10 cm x 10 cm quadrats to a depth of 15 cm. Samples were transferred to a bucket, 5% formalin was added. The amphipods were collected as they were driven from the debris. This was usually done on site. Seagrasses were usually found associated with sand. Seagrass samples were collected from a 10 cm x 10 cm quadrat dug to a depth of 15 cm.

A sediment grab was tried on one occasion to collect subtidal samples at Trou aux Biches. However because the substrate consisted of a mixture of sand and coral rubble, the grab did not usually close and samples were lost. A few samples of sand and coral mixture were collected by snorkelling to the bottom and using a plastic scoop (10 cm diameter and 20 cm length) to pick up the substrate. Once back in the boat the contents of the scoop were placed in a plastic bag and 5% formalin was added.

At some sites, samples were collected at random on different substrates, usually sand, the species of algae present, and coral rubble.

2.4 Sorting

Most tropical amphipods are 1 to 8 mm in length and are rarely as large as 12 mm Barnard (1976), and from preliminary observations on the size of the amphipods in samples it was found appropriate to use a sieve with a mesh size of 0.7 mm for sorting.

Samples that were transported to the laboratory were sorted by placing each sample in a bucket and washing with tapwater. The contents were then poured over a 20-cm diameter sieve of 0.7mm mesh size. The sieve was then placed over a shallow tray which contained sufficient water to cover the contents. By vigorous, vertical agitation of the sieve and aeration of the submerged sample, the amphipods floated to the surface where they were picked up with fine forceps and transferred to vials containing 5 % buffered formalin (Stoner, 1983). The procedure was repeated 4 or 5 times depending on the sample to ensure that all amphipods were collected. Algal surfaces were then checked for amphipods which may have remained on them. A sample of each type of alga and seagrass was also preserved in 5% formalin for later identification.

The amphipods in some coral rubble and seagrass substrates had to be extracted in the field because of logistical problems. As a result some of the smaller specimens were probably missed. This potential bias should be kept in mind in the discussion of these substrates.

2.5 Marine flora identification procedure and groupings

Algae and seagrasses were identified to genus or species by the author with the assistance of Dr. A. Whittick. Reference literature included the works by Boergesen (1940-1957), Jaasund (1976), Mshigeni (1985) and Jagtap (1993). The publication by Littler et al. (1989) on marine algae of the Caribbean was quite helpful during the identification process. Samples were also compared with specimens in the Memorial University of Newfoundland Phycological Herbarium .

Algae were grouped into morphological categories following a modification of the groups suggested by Hacker and Steneck (1990) and Steneck and Watling (1982). Algae were grouped into toughness categories following the classification used by Steneck and Watling (1982).

2.6 Amphipod identification procedure

The protocol for amphipod identification was based on some of the guidelines set by Ledoyer (1979b). Amphipods were first sorted into families and groups (for individuals which were partly damaged or for individuals for which family identification was not immediately apparent) based on gross external morphology by viewing them under a stereomicroscope. The number of amphipods in each category was counted and the families Talitridae, Hyalidae, Ampithoidae, Gammaridae, Melitidae and Corophiidae were chosen in that order for species identification. The choice of this order was based on the number of samples containing a family, the abundance of amphipods in the family in the whole collection and, also, if the family appeared to be less complex (having individuals appearing to belong to one or two species).

At the family level, the specimens in a sample were sorted into genera or groups of species. For each of these groups male specimens which had most of their appendages were first dissected followed by female specimens. The protocol adopted for species identification dissections was a modified version of the dissection technique outlined by Barnard and Karaman (1991). Prior to dissection the body length of the specimen was recorded by holding it straight and measuring the distance along the dorsal side of the body from the base of the first antennae to the base of the telson (Ward, 1985). A micrometer scaled eyepiece fixed to the stereomicrosocope was used to make this measurement. This method of measurement excludes the telson and the rostrum, the lengths of which vary with families of amphipods. Notes on the general appearance of the specimen, its sex and maturity were also made. For dissection the amphipod was laid on its left side in a Petri-dish with its legs projecting away from the author. The body was covered to more than twice its depth with a solution of glycerine to reduce the effects of surface tension during dissection. A pair of jeweller's forceps with very fine tips, a blunt pair of forceps, and insect needles mounted on glass rods, were used during dissection.

Pereopods 4 and 5 of the amphipod were removed together by gently pulling them from the body surface. Similarly the remaining pereopods, gnathopod 1 and gnathopod 2, were removed and placed on a slide containing permanent mounting medium [a mixture of CMC-9 (Low viscosity, Carboxy-methyl cellulose) previously stained with Lignin pink dye] and spread to the size of a cover slip. Antennae 1 and 2 were also removed and placed on the same slide. Before placing the cover slip the parts were viewed under a stereomicroscope to make sure they were spread out and not overlapping. A second slide was made by removing the telson and uropods 1, 2 and 3, of the same side as the legs. When making this slide care was taken to make sure the uropods were mounted dorsal side up. The third permanent slide was made by first removing the maxilliped, then maxilla 2, followed by maxilla1 and the lower lip (which is transverse and requires a stronger pull) and finally the mandible. The upper lip was not removed. The remaining carcass usually had a complete set of pereonal and pleonal parts, except for the telson, and it was placed in a vial containing 5% formalin. In the case of very small specimens the uropods and the telson were placed on the slide as a unit and then gently teased apart. This procedure was also used when dissecting the mouth parts of very small specimens as it prevented loss of parts while transferring them from the Petri-dish to the slide.

Slides were allowed to dry overnight at room temperature and then examined using a compound microscope. Specimens were identified by the author and Prof. D.H. Steele by comparing their external morphology to amphipod species known to exist in the Indo-pacific region .

Once a species was identified, notes on its special features and how to distinguish it from other species were made. Identification of specimens of the same species was generally possible without dissection once the author was familiar with the characteristics of a species. However, in case of doubts, specimens were dissected for confirmation of their identity. The major problem faced was that in many specimens the antennae were broken and one had to look for other diagnostic features to identify them.

A total of 34,441 specimens were collected, examined and identified in this study.

A number of specimens differed significantly from all known species and they are likely to represent undescribed taxa. These have been designated with a number (e.g. *Ampithoe sp. 1*).

The species are reported following the superfamily classification of amphipod families given by Bousfield (1983) with additions of some of the families as reported by Barnard and Karaman (1991).

2.7 Data analysis

For all 486 samples (280 quadrats and 206 non-quadrat) information on date, site of collection, method of collection, type of substrate and total number of amphipods was recorded. For those samples containing amphipods (465), a list of amphipod species together with the number of specimens of each species was compiled. The number of quadrat (10 cm x 10 cm) and non-quadrat samples from the various types of substrate are shown in Tables 2.1 and 2.2 respectively.

Table 2.1 Number of samples collected using a 10 cm x 10 cm quadrat according to the type of substrate.

Substrates	Number of samples containing amphipods	Number of samples without amphipods	Total number of samples
Algae (pure stands)	208	13	221
Algae (mixtures)	23	4	27
Seagrasses*	20	0	20
Coral rubble	5	2	7
Sand	3	2	5
Total	259	21	280

*: *Halodule univeris* (Forsk.) Aschers. in Boissier
Halodule ovata Guad. in Freycin

Table 2.2 Number of non-quadrat samples containing amphipods

Substrates	Number of samples
Algae (pure stands)	100
Algae (mixtures)	24
Seagrasses*	3
Coral rubble	3
Sand	5
Debris	20
Coral and algae mixture	35
Bivalves	2
Sponge	5
Sponge and algae mixture	7
Mangrove **	2
Total	206

* : *Halodule uninervis* (Forsk.) Aschers. in Boissier
Halophila ovata Guad. in Freycin

**: *Rhizophora mucronata* Lamk.

2.7.1 Occurrence of amphipod species in collections from algae, seagrasses, debris, coral rubble and sand

A subset of the data consisting of samples containing amphipods was used to determine the percentage frequency of occurrence of amphipod species in the five most frequently sampled substrates (Table 2.3).

Table 2.3 Number of samples of each substrate type used in computing percentage frequency of occurrence (A_{sub}) of amphipod species.

Substrate categories	Pooled number of quadrat and non-quadrat samples (N_{tots})
Algae (pure stands and mixtures)	355
Seagrass	23
Debris	20
Coral rubble	10
Sand	8

A_{sub} was computed for 11 species of amphipods for quadrat and no-quadrat samples separately. Since the patterns of the percentage frequency of occurrence were similar for both types of smapling, the data sets were pooled for the analysis.

For 64 amphipod species which occurred at least once in one of these five substrates the percentage frequency of occurrence was computed using the formula

$$A_{sub} = (N_{sub} / N_{tots}) * 100$$

where N_{sub} is the number of samples of the particular substrate containing the amphipod species and N_{tots} is the total number of samples of that substrate.

2.7.2 Occurrence of amphipod species on algae

Thirty-five of the 64 amphipod species were used to compute their percentage frequency of occurrence on specific algal substrates. Amphipod species occurring only on algae (except the leucothoids, amphilochids and oedicerotids) and those ubiquitous species with a percentage frequency of occurrence (A_{sub}) of at least 2 % in algae (but excluding the ampeliscids and lysiannassids) were used. The leucothoids, amphilochids, oedicerotids, ampeliscids and lysiannassids were excluded because their occurrence on algae is only incidental (Prof. D.H. Steele, pers. comm.).

In this analysis 17 algal categories were used. Those algae with less than 5 samples were excluded. Algae of the genus *Padina* were pooled together as were algae belonging to the genus *Gracilaria* (except *Gracilaria salicornia* which had a different morphology) because the species within each of these genera had similar morphologies. All other categories consisted of a single algal species. For these 17 categories (Table 2.4) only samples containing amphipods were used. The percentage frequency of occurrence of particular amphipod species (A_{alg}) was computed using the formula

$$A_{alg} = (N_{alg} / N_{talg}) * 100$$

where N_{alg} is the number of samples of a particular alga on which the amphipod occurred and N_{talg} is the number of samples of that alga as shown in Table 2.4.

Table 2.4 Categories of algae and the number of samples of each used to compute the percentage frequency of occurrence of amphipod species (A_{alg})

Algal groups	Symbol	Number of samples (pooled pure stands of quadrat and non-quadrat samples) (N_{talg}) *
Acanthophora spicifera (Vahl) Borgesen	As	5
Amansia glomerata C. Agardh	Ag	9
Amphiroa flagilissima (L.) Lamouroux	Af	6
Boodlea composita (Harvey) Brand	B	6
Caulerpa sertulariodes (Gmelin) Howe	Cs	5
Caulerpa racemosa (Forsk.) J. Agardh	Co	7
Centroceras clavulatum (C. Agardh) Montagne	Cc	23
Digenia simplex (Wulfen) C. Agardh	Ds	18
Enteromorpha flexuosa (Wulfen) J. Agardh	E	29
Gracilaria spp. **	Gp	17
Gracilaria salicornia (J. Agardh) Dawson	Gs	26
Laurencia papillosa (Forsk.) Greville	L	12
Padina spp. ***	P	24
Sargassum densifolium Zan.	Sr	12
Turbinaria ornata (Turn.) J. Agardh	T	11
Ulva lactuca L.	U	44
Wurdemania miniata (Draparaud) Feldmann & Hamel	W	5

* : Quadrat and non-quadrat samples were again pooled for this analysis after checking the patterns for the percentage frequency of occurrence (A_{alg}) in 11 species of amphipods for samples collected by the two methods.

** : includes *Gracilaria corticata* J. Agardh, *Gracilaria crassa* Harvey, *Gracilaria edulis* (J. Agardh) Silva, *Gracilaria millardetii* J. Agardh, *Gracilaria sp.*

*** : includes *Padina boryana* Thivy, *Padina gymnospora* (Kutzing) Vickers, *Padina tetrostromatica* Hauck, *Padina sp.*

2.7.3 Mean abundance of amphipod species on different species of algae

Analysis of variance (ANOVA) was used to test for differences in the mean number of amphipods of particular species in 10 cm x 10 cm quadrats of algae. Analyses were performed only on data from Souillac (SOU) (12 algal categories) where replicate samples of algae were collected.

2.7.4 Mean abundance of amphipodspecies on algae of different morphologies

Analysis of variance was used to test if the mean number of individuals of particular species of amphipods in 10 cm x 10 cm quadrats was significantly different among algae of different morphologies. The analysis was performed using data on the number of amphipods from algae collected using quadrats at Souillac (SOU). Algal taxa were sorted according to morphology into 3 classes as shown in Table 2.5.

Table 2.5 Categories into which algal taxa were placed to compare abundance of amphipods in algal morphological categories [based on a modification of Hacker and Steneck (1990) and Steneck and Watling (1982)]

Algae morphology	Class	Algae taxa
Filamentous (Fi)	1	*Enteromorpha flexuosa*
Foliose (Fo)	2	*Padina spp., Ulva lactuca*
Branched (Br)	3	*Acanthophora spicifera, Amansia glomerata, Amphiroa flagelissima, Caulerpa racemosa, Digenia simplex, Gracilaria spp., Gracilaria salicornia, Sargassum densifolium, Wurdemania miniata*

(Note: Groupings are shown only for the algae used in the analysis)

2.7.5 Mean abundance of amphipods on algae of different toughness

The purpose of the analysis was to determine if algal samples sorted according to the toughness of their tissues (Table 2.6) supported different mean numbers of amphipods.

Table 2.6 Categories into which algal taxa were placed based on toughness of their tissues [using classification given by Steneck and Watling (1982)]

Algal toughness	Algae categories
1 (low)	*Enteromorpha flexuosa* , *Ulva lactuca*
2 (intermediate)	*Acanthophora spicifera, Caulerpa racemosa, Digenia simplex*
3 (high)	*Amansia glomerata, Amphiroa flagelissima, Gracilaria spp., Gracilaria salicornia, Padina spp., Sargassum denisfolium, Wurdemania miniata*

(Note: The groupings are shown only for algal categories used in the analysis)

This analysis was carried out using data collected from 10 cm x 10 cm algal quadrat samples at Souillac (SOU).

For all the tests carried out the general linear model (GLM) (MINITAB, 1992a) approach was used. The assumptions made when running a GLM is that the mean value of the residuals is zero, the variance of the residuals is constant, the residuals are independent of each other and the residuals follow a normal distribution. For count data, the residuals usually follow a Poisson distribution where the mean is equal to the variance and the latter increases as the mean increases, causing heterogeneity of variance (Sokal and Rohlf, 1995). However, plots of residuals on fitted values did not show bows and arcs implying that the general linear model and residuals are not associated and one could proceed with the analysis.

The residuals were checked for normality both by using a histogram to see if they were normally distributed, and by a plot of the normal equivalent deviates (n scores) against the residuals - a straight line implies that the residuals are normally distributed.

In cases where the residuals were not normally distributed, randomisation tests were carried out. This permits the computation of a p-value from an empirical distribution generated from the data rather than from a theoretical distribution. The test involves calculation of the observed F-ratio ($F_{obs.}$), then randomising the data and recalculating the F-statistic to obtain an outcome when the null hypothesis is true. The process was repeated 1000 times (in the present case) to obtain a frequency distribution for F-ratios when the null hypothesis is true. The observed outcome ($F_{obs.}$) was then compared with this distribution and the p-value computed as the probability of obtaining an F-ratio above F_{obs}.

The type I error (α) was set at 5 % and a p value of less than 0.05 leads to the rejection of the null hypothesis. All computations were done using the statistical software MINITAB (1992b).

2.7.6 Analysis of amphipod community on algae

2.7.6 .1 Species diversity

2.7.6.1.1 Species richness and rarefaction

Species richness is the number of species in a community (Krebs, 1989). Magurran (1988) noted that species richness provides an "extremely useful measure" of diversity if a study area can be successfully delimited in space and time and the constituent species enumerated and identified. However, it is difficult to enumerate all the species in a community and the number of species invariably increases as the number of samples and sampling effort increase.

Rarefaction is a statistical method for estimating the number of species (s) expected in a random sample of individuals (n) taken from a collection. If the total sample has S species and N individuals, the rarified sample must always have $n < N$ and $s < S$ (Krebs, 1989).

Rarefaction curves were plotted for each of the different categories of algae at Souillac (SOU) and Trou aux Biches (TAB).

At each site and for each algal category, the number of amphipods of each species was pooled for pure stands of quadrat and non-quadrat samples, and total number of specimens computed. This information was then used to compute the expected number of species for samples of different sizes using the program RAREFACT (Krebs, 1991).

2.7.6.1.2 Heterogeneity measures

The **Shannon-Wiener index** was used as a measure of diversity. It was chosen because it has a fairly good discriminant ability, it is widely used and it is only moderately sensitive to sample size (Magurran,1988). This index assumes that individuals are randomly sampled from an indefinitely large population (Magurran, 1988). The index also assumes that all species are represented in a sample. It is computed using the formula

$$H' = -\sum_{i=1}^{S} p_i \log_e p_i$$

where S is the number of species in a sample and p_i is the proportion of observations in species i.

Denoting n to be the sample size, and f_i to be the number of observations in species i, then $p_i = f_i / n$. The function can be rewritten as

$$H' = \frac{n\log_e n - \sum_{i=1}^{S} f_i \log_e f_i}{n}$$

(Source: Zar, 1996)

Although as a measure of heterogeneity the Shannon-Wiener index takes into account the evenness or abundance of the different categories, it is possible to calculate a separate additional measure of evenness (J).

$$J = H' / H'_{max}$$

where H'_{max} = $\log_e S$, the maximum possible diversity for a sample consisting of S species.

J is a measure of **relative diversity** and is constrained between 0 and 1 with 1 representing a situation in which all species are equally abundant (Magurran, 1988). As with H', the evenness measure J assumes that all species in a community are accounted for in the sample.

The calculation of S, H', and J was done by writing a batch file in MINITAB (1992b).

The indices were computed for each algal category at Souillac (SOU) and Trou aux Biches (TAB). For each algal category, only samples collected by the quadrat method were used.

2.7.6.2 Mean total number of amphipods

2.7.6.2.1 Algal categories

An analysis of variance was performed on the total number of amphipods in the 12 algal categories at Souillac (SOU) to determine if the means were significantly different. The analysis was repeated for the four algal categories present at Trou aux Biches (TAB).

2.7.6.2.2 Algal morphological categories

Algal taxa were sorted according to morphology into 3 classes as shown in Table 2.5. for Souillac (SOU) and Table 2.7 for Trou aux Biches (TAB). The test was performed to determine if algae having different morphology supported different mean numbers of amphipods per 10 cm x 10 cm quadrats.

Table 2.7 Categories into which algal taxa were placed to compare abundance of amphipods in algal morphological groups

Algal morphology	Class	Algae taxa
Filamentous (Fi)	1	*Centroceras clavulatum*
Foliose (Fo)	2	*Ulva lactuca*
Branched (Br)	3	*Boodlea composita, Gracilaria salicornia*

(Note: Groupings are shown only for the algae used in the analysis for TAB)

2.7.6.2.3. Algal toughness categories

The purpose of the analysis was to determine if algal samples sorted according to toughness of their tissues supported different mean total numbers of amphipods. This analysis was carried out using the algal categories available at Souillac and the groupings based on toughness shown in Table 2.6.

2.7.6.3 Community structure of amphipods at sites of different wave exposure.

2.7.6.3.1. *Ulva lactuca* at Souillac (SOU) and Trou aux Biches (TAB)

At two sites, Souillac (SOU) and Trou aux Biches (TAB), the amphipod fauna on the alga *Ulva lactuca* was compared in terms of total number of amphipods (using one-way ANOVA), species richness (using rarefaction) and species heterogeneity (Shannon-Wiener index and Evenness index). *Ulva lactuca* was chosen because it was the only species from which a suitable number of replicate samples had been collected from both sites.

Two-way analysis of variance was used to test if relative abundance of amphipod species in quadrat samples was significantly different at the two sites. If the interaction term was significant, one-way analysis of variance was used to test if the mean numbers of amphipods of particular species was significantly different at the two sites.

2.7.6.3.2 Cluster analysis of amphipod fauna of algae from sites of different exposure

The amphipod fauna of 17 algal categories collected from sites of different exposure (protected, moderately exposed and exposed) (Table 2.8) was compared using hierarchical cluster analysis. Cluster analysis is a technique for grouping samples which are similar to one another (Krebs, 1989).

The analysis was run using presence and absence of amphipod species. The data for each of the algal categories present at each of the site exposure groups were first aggregated and then converted to binary form. The clustering method used was "between group linkage" on Jaccard's similarity measure for binary data. This similarity index excludes joint absences and matches and non-matches are given equal weight (SPSS, 1996). All computations and dendrograms were constructed using SPSS (1996).

Table 2.8 Twenty-seven sites sorted according to degree of wave exposure (For full names see Figure 2.2)

	Exposure category	Sites
1	Protected (sheltered) (S)	FEF, ALB, ALR, BALA, BDT, BM, CUV,GB, GG, MAH, MCHOI, PAP, PAS, PDL, RDG, TAB, TAM, WOL
2	Moderately exposed (ME)	PDF, BOU, PLFF
3	Exposed (E)	GRI, PAC, PAR, PLF, RN, SOU

3.0 RESULTS

3.1 Amphipod fauna of Mauritius recorded in the present study

The gammaridean amphipod fauna collected in this study includes 69 species in 37 genera and 18 families (Table 3.1). Forty-one species are reported for the first time from the islands of which 19 are undescribed. The undescribed species are similar to, but distinct from, known species. Including those reported by Ledoyer (1978), 130 species of amphipods have now been recorded from Mauritius (Table 3.2).

Table 3.1 Gammaridean amphipod species collected from Mauritius in the present study (* : species recorded for the first time on the island; numbers in brackets indicate the number of specimens in the collection).

- Superfamily Eusiroidea
  - Family Eusiridae
    - *Tethygeneia pacifica* (Schellenberg, 1938) * (332)

- Superfamily Oedicerotoidea
  - Family Oedicerotidae
    - *Perioculodes longimanus* (Bate & Westwood 1868) * (3)

- Superfamily Leucothoidea
  - Family Amphilochidae
    - *Amphilochus sp. 1* Undescribed species * (3)
    - *Amphilochus sp. 2* Undescribed species * (9)
    - *Gitanopsis sp. 1* Undescribed species * (9)

  - Family Leucothoidae

    - *Leucothoe crenatipalma* Ledoyer, 1972 (3)
    - *Leucothoe hyhelia* J.L. Barnard, 1965 (1)
    - *Leucothoe madrasana* Sivaprakasam 1967 (2)
    - *Leucothoe predenticulata* Ledoyer, 1978 ? (9)

Leucothoe sp. 1 Undescribed species * (3)
Leucothoe sp. 2 Undescribed species * (1)
Leucothoella bannwarthi Schellenberg, 1938 (6)

Family Anamixidae
Anamixis pottsi (Shoemaker, 1933) (23)
Paranamixis bocki Schellenberg, 1938 (15)

Superfamily Talitroidea

Family Hyalidae
Hyale ayeli J.L. Barnard, 1955 * (4035)
Hyale chevreuxi K.H. Barnard, 1916 * (5091)
Hyale grandicornis (Kroyer, 1845) * (2684)
Parhyallela indica K.H. Barnard, 1935 * (161)

Family Talitridae
Orchestia anomala Chevreux, 1901 * (4465)

Superfamily Lysianassoidea
Family Lysianassidae
Lysianassa ewa J.L. Barnard, 1970 (109)
Lysianassa sp. 1 Undescribed species * (7)

Superfamily Liljeborgioidea
Family Sebidae
Seba typica (Chilton,1884) (17)

Superfamily Dexaminoidea
Family Dexaminidae
Dexaminella aegytiaca var. rotundicoxa Ledoyer, 1972 (1)
Paradexamine micronesica Ledoyer, 1979 (1)
Paradexamine orientalis (Spandl, 1923)* ? (1)

Superfamily Ampeliscoidea
Family Ampeliscidae
Ampelisca sp. 1 Undescribed species * (3469)

Superfamily Hadzioidea
Family Hadziidae
Hadzia dentifera Ledoyer, 1982 * ? (175)

Family Melitidae

Ceradocus mahafalensis Ledoyer, 1979 (17)
Ceradocus sp. 1 Undescribed species * (11)

Elasmopus ecuadorensis hawaiensis Schellenberg 1938 (309)
Elasmopus hooheno J.L. Barnard, 1970 (337)
Elasmopus pectenicrus (Bate, 1862) * (56)
Elasmopus spinidactylus Chevreux, 1908 * (227)
Elasmopus sp. 1 Undescribed species * (146)

Maera mannarensis Sivaprakasam, 1968 * (12)
Maera octodens Sivaprakasam, 1968 (10)
Maera pacifica Schellenberg, 1938 (136)
Maera quadrimana (Dana, 1853) (32)
Maera serrata Schellenberg, 1938 (74)
Maera sp. 1 Undescribed species * (1)
Maera sp. 2 Undescribed species * (1)
Maera tulearensis Ledoyer, 1972 (2)

Melita appendiculata (Say, 1818) (46)
Melita zeylanica Stebbing , 1904 * (132)

Mallacoota insignis (Chevreux, 1901) (644)
Mallacoota sp. 1 Undescribed species * (1021)
Mallacoota subcarinata (Haswell, 1880) (3480)

Nuuanu sp.1 Undescribed species * (17)

Superfamily Corophioidea

Family Ampithoidae

Ampithoe cavimana[1] Sivaprakasam, 1970 (909)
Ampithoe kulafi J.L. Barnard, 1970 * (62)
Ampithoe ramondi Audouin, 1826 (117)
Ampithoe sp. 1 Undescribed species * (1038)
Ampithoe sp. 2 Undescribed species * (417)

Cymadusa filosa Savigny, 1816 * (922)
Cymadusa microphthalma (Chevreux, 1901)* (393)

Paradusa mauritiensis Ledoyer, 1978 (53)

Paragrubia vorax Chevreux, 1901 (136)

Perampithoe falsa (K.H. Barnard, 1932) * (50)

Family Isaeidae

Gammaropsis atlantica Stebbing 1888 (31)
Ledoyerella sp. 1 Undescribed species * (80)

Family Ischyroceridae

Erichthonius brasiliensis (Dana 1853) * ? (15)
Jassa sp. 1 Undescribed species * (480)
Jassa sp. 2 Undescribed species * (285)

Family Aoridae

Bemlos waipio (J.L. Barnard, 1970)* (67)

Globosolembos indicus (Ledoyer, 1967) (15)

Grandidierella bonnieri[2] Stebbing 1908 * (292)
Grandidierella grossimana Ledoyer, 1968 * (603)

Lembos sp. 1 Undescribed species * (1)

Family Corophiidae

Corophium acherusicum (Costa , 1851) * (1146)

Note: [1] : *Ampithoe cavimana* Sivaprakasam, 1970 is synonymized with *Cymadusa brevidactyla* (Chevreux, 1907) in Barnard and Karaman (1991). Ledoyer (1978) suggests that these may be two different species.

[2] : *Grandidierella bonnieri* is synonymised to *Grandidierella megnae* (Giles, 1888) in Barnard and Karaman (1991).

'?' : identification uncertain

3.2 Biogeography

3.2.1 Indo-Pacific distribution of amphipods reported from Mauritius

Based on a review of work done before 1986, Barnard and Karaman (1991) reported that 714 species of gammaridean amphipods were known from the Indo-pacific including the Red Sea. The number of amphipod species currently reported in the Indo-pacific is more than 1000 species (Lowry and Stoddart, 1995).

For the 130 species of amphipods recorded from Mauritius, their occurrence in 10 Indo-pacific locations is shown in Table 3.2. The amphipod fauna of the Maldives and Laccadives archipelagoes, Moluccas, Mozambique, Philippines, Seychelles and Sri Lanka are not well documented and one can compare them only in terms of the species that have been reported. The amphipod faunas of Fiji, Hawaii, India and Madagascar, on the other hand, have been fairly well documented and can be compared to the Mauritian amphipod fauna. Several species are shared and some of the species show wide Indo-pacific distribution. For example, the eusirid, *Eusiroides diplonyx*, the anamixid, *Anamixis pottsii*, the stenothoid, *Stenothoe gallensis* have been reported from Madagascar, India and as far east as Hawaii. Among the Melitidae, *Elasmopus pectenicrus*, *Elasmopus spinidactylus*, *Maera octodens*, *Maera pacifica*, *Maera quadrimana* are also seen in these four locations.

The beach hopper, *Orchestia anomala* has been reported from India, Madagascar, Mozambique, Seychelles and as far east as the Moluccas. From the compilation in Table 3.2, *Mallacoota subcarinata*, *Ampithoe ramondi*, *Cymadusa filosa* and *Paragrubia vorax* are among the species that have been reported from several regions in the Indo-pacific.

A comparison of the species recorded in Mauritius and known to occur in Fiji, Hawaii, India and Madagascar indicates that more than 50% of gammaridean amphipods found in Mauritius occur in its closest large land mass, Madagascar (Table 3.3). Species that are shared between Mauritius and Madagascar encompass 25 of the 30 families listed in Table 3.2.

Twenty-eight of the amphipod species reported in Mauritius have also been reported from India. A close similarity, especially in species of the families Ampithoidae and Hyalidae, is apparent.

Fiji and Hawaii are island archipelagoes very far from Mauritius. However, the species shared between Mauritius and Hawaii is notable, for example, 5 of the 9 species of *Elasmopus* of the family Melitidae in Mauritius have been reported from Hawaii.

Table 3.2 Occurrence of amphipods recorded from Mauritius (MRU) in the present study and by Ledoyer (1978) (species not found in the present study indicated as **) and other Indo-pacific regions: FIJ, Fiji; HAW, Hawaii; IND, India; MAD, Madagascar; MAL, Maldives and Laccadives archipelago; MOL, Moluccas; MOZ, Mozambique; PHI, Philippines; SEY, Seychelles; SRL, Sri Lanka. Species' names have been abbreviated. (See Appendix C and Table 3.1 for complete spelling). The columns are arranged in the order of geographical distance from Mauritius.

Species	MRU	MAD	MOZ	SEY	MAL	SRL	IND	PHI	MOL	FIJ	HAW
Family Eusridae											
Eusi.dipl. **	+	+	-	-	-	-	+	-	-	+	+
Teth paci.	+	+	-	-	-	-	-	-	+	-	+
Family Exoedicerotidae											
Kana.mano **	+	+	-	-	-	-	-	-	-	-	+
Family Oedicerotidae											
Peri.long.	+	+	+	-	-	-	+	-	-	-	-
Family Pleustidae											
Tepi.barn. **	+	+	-	-	-	-	-	-	-	-	-
Family Amphilochidae											
Amph.lati. **	+	-	-	-	-	-	-	-	-	-	-
Amph.neop. **	+	+	-	-	-	+	+	-	+	-	-
Amph.sp. 1	+	-	-	-	-	-	-	-	-	-	-
Amph.sp. 2	+	-	-	-	-	-	-	-	-	-	-
Gita.pele **	+	+	-	-	-	-	-	-	-	-	+
Gita.sp. 1	+	-	-	-	-	-	-	-	-	-	-
Family Cyprodeidae											
Cypr.orna. **	+	+	-	-	-	-	+	-	+	-	-
Unya.dabb. **	+	-	-	-	-	-	-	-	-	-	-
Family Leucothoidae											
Leuc.acut. **	+	-	-	-	-	-	-	-	-	-	-
Leuc.angu. **	+	+	-	-	-	-	-	-	-	-	-
Leuc.cren.	+	+	-	-	-	-	-	-	-	-	-
Leuc.hyhe.	+	+	-	-	-	-	-	-	-	-	+
Leuc.lihu **	+	+	-	-	-	-	-	-	-	-	+
Leuc.micr. **	+	-	-	-	-	-	-	-	-	-	-
Leuc.madr.	+	+	-	-	-	-	+	-	-	-	-
Leuc.pred.	+	-	-	-	-	-	-	-	-	-	-

Table 3.2 contd.

Species	MRU	MAD	MOZ	SEY	MAL	SRL	IND	PHI	MOL	FIJ	HAW
Leuc.sp.1	+	-	-	-	-	-	-	-	-	-	-
Leuc.sp. 2	+	-	-	-	-	-	-	-	-	-	-
Leua.bann.	+	+	-	-	-	-	-	+	-	+	-
Family Anamixidae											
Anam.gros. **	+	-	-	-	-	-	-	-	-	-	-
Anam.pott.	+	+	-	-	-	-	+	-	+	-	+
Para. bock.	+	+	-	-	-	-	-	-	-	-	-
Para.esca. **	+	+	-	-	-	-	-	-	-	-	-
Family Colomastigidae											
Colo.luna. **	+	+	-	-	-	-	-	-	-	+	+
Colo.trun. **	+	+	-	-	-	-	-	-	+	-	-
Family Stenothoidae											
Sten.gall. **	+	+	+	-	-	+	+	-	-	-	+
Family Hyalidae											
Hyal ayel.	+	-	-	-	-	-	+	-	-	-	+
Hyal. chev.	+	+	-	-	-	-	+	-	-	+	-
Hyal.gran.	+	-	+	-	-	-	-	-	-	-	+
Hyal.iner. **	+	-		-	-	-		-	-	-	-
Parh.indi.	+	-	-	-	-	-	+	-	-	-	-
Family Talitridae											
Orch.anom.	+	+	+	+	-	-	+	-	+	-	-
Family Eophliantidae											
Cein.lati. **	+	-	-	-	-	-	-	-	-	-	-
Family Phliantidae											
Pere.alan. **	+	+	-	-	-	-	-	-	-	+	+
Family Lysianassidae											
Amar.macr **	+	+	+	-	-	-	-	-	-	-	-
Ensa.angu. **	+	-	-	-	-	-	-	-	-	-	-
Lysi.ewa	+	+	-	-	-	-	-	+	-	-	+
Lysi.sp. 1	+	-	-	-	-	-	-	-	-	-	-
Parl.maur. **	+	-	-	-	-	-	-	-	-	-	-
Family Iphimediidae											
Iphi.comp. **	+	-	-	-	-	-	-	-	-	-	-
*Iphi. sp**	+	-	-	-	-	-	-	-	-	-	-
Family Liljeborgiidae											
Lilj.heei. **	+	+	-	-	-	-	-	-	-	-	+
Lilj.prox. **	+	-	-	-	-	-	-	-	-	-	-
Family Sebidae											
Seba.hirs. **	+	-	-	-	-	-	-	-	-	-	-

Table 3.2 contd.

Species	MRU	MAD	MOZ	SEY	MAL	SRL	IND	PHI	MOL	FIJ	HAW
Seba.typi.	+	-	-	-	-	-	-	-	-	-	-
Family Dexaminidae											
Dexa.aegy.	+	+	-	-	-	-	-	-	-	-	-
Para.inde. **	+	+	-	-	-	-	-	-	-	-	-
Para.micr.	+	+	-	-	-	-	-	-	-	-	-
Para.orie.	+	+	-	-	-	-	-	-	+	-	-
Family Ampeliscidae											
Ampe.pygm. **	+	+	-	-	-	-	-	-	-	+	-
Ampe.sp. 1	+	-	-	-	-	-	-	-	-	-	-
Family Hadziidae											
Hadz.dent	+	+	-	-	-	-	-	-	-	-	-
Family Melitidae											
Cera.hawa. **	+	+	-	-	-	-	-	-	-	-	+
Cera.maha.	+	+	-	-	-	-	-	-	-	-	-
Cera.sp. 1	+	-	-	-	-	-	-	-	-	-	-
Elas.ecua.	+	+	-	-	-	-	-	-	-	-	+
Elas.hooh.	+	+	-	-	-	-	-	-	+	-	+
Elas.molo. **	+	+	-	-	-	-	-	-	-	+	+
Elas.pect.	+	+	-	-	-	-	+	-	-	-	+
Elas.pseu. **	+	+	-	-	-	-	-	-	-	+	-
Elas.spin.	+	+	-	-	-	-	+	-	-	+	+
*Elas.sp. **	+	-	-	-	-	-	-	-	-	-	-
Elas.sp.1	+	-	-	-	-	-	-	-	-	-	-
Erio.dent. **	+	-	-	-	-	-	-	-	-	-	-
Maer.aequ. **	+	+	-	-	-	-	-	-	-	-	-
Maer.mann.	+	-	-	-	-	-	+	-	-	-	-
Maer.octo.	+	+	-	-	-	-	+	-	-	+	-
Maer.paci.	+	+	-	-	-	-	+	-	-	+	+
Maer. quad.	+	+	-	-	-	-	+	-	-	+	+
Maer.serr.	+	+	+	-	-	-	-	-	-	+	+
Maer.sp. 1	+	-	-	-	-	-	-	-	-	-	-
Maer.sp. 2	+	-	-	-	-	-	-	-	-	-	-
Maer.tulu.	+	+	-	-	-	-	-	-	-	-	-
Meli.appe.	+	+	+	-	-	-	-	-	-	-	+
Meli.zeyl.	+	-	+	-	-	-	+	-	+	+	-
Mall.insi.	+	+	-	+	-	-	-	-	-	-	-
Mall.subc.	+	-	+	-	-	+	+	-	-	+	-
Mall.sp. 1	+	-	-	-	-	-	-	-	-	-	-
Nuua.amik. **	+	+	-	-	-	-	-	-	-	-	+

Table 3.2 contd.

Species	MRU	MAD	MOZ	SEY	MAL	SRL	IND	PHI	MOL	FIJ	HAW
Nuua.sp. 1	+	-	-	-	-	-	-	-	-	-	-
Pseu.chel.**	+	-	-	-	-	-	-	-	-	-	-
Family Biancolinidae											
Bian.maui.**	+	-	-	-	-	-	-	-	+	-	+
Family Ampithoidae											
Ampi.cavi.	+	+	-	-	-	-	+	-	+	-	-
Ampi.kula.	+	+	-	-	-	-	+	-	+	-	-
Ampi.poll.**	+	+	-	-	-	-	-	-	-	-	-
Ampi.ramo.	+	+	+	-	-	-	+	-	+	+	+
*Ampi.sp.**	+	-	-	-	-	-	-	-	-	-	-
Ampi.sp. 1	+	-	-	-	-	-	-	-	-	-	-
Ampi.sp. 2	+	-	-	-	-	-	-	-	-	-	-
Cyma.brev.**	+	+	-	-	-	-	-	-	-	+	-
Cyma.filo.	+	+	+	-	-	-	+	-	+	-	+
Cyma.micro.	+	-	-	+	+	-	+	-	-	-	-
Para.maur	+	+	-	-	-	-	-	-	-	-	-
Para.vora	+	+	+	+	+	-	-	-	-	+	+
Pera.fals.	+	-	-	-	-	-	+	-	-	-	-
Family Isaeidae											
Aorc.curv.**	+	-	-	-	-	-	-	-	-	-	-
Gamm.abbo.**	+	+	-	-	-	-	-	-	+	-	-
Gamm.afra.**	+	+	+	-	-	-	-	-	-	-	+
Gamm.atla.	+	+	+	-	-	-	-	-	-	+	+
Gamm.gran.**	+	-	-	-	-	-	-	-	-	-	-
Gamm.holm.**	+	-	-	-	-	-	-	-	-	-	-
Gamm.maur.**	+	-	-	-	-	-	-	-	-	-	-
Gamm.phot.**	+	+	-	-	-	-	-	-	-	-	-
Gamm.poki.**	+	-	-	-	-	-	-	-	-	+	+
Ledo.sp.1	+	-	-	-	-	-	-	-	-	-	-
Family Ischyroceridae											
Eric.bras.	+	+	+	-	-	-	+	-	+	-	-
Eric.lati.**	+	+	-	-	-	-	-	-	-	-	-
Jassa.sp. **	+	-	-	-	-	-	-	-	-	-	-
Jass.sp. 1	+	-	-	-	-	-	-	-	-	-	-
Jass.sp. 2	+	-	-	-	-	-	-	-	-	-	-
Para.chil.**	+	+	-	-	-	-	-	-	-	-	-
Para.spin.**	+	+	-	-	-	-	-	-	-	-	-
Vent.vent**	+	+	-	-	-	-	-	-	-	+	+

Table 3.2 contd.

Family Aoridae											
Species	MRU	MAD	MOZ	SEY	MAL	SRL	IND	PHI	MOL	FIJ	HAW
Beml.pseu. **	+	-	-	-	-	-	-	-	-	-	-
Beml.waip.	+	+	-	-	-	-	-	-	-	-	+
Glob. indi.	+	+	-	-	-	-	-	-	-	-	-
Gran..bonn.	+	+	+	-	-	+	+	-	-	-	-
Gran. gross.	+	+	-	-	-	-	-	-	-	-	-
Lemb. sp. 1	+	-	-	-	-	-	-	-	-	-	-
Lemb.trid. **	+	+	-	-	-	-	-	-	-	-	-
Rita.long. **	+	-	-	-	-	-	-	-	-	-	-
Family Corophiidae											
Coro.asch.	+	-	-	-	-	-	+	-	-	-	-
Laet.acut. **	+	-	-	-	-	-	-	-	-	-	-
Family Podoceridae											
Podo.cris. **	+	+	+	-	-	-	-	-	-	-	-
Podo.pali. **	+	+	-	-	-	-	-	-	-	-	-
Total	130	74	17	4	2	4	28	2	16	21	34

The table was prepared by compiling data from the following sources

Fiji (FIJ) : Myers, 1985

Hawaii (HAW): Barnard, 1970, 1971

India (IND): Barnard, 1935; Nayar, 1959, 1966; Rabindranath, 1972b, 1972c,1972d; Sivaprakasam, 1966, 1967a, 1967b, 1968a, 1968b, 1969a, 1969b, 1970a, 1970b.

Madagascar (MAD): Ledoyer, 1967, 1972, 1979b, 1982

Maldives and Laccadives archipelago (MAL): Walker, 1905

Moluccas (MOL): Ledoyer, 1979a

Mozambique (MOZ): Griffiths, 1973

Philippines (PHI): Olerod, 1970

Seychelles (SEY) : Chevreux, 1901

Sri Lanka (SRL): Walker, 1904; Karaman, 1985

('+' : indicates reported from these sources and '-' indicates not reported based on the sources above; '*' prior to the species name is used for those reported by Ledoyer (1978) whose status still undetermined and the fact that they are not recorded elsewhere is not significant.

Table 3.3 Comparison of amphipod fauna of Mauritius (130 species) with Fiji, Hawaii, India and Madagascar using data tabulated in Table 3.2.

Location	Number of amphipod species common with Mauritius	% of amphipod species shared with Mauritius
Madagascar (MAD)	74	56.9
India (IND)	28	21.5
Fiji(FIJ)	21	16.2
Hawaii (HAW)	34	26.2

3.2.2 Species diversity at the family level

The number of species in the gammaridean families represented in Mauritius are comparable to those present in these families in Hawaii and Fiji (Table 3.4).

The largest number of species occurs in the family Melitidae in all three islands (Mauritius, 29; Fiji, 18; Hawaii, 28). In Mauritius the Ampithoidae (13 species) and the Leucothoidae (11 species) are the second and third most speciose families, followed by the Isaiedae (10 species). The number of species in the speciose families Isaeidae and Ampithoidae is comparable for the three countries. A conspicuous difference between the countries is in the number of leucothoid species where 11 species are reported from Mauritius compared to only 3 each in Fiji and Hawaii. The number of species in the families Lysianassidae and Dexaminidae is also higher in Mauritius than in Fiji and Hawaii. On the other hand, the families Hyalidae, Aoridae, Eusiridae and Stenothoidae tend to be more diverse in Hawaii than in Mauritius.

Table 3.4 Number of species in the families of gammaridean amphipods of Mauritius as compared to two Indo-pacific islands (Hawaii and Fiji).

Families	Mauritius (present study)	Mauritius (present study and Ledoyer (1978)	Fiji (Myers, 1985)	Hawaii (As cited from Myers, 1985)
Eusiridae	1	2	1	5
Oedicerotidae	1	1	0	0
Exoedicerotidae	0	1	0	1
Pleustidae	0	1	0	2
Amphilochidae	3	6	4	5
Cyproideidae	0	2	1	1
Leucothoidae	7	11	3	3
Anamixidae	2	4	1	1
Colomastigidae	0	2	1	4
Stenothoidae	0	1	1	5
Hyalidae	4	5	5	10
Talitridae	1	1	1	0
Eophliantidae	0	1	1	0
Phliantidae	0	1	1	1
Lysianassidae	2	5	2	1
Iphimediidae	0	2	0	0
Liljeborgidae	0	2	0	2
Sebidae	1	2	0	1
Dexaminidae	3	4	1	2
Ampeliscidae	1	2	2	1
Hadziidae	1	1	0	0
Melitidae	21	29	18	28
Ampithoidae	10	13	11	11
Isaeidae	2	10	10	10
Ischyroceridae	3	8	2	7
Aoridae	5	8	7	16
Corophiidae	1	1	1	3
Podoceridae	0	3	3	4

3.2.3 Endemism

Ledoyer (1978) identified 89 species of gammaridean amphipods in Mauritius and he reported 24 new species; one of the new species, *Paradusa mauritiensis*, has now been reported from Madagascar (Ledoyer, 1982). In the present work, 69 species are reported, 41 of which were not reported by Ledoyer (1978).

Forty-two of the 130 (32.3%) amphipod species now reported from Mauritius appear to be endemic. Eight of the 42 species belong to the family Melitidae, 5 to the Leucothoidae, 5 to the Isaeidae and 4 to the Amphilochidae. The Lysianassidae, Ischyroceridae and Aoridae each have three apparently endemic species; the Ampithoidae and the Sebidae have two endemic species each.

3.3 Ecology of amphipods from Mauritius

3.3.1 Occurrence of amphipods on different substrates

The percentage frequency of occurrence (A_{sub}) of amphipod species in five substrate types (sand, debris, coral rubble, seagrass and algae) are tabulated in Appendix D and examples are shown in Figures 3.1-3.4. Some amphipod species had a high percentage frequency of occurrence on a single substrate while others had a high percentage frequency of occurrence on a number of substrates (Figures 3.1-3.4). For example, *Orchestia anomala* (debris), *Seba typica* (coral rubble), *Ledoyerella sp. 1* (sand) (Figure 3.1) represent species occurring mostly on one substrate. *Tethygeneia pacifica, Parhyallela indica, Hyale chevreuxi, Elasmopus spinidactylus, Elasmopus hooheno, Elasmopus pectenicrus, Elasmopus sp. 1, Maera octodens, Maera tuluarensis, Paradusa mauritiensis, Mallacoota insignis, Paragrubia vorax, Perampithoe falsa, Ericthonius brasiliensis, Jassa sp. 1, Jassa sp. 2* are examples of species having a high percentage frequency of occurrence only on algae.

Species occurring mainly in plant substrates (algae and seagrass) were *Hyale ayeli, Ampelisca sp. 1, Maera quadrimana, Melita zeylanica, Ampithoe kufali, Ampithoe sp. 1, Ampithoe sp. 2, Cyamadusa filosa, Cyamadusa micropthalma, Gammaropsis atlantica,Bemlos waipio,Globosolembos indicus, Grandidierella bonnieri* and *Corophium acherusicum* (Figure 3.2). A number of species occurred on two substrates: *Hadzia dentifera* on sand and coral rubble; *Malacoota sp. 1, Ampithoe ramondi* (Figure 3.3) and *Lysianaassa* sp. 1 on coral rubble and algae; *Elasmopus ecuadoriensis hawaiensis,*

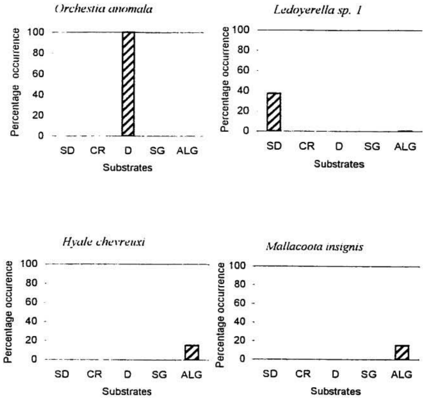

Figure 3.1 **Examples of amphipod species having a high percentage frequency of occurrence on one substrate (SD: sand; CR: coral rubble; D: debris; SG: seagrasses; ALG: algae)**

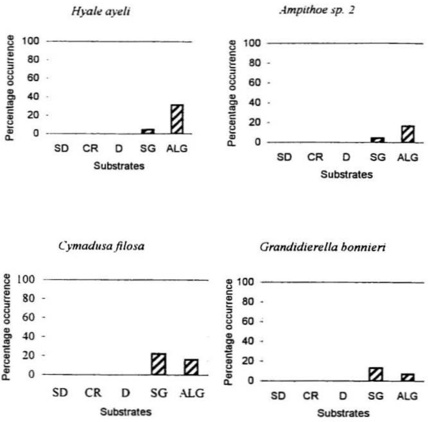

Fig 3.2 Examples of amphipod species showing a high percentage frequency of occurrence on plant substrates (SD: sand; CR: coral rubble; D: debris; SG: seagrasses; ALG: algae)

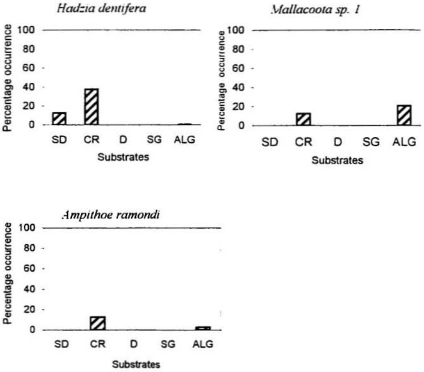

Figure 3.3 Examples of amphipod species showing a high percentage frequency of occurrence on two substrates (SD: sand; CR: coral rubble; D: debris; SG: seagrasses; ALG: algae)

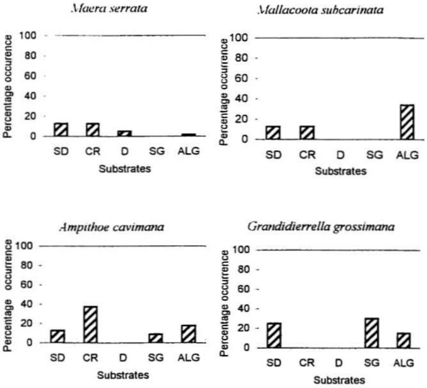

Figure 3.4 Examples of amphipod species showing a high percentage frequency of occurrence on at least 3 of the 5 substrates (SD: sand; CR: coral rubble; D: debris; SG: seagrasses; ALG: algae)

Maera mannarensis and *Gitanopsis sp.1* on sand and algae and *Nuuanu sp.1* on sand and seagrass. *Lysianassa ewa* occurred predominantly on sand but it also occurred on seagrass and algae.

Species occurring on at least three of the substrates included *Hyale grandicornis, Maera pacifica, Maera serrata, Malacoota subcarinata, Ampithoe caviaman* and *Grandidierella grossimana* (Figure 3.4).

3.3.2 Occurrence ofamphipod species on specific algalsubstrates

The percentage frequency of occurrence (A_{alg}) was computed for 35 amphipod species belonging to the families Eusiriidae, Hyalidae, Melitidae, Ampithoidae, Isaeidae, Ischyroceridae, Aoridae and Corophidae found mostly on algae (Appendix E). These amphipods showed varied patterns of distribution among algae, some being found on only a few species while others occurred on many species (Figs. 3.5-3.39).

Of the 17 algal taxa considered, the eusirid, *Tethygeneia pacifica* (Figure 3.5) had a high percentage frequency of occurrence on *Padina spp.*, *Sargassum densifolium*, *Turbinaria ornata*, *Ulva lactuca* and *Digenia simplex*.

The Hyalidae, *Hyale ayeli, Hyale chevreuxi* and *Hyale grandicornis* (Figure 3.6-3.8) had a high percentage frequency of occurrence on almost all the algae except for *Turbinaria ornata* and *Caulerpa sertulariodes*. At the species level, however, *Hyale ayeli* had a high percentage frequency of occurrence (A_{alg}) on *Digenia simplex*; *Hyale chevreuxi* had a high A_{alg} on *Sargassum densifolium* and *Hyale grandicornis* had high A_{alg} on *Amansia glomerata* and *Ulva lactuca*. The hyalid, *Parhyallela indica* had a high frequency of occurrence only on a few algae (*Centroceras clavulatum*, *Gracilaria spp.*, *Gracilaria salicornia*, *Wurdemannia miniata* and *Enteromorpha sp.*) (Figure 3.9).

The melitids, of the genus *Elasmopus* (Figures 3.10-3.14) had a high percentage frequency of occurrence on all algae except *Caulerpa sertulariodes*. Within the genus *Elasmopus*, *Elasmopus ecuadorensis hawaiensis* had a high frequency of occurrence on *Sargassum densifolium* while *Elasmopus hooheno* and *Elasmopus pectenicrus*, had a high A_{alg} on *Laurencia papillosa*. *Elasmopus sp. 1* had a high A_{alg} on the alga *Amansia glomerata*. The *Elasmopus* species had low percentage frequencies of occurrence on *Gracilaria spp.* and *Gracilaria salicornia*. The genus *Mallacoota*, on the other hand, (Figures 3.15-3.17), had a high percentage frequency of occurrence on these two algae. The *Mallacoota* species had a high A_{alg} on most algae except for *Caulerpa sertulariodes* and *Turbinaria ornata*. The percentage frequency occurrence on the alga *Amansia glomerata* for the three species was high. At the species level, however, *Mallacoota insignis* (Figure 3.15) had a high frequency of occurrence on *Digenia simplex* and *Gracilaria salicornia*, while *Mallacoota sp.1* (Figure 3.16) was found mostly on *Caulerpa racemosa* and *Digenia simplex*. *Mallacoota subcarinata* (Figure 3.17) had a high percentage frequency of occurrence on *Gracilaria salicornia*, *Centroceras clavulatum* and *Ulva lactuca*.

The melitids of the genus *Maera* (Figures 3.18-3.19) had a high percentage frequency of occurrence on *Turbinaria ornata* and a relatively high percentage frequency of occurrence on few other algal categories. The genus *Melita*, as shown by *Melita zeylanica* (Figure 3.20), had a high percentage frequency of occurrence on *Padina spp.*, *Ulva lactuca* and *Amansia glomerata*.

The Ampithoidae considered for the analysis, namely *Ampithoe cavimana*, *Ampithoe kulafi*, *Ampithoe ramondi*, *Ampithoe sp. 1*, *Ampithoe sp. 2*, *Cymadusa filosa*, *Cymadusa microphthalma*, *Paradusa mauritiensis*, *Paragrubia vorax* and *Perampithoe falsa* had high percentage frequency of occurrence on a wide variety of algae. *Ampithoe cavimana* (Figure 3.21) and *Ampithoe ramondi* (Figure 3.22) had a high percentage frequency of occurrence on *Turbinaria ornata* while *Ampithoe kulafi* (Figure 3.23) had a high percentage frequency of occurrence on *Sargassum densifolium*. *Ampithoe sp. 1* (Figure 3.24) and *Ampithoe sp. 2* (Figure 3.25) had high A_{alg} on *Acanthophora spicifera* and *Ulva lactuca*. *Ampithoe sp. 2*, however, had a high percentage frequency of occurrence on *Digenia simplex*.

For the ampithoids of the genus *Cymadusa* (Figures 3.26-3.27), the species were more common on *Padina spp.* and *Turbinaria ornata*. *Cymadusa filosa* had high A_{alg} on *Caulerpa sertulariodes* while *Cymadusa microphthalma* had high percentage frequency of occurrence on *Digenia simplex*. *Paragrubia vorax* (Figure 3.28) had a high percentage frequency of occurrence on a few algae, namely *Turbinaria ornata*, *Padina spp.* and *Amansia glomerata*. *Paradusa mauritiensis* (Figure 3.29) had a high percentage frequency of occurrence only on *Padina spp*. *Perampithoe falsa* (Figure 3.30) tended to have a high frequency of occurrence mostly on *Sargassum densifolium* and *Turbinaria ornata*. It also had a fairly high frequency of occurrence on *Caulerpa racemosa*.

The isaeid, *Gammaropsis atlantica* (Figure 3.31) had a high percentage frequency of occurrence on only five of the 17 algal groups, being associated mostly with *Caulerpa* *racemosa*, *Digenia simplex*, *Gracilaria salicornia*, *Padina spp.* and *Sargassum densifolium*.

Among the Ischyroceridae, *Erichthonius brasiliensis* (Figure 3.32) had a high percentage frequency of occurrence on only 4 of the 17 algal groups, namely *Gracilaria salicornia*, *Padina spp.*, *Turbinaria ornata* and *Ulva lactuca*. The genus *Jassa* (Figure 3.33-3.34) however had a high percentage frequency of occurrence on a wider range of algal species. The species *Jassa sp. 1* had a high percentage frequency of occurrence in 10 of the 17 algal categories with highest frequency of occurrence on *Amansia glomerata*, *Gracilaria salicornia* and *Sargassum densifolium*. *Jassa sp. 2* was not so ubiquitous having a high percentage frequency of occurrence on only 3 of the 17 algal categories (*Amansia glomerata*, *Gracilaria spp.* and *Sargassum densifolium*).

Among the aorids, *Bemlos waipio* (Figure 3.35) had a high percentage frequency of occurrence only on three algae, *Laurencia papillosa*, *Padina spp.* and *Gracilaria salicornia*. *Globolembos indicus* (Figure 3.36) had a high percentage frequency of occurrence only on the green algae *Enteromorpha flexuosa* and *Ulva lactuca*. The Aoridae of the genus *Grandidierella* (Figure 3.37-3.38) had a high frequency of occurrence on *Caulerpa sertulariodes* and *Grandidierella bonnieri* (Figure 3.37) had a high percentage frequency of occurrence on *Enteromorpha flexuosa*, while *Grandidierella grossimana* (Figure 3.38) had a high percentage frequency of occurrence on *Gracilaria spp.*

The Corophiid, *Corophium acherusicum* had a high percentage frequency of occurrence on 8 of the 17 algal groups. The highest percentage frequencies of occurrence were observed on *Laurencia papillosa*, *Enteromorpha flexuosa* and *Caulerpa sertulariodes* (Figure 3.39).

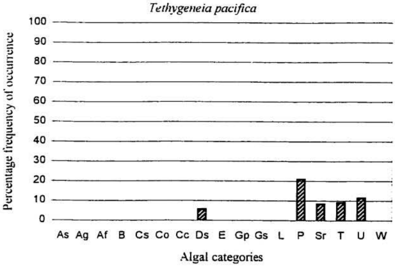

Figure 3.5 Percentage frequency occurrence of *Tethygeneia pacifica* in algal categories (refer to Table 2.4 for full names)

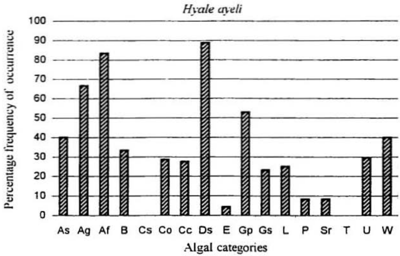

Figure 3.6 Percentage frequency of occurrence of *Hyale ayeli* in algal categories (refer to Table 2.4 for full names)

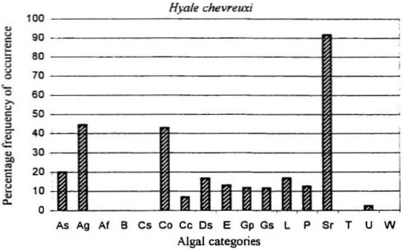

Figure 3.7 Percentage frequency of occurrence of *Hyale chevreuxi* in algal categories (refer to Table 2.4 for full names)

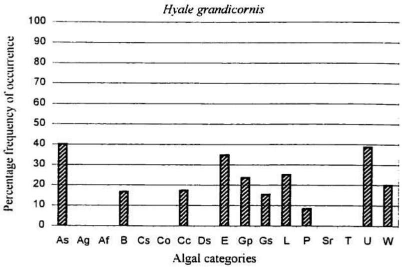

Figure 3.8 Percentage frequency of occurrence of *Hyale grandicornis* in algal categories (refer to Table 2.4 for full names)

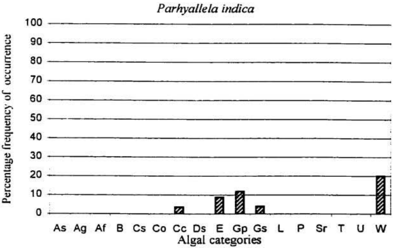

Figure 3.9 Percentage frequency of occurrence of *Parhyallela indica* in algal categories (refer to Table 2.4 for full names)

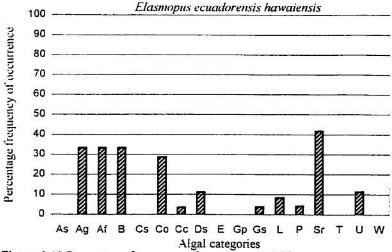

Figure 3.10 Percentage frequency of occurrence of *Elasmopus ecuadorensis hawaiensis* in algal categories (refer to Table 2.4 for full names)

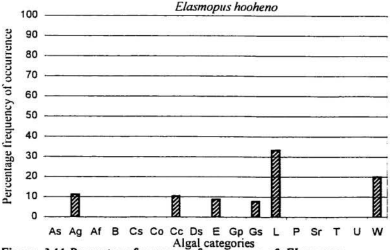

Figure 3.11 Percentage frequency of occurrence of *Elasmopus hooheno* in algal categories (refer to Table 2.4 for full names)

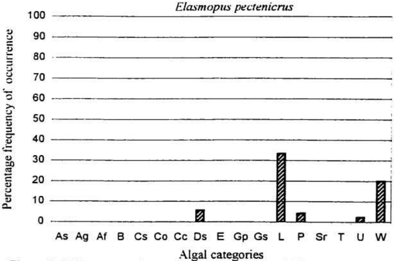

Figure 3.12 Percentage frequency of occurrence of *Elasmopus pectenicrus* in algal categories (refer to Table 2.4 for full names)

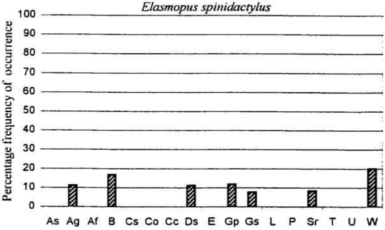

Figure 3.13 Percentage frequency of occurrence of *Elasmopus spinidactylus* in algal categories (refer to Table 2.4 for full names)

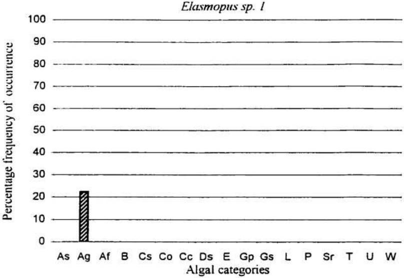

Figure 3.14 Percentage frequency of occurrence of *Elasmopus sp.1* in algal categories (refer to Table 2.4 for full names)

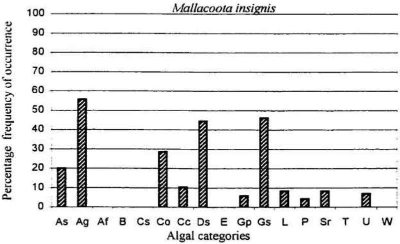

Figure 3.15 Percentage frequency of occurrence of *Mallacoota insignis* in algal categories (refer to Table 2.4 for full names)

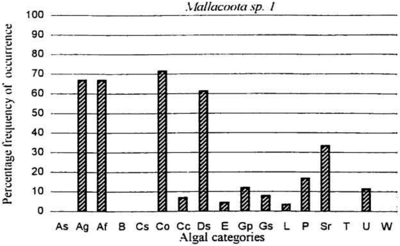

Figure 3.16 Percentage frequency of occurrence of *Mallacoota sp. 1* in algal categories (refer to Table 2.4 for full names)

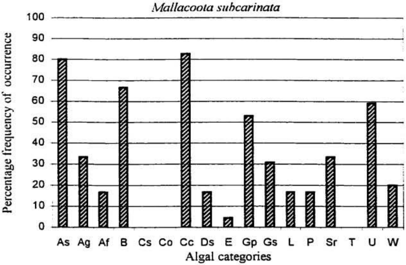

Figure 3.17 Percentage frequency of occurrence of *Mallacoota subcarinata* in algal categories (refer to Table 2.4 for full names)

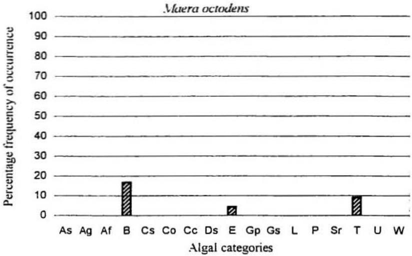

Figure 3.18 Percentage frequency of occurrence of *Maera octodens* in algal categories (refer to Table 2.4 for full names)

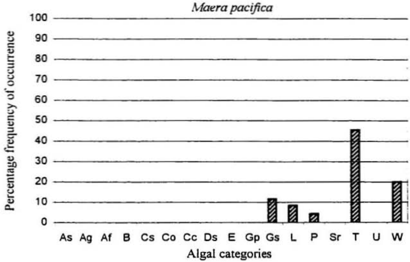

Figure 3.19 Percentage frequency of occurrence of *Maera pacifica* in algal categories (refer to Table 2.4 for full names)

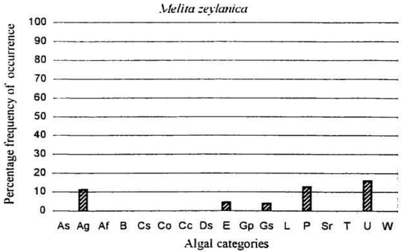

Figure 3.20 Percentage frequency of occurrence of *Melita zeylanica* in algal categories (refer to Table 2.4 for full names)

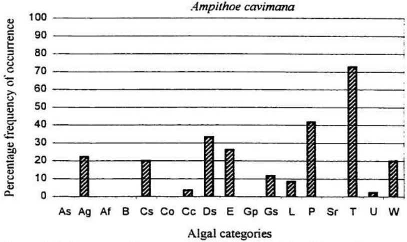

Figure 3.21 Percentage frequency of occurrence of *Ampithoe cavimana* in algal categories (refer to Tabel 2.4 for full names)

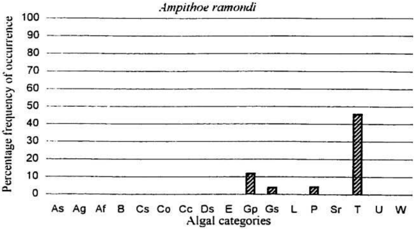

Figure 3.22 Percentage frequency of occurrence of *Ampithoe ramondi* in algal categories (refer to Table 2.4 for full names)

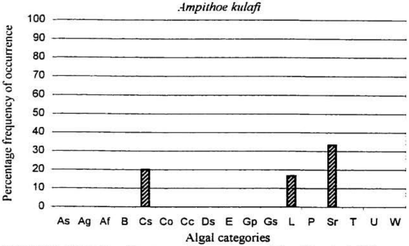

Figure 3.23 Percentage frequency of occurrence of *Ampithoe kulafi* in algal categories (refer to Table 2.4 for full names)

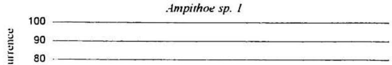

Figure 3.24 Percentage frequency of occurrence of *Ampithoe sp. 1* in algal categories (refer to Table 2.4 for full names)

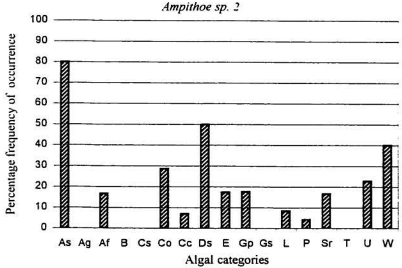

Figure 3.25 Percentage frequency of occurrence of *Ampithoe sp. 2* in algal categories (refer to Table 2.4 for full names)

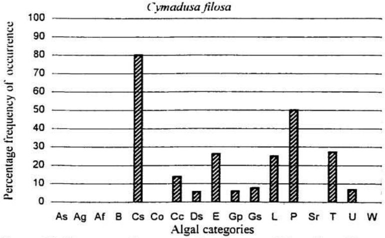

Figure 3.26 Percentage frequency of occurrence of *Cymadusa filosa* in algal categories (refer to Table 2.4 for full names)

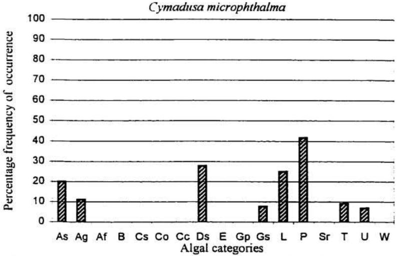

Figure 3.27 Percentage frequency of occurrence of *Cymadusa microphthalma* in algal categories (refer to Table 2.4 for full names)

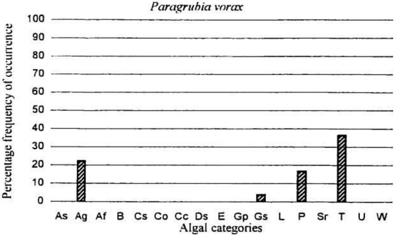

Figure 3.28 Percentage frequency of occurrence of *Paragrubia vorax* in algal categories (refer to Table 2.4 for full names)

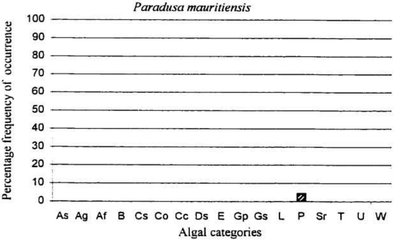

Figure 3.29 Percentage frequency of occurrence of *Paradusa mauritiensis* in algal categories (refer to Table 2.4 for full names)

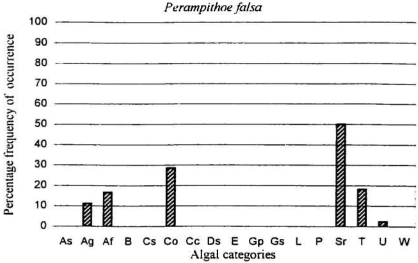

Figure 3.30 Percentage frequency of occurrence of *Perampithoe falsa* in algal categories (refer to Table 2.4 for full names)

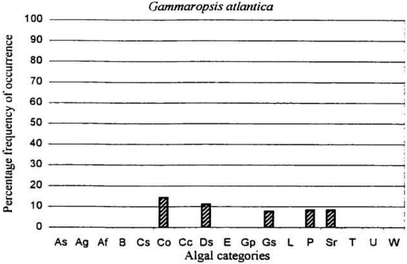

Figure 3.31 Percentage frequency of occurrence of *Gammaropsis atlantica* in algal categories (refer to Table 2.4 for full names)

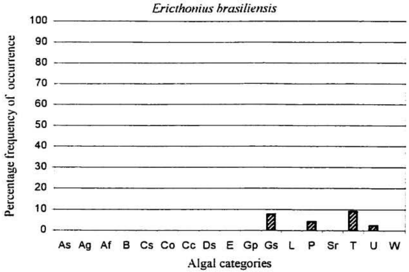

Figure 3.32 Percentage frequency of occurrence of *Ericthonius brasiliensis* in algal categories (refer to Table 2.4 for full names)

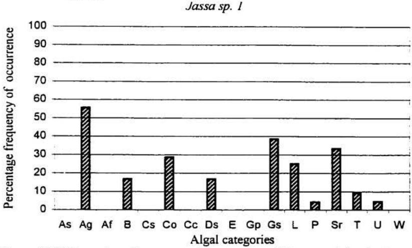

Figure 3.33 Percentage frequency of occurrence of *Jassa sp. 1* in algal categories (refer to Table 2.4 for full names)

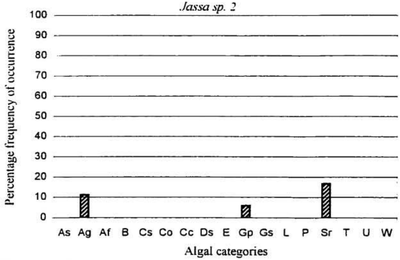

Figure 3.34 Percentage frequency of occurrence of *Jassa sp. 2* in algal categories (refer to Table 2.4 for full names)

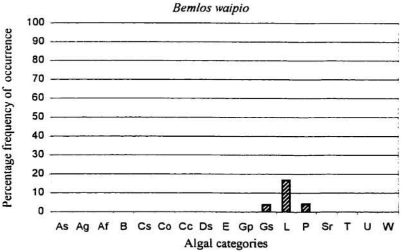

Figure 3.35 Percentage frequency of occurrence of *Bemlos waipio* in algal categories (refer to Table 2.4 for full names)

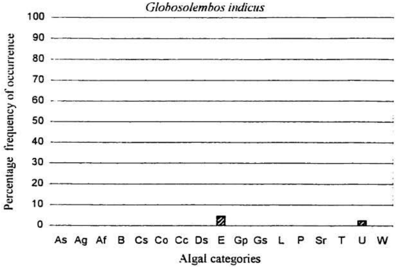

Figure 3.36 Percentage frequency of occurrence of *Globosolembos indicus* in algal categories (refer to Table 2.4 for full names)

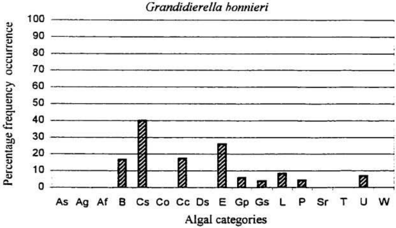

Figure 3.37 Percentage frequency of occurrence of *Grandidierella bonnieri* in algal categories (refer to Table 2.4 for full names)

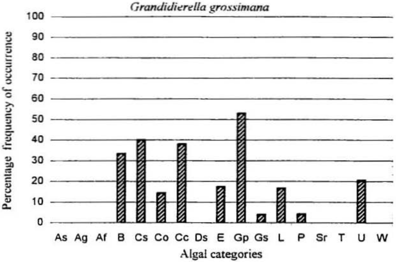

Figure 3.38 Percentage frequency of occurrence of *Grandidierella grossimana* in algal categories (refer to Table 2.4 for full names)

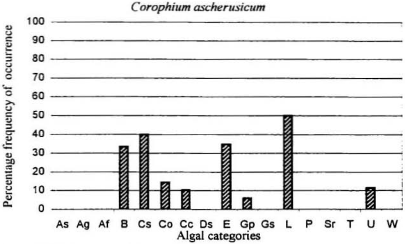

Figure 3.39 Percentage frequency of occurrence of *Corophium ascherusicum* in algal categories (refer to Table 2.4 for full names)

3.3.3 Mean abundance of amphipods on different species of algae

Twelve algal categories (*Acanthophora spicifera*, *Amansia glomerata*, *Amphiroa flagellissima*, *Caulerpa racemosa*, *Digenia simplex*, *Enteromorpha flexuosa*, *Gracilaria* spp, *Gracilaria salicornia*, *Padina* spp., *Sargassum densifolium*, *Ulva lactuca* and *Wurdemania miniata*) collected by quadrats at Souillac (SOU) were analysed to determine if the mean numbers of amphipod species associated with these algae were significantly different.

For the hyalids studied (Figure 3.40), the mean number of amphipods was significantly different among the twelve algal categories for *Hyale chevreuxi* ($F_{(11, 56)}$ = 3.29, $p_{\text{randomised}}$ = 0.011). The highest mean number of individuals was on *Sargassum densifolium*. *Hyale ayeli* ($F_{(11, 56)}$ = 1.68, $p_{\text{randomised}}$ = 0.176) and *Hyale grandicornis* ($F_{(11,56)}$ = 2.04, $p_{\text{randomised}}$ = 0.062) did not show a significant difference in the mean number of individuals among the algal categories. Inspection of the mean number of amphipods in the different algal categories showed that the highest mean numbers of each of the *Hyale* species were on different algae (Figure 3.40).

For the melitids of the genus *Elasmopus* (Figure 3.41), a significant difference in the mean number of amphipods was observed in *E. ecuadorensis hawaiensis* ($F_{(11, 56)}$ = 2.30, $p_{\text{randomised}}$ = 0.038). *Elasmopus spinidactylus* did not show a significant difference among algal categories. *Elasmopus sp. 1* was found almost exclusively on *Amansia glomerata* but the high variance in the latter led to the failure to detect a significant

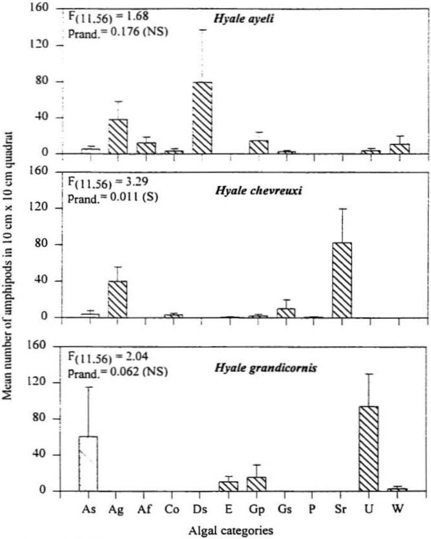

Figure 3.40 Mean number of amphipods per quadrat for *Hyale* species in 12 algal categories at Souillac (SOU) (S: significant, NS: no significant difference; Vertical lines: standard error)

difference among algal species. The highest mean number of amphipods occurred on different algal taxa for the three species (Figure 3.41).

For the melitids of the genus *Mallacoota* (Figure 3.42) the mean number of *Mallacoota subcarinata* was significantly different among algal categories ($F_{(11,56)} = 5.56$, $p_{\text{randomised}} < 0.0004$) with the highest mean number on *Acanthophora spicifera* . The mean number of *Mallacoota insignis* was also significantly different among algal categories ($F_{(11,56)} = 2.27$, $p_{\text{randomised}} = 0.041$). The mean number of *Mallacoota sp. 1* did not vary significantly among algal categories ($F_{(11,56)} = 1.63$, $p_{\text{randomised}} = 0.135$).

For the four ampithoid species analysed at Souillac (SOU) (Figure 3.43), the mean number of amphipods was significantly different among algae species for *Ampithoe cavimana* ($F_{(11,56)} = 8.28$, $p_{\text{randomised}} < 0.0004$) and *Ampithoe sp. 2* ($F_{(11,56)} = 2.87$, $p_{\text{randomised}} = 0.023$). Highest mean numbers were recorded on different algae for the different species. For example, *Ampithoe cavimana* had a high mean abundance on *Padina spp.* while *Ampithoe falsa* had highest mean numbers on *Sargassum densifolium*.

The mean number of *Jassa sp. 1* (Figure 3.44) was significantly different among algal categories ($F_{(11,56)} = 3.16$, $p_{\text{randomised}} = 0.009$); the highest mean number of amphipods occurred on *Amansia glomerata*.

The mean number of *Grandidierella grossimana* was not significantly different among algae ($F_{(11, 56)} = 0.77$, $p_{\text{randomised}} = 0.825$). The highest mean number occurred on *Ulva lactuca* (Figure 3.45) .

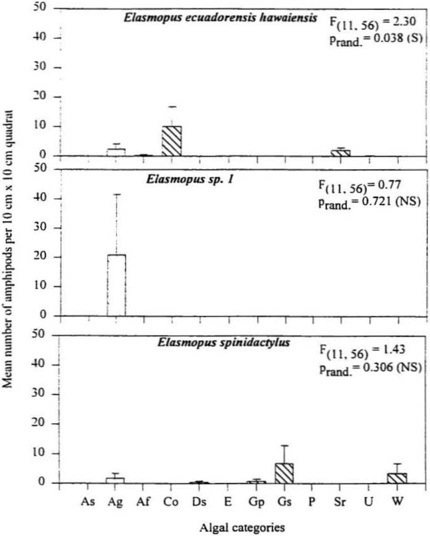

Figure 3.41 Mean number of amphipods per quadrat for *Elamopus* species in 12 algal categories at Souillac (SOU) (S: significant, NS: no significant difference; Vertical lines: standard error)

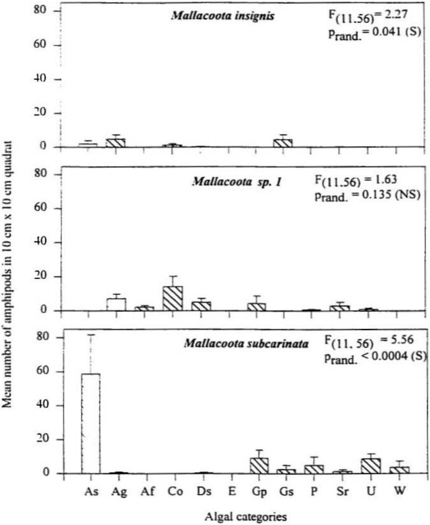

Figure 3.42 Mean number of amphipods per quadrat for *Mallacoota* species in 12 algal categories at Souillac (SOU)
(S: significant, NS: no significant difference;
Vertical lines : standard error)

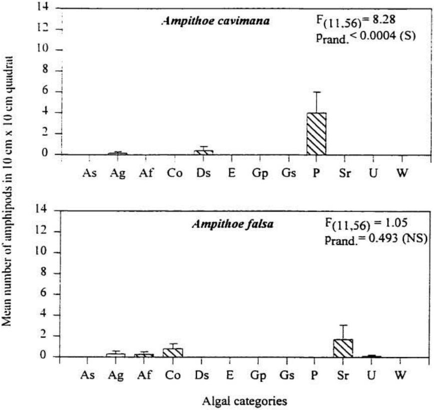

Figure 3.43 Mean number of amphipods per quadrat for *Ampithoe* species in 12 algal categories at Souillac (SOU) (S: significant, NS: no significant difference) (Vertical lines : standard error)

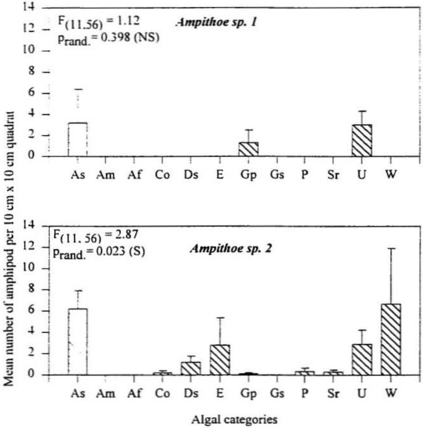

Figure 3.43 (contd) Mean number of amphipods per quadrat for *Ampithoe* species in 12 algal categories at Souillac (SOU)

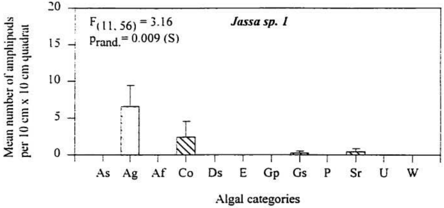

Figure 3.44 Mean number of amphipods per quadrat for *Jassa sp. 1* in 12 algal categories at Souillac (SOU) (S: significant difference; Vertical lines: standard error)

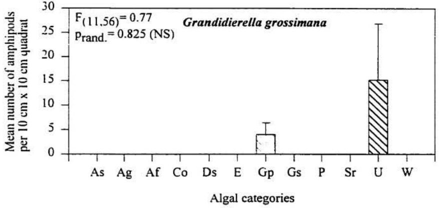

Figure 3.45 Mean number of amphipods per quadrat for *Grandidierella grossimana* in 12 algal categories at Souillac(SOU) (NS: no significant difference;Vertical lines: standard error)

3.3.4 Mean abundance of amphipods in algal morphological categories

The mean number of individuals per quadrat was not significantly different among algal morphological categories among the *Hyale* species except for *Hyale grandicornis*. In the latter a high mean number of amphipods was found in the foliose category ($F_{(2, 65)} = 5.83$, $p_{randomised} = 0.041$). None of the species of the genera *Elasmopus, Mallacoota* or *Ampithoe* showed a significant difference in the mean number of individuals per quadrat in the algal morphological categories (Table 3.5).

Table 3.5 Mean and standard error of the mean number of individuals of 15 species of amphipods in algal morphological categories at Souillac (SOU)

Species	Filamentous	Foliose	Branched	$F_{(2,65)}$	$P_{randomised}$
Hyale ayeli	0.00	2.77±1.91	18.90±7.01	1.02	0.983
Hyale chevreuxi	0.60±0.60	0.15±0.15	19.00±6.75	1.35	0.685
Hyale grandicornis	10.40±6.04	72.30±29.7	9.26±6.18	5.83	0.041*
Elasmopus ecuadorensis hawaiensis	0.00	0.08±0.08	1.64±0.78	0.73	0.801
Elasmopus sp. 1	0.00	0.00	2.92±2.90	0.18	0.999
Elasmopus spinidactylus	0.00	0.00	1.16±0.59	0.67	0.828
Mallacoota insignis	0.00	0.00	1.40±0.51	1.34	0.729
Mallacoota sp.1	0.00	0.85±0.54	4.40±1.25	1.60	0.217
Mallacoota subcarinata	0.00	7.92±2.44	8.44±3.35	0.37	0.999
Ampithoe cavimana	0.00	0.92±0.63	0.06±0.04	3.93	0.082
Ampithoe falsa	0.00	0.08±0.08	0.38±0.21	0.42	0.999
Ampithoe sp. 1	0.00	2.31±1.05	0.58±0.40	2.03	0.361
Ampithoe sp. 2	2.80±2.56	2.31±1.06	1.22±0.45	0.84	0.999
Jassa sp. 1	0.00	0.00	1.24±0.54	0.94	0.650
Grandidierella grossimana	0.00	11.69±9.04	0.80±0.51	3.08	0.119

*: $p < 0.05$, significant difference among means

3.3.5 Mean abundance of amphipods in algal toughness categories

The mean number of individuals was significantly different among algal toughness categories only for *Hyale grandicornis* ($F_{(2, 65)} = 5.75$, $p_{\text{Prandomised}} = 0.007$) of the *Hyale* species and for *Mallacoota subcarinata* ($F_{(2, 65)} = 3.55$, $p_{\text{Prandomised}} = 0.025$) of the *Mallacoota* species. In the case of *Hyale grandicornis*, the highest mean number was on algae of lowest toughness while for *Mallacoota subcarinata* the highest mean number was in the intermediate toughness category. No significant difference in the mean number of individuals among the three toughness groups was observed in the other species tested (Table 3.6).

Table 3.6 Mean and standard error of the mean number of individuals of 15 amphipod species in algal toughness groups (low, intermediate and high) at Souillac (SOU)

Species	Low	Intermediate	High	$F_{(2, 65)}$	$P_{randomised}$
Hyale ayeli	2.40±1.66	29.30±20.30	13.32±4.80	1.50	0.285
Hyale chevreuxi	0.20±0.20	2.33±1.35	24.1±8.73	2.66	0.087
Hyale grandicornis	66.10±26.00	20.10±18.60	4.26±3.66	5.75	0.007*
Elasmopus ecuadorensis hawaiensis	0.07±0.07	3.33±2.40	0.84±0.38	2.12	0.154
Elasmopus sp. 1	0.00	0.00	3.84±3.82	0.39	0.999
Elasmopus spinidactylus	0.00	0.13±0.13	1.47±0.77	1.28	0.347
Mallacoota insignis	0.00	1.13±0.69	1.40±0.62	1.09	0.584
Mallacoota sp.1	0.60±0.48	6.40±2.52	3.32±1.32	2.14	0.144
Mallacoota subcarinata	5.87±2.19	19.7±10.3	3.71±1.42	3.55	0.025*
Ampithoe cavimana	0.00	0.13±0.13	0.34±0.22	0.63	0.802
Ampithoe falsa	0.07±0.07	0.27±0.18	0.40±0.27	0.35	0.92
Ampithoe sp. 1	2.00±0.93	1.07±1.07	0.34±0.32	1.76	0.22
Ampithoe sp. 2	2.87±1.17	2.53±0.90	0.63±0.45	3.16	0.061
Jassa sp. 1	0.00	0.80±0.73	1.32±0.65	0.87	0.61
Grandidierella grossimana	10.13±7.86	0.00	1.05±0.67	2.48	0.08

***: $p < 0.05$, significant difference among means of toughness categories.**

Amphipod assemblages on algae

3.3.6.1 Species diversity

3.3.6.1.1 Species richness

Algal substrates contained the highest number of species, followed by seagrasses, sand, coral rubble and debris substrates (Table 3.7).

Table 3.7 Number of amphipod species recorded in 5 substrates (quadrat and non-quadrat samples)

Substrates	Number of species recorded
Algae	62
Seagrass	20
Sand	14
Coral rubble	9
Debris	3

The rarefaction curves for 12 algal species at Souillac (SOU) and 4 algal species at Trou aux Biches (TAB) indicate the number of amphipod species expected in samples of various sizes. For the purpose of clarity two graphs (Figure 3.46) are shown for algae at Souillac (SOU) (note that the two graphs have different scales for the x-axis). For five algae *Acanthophora spicifera*, *Amansia glomerata*, *Gracilaria spp.*, *Sargassum densifolium* and *Ulva lactuca*, it appears that a higher number of species is expected to occur in *Amansia glomerata*, *Gracilaria spp.* and *Ulva lactuca* than in *Sargassum densifolium* and *Acanthophora spicifera*. As regards the other algae, a high number of species is expected in *Gracilaria salicornia* and *Caulerpa racemosa* whereas *Enteromorpha flexuosa* and *Padina spp.* have lower expected numbers of species.

At Trou aux Biches (TAB), rarefaction curves were plotted for four algae; *Gracilaria salicornia* had a higher expected number of species than *Boodlea composita*, *Centroceras clavulatum* and *Ulva lactuca* (Figure 3.47) for the same number of individuals collected.

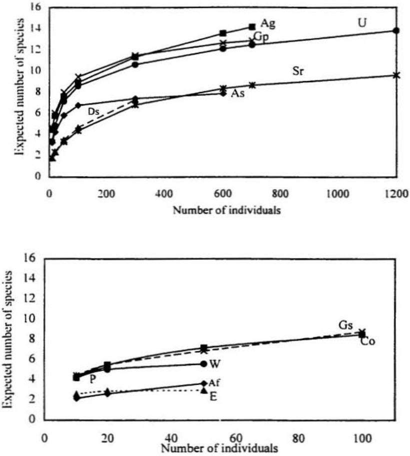

Figure 3.46 Rarefaction curves showing expected number of amphipod species on 12 algal taxa at Souillac (SOU) (refer to Table 2.4 for full names) (Note: the x-axis is not of the same scale for the two graphs)

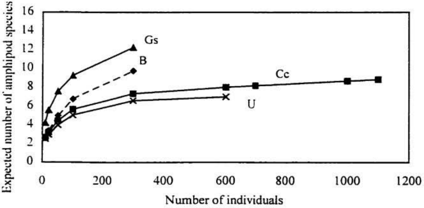

Figure 3.47 Rarefaction curves showing expected number of amphipod species on 4 algae at Trou aux Biches (refer to Table 2.4 for full names of algae)

3.3.6.1.2 Species heterogeneity measures

The Shannon-Wiener diversity index (H'), the evenness index (J) and the number of species were calculated for 12 algal categories at SOU (Table 3.8) and 4 algal categories at TAB (Table 3.9). The data for all amphipod species collected by quadrat for each alga were pooled for the computation.

Table 3.8 Shannon-Wiener diversity index (H'), Evenness index (J) and number of species (S) of amphipods for 12 algal taxa collected by the quadrat method at Souillac (SOU)

Algal category	H'	S	J
Gracilaria spp.	1.84	13	0.72
Amansia glomerata	1.7	15	0.5
Gracilaria salicornia	1.63	9	0.74
Padina spp.	1.63	7	0.84
Caurlepa racemosa	1.58	10	0.68
Wurdemania miniata	1.51	6	0.85
Acantophora spicifera	1.24	8	0.60
Ulva lactuca	0.99	10	0.43
Enteromorpha sp.	0.68	3	0.62
Amphiroa flagelissima	0.59	4	0.42
Sargassum densifolium	0.52	11	0.22
Digenia simplex	0.42	8	0.20

The highest H' and J values were observed in *Gracilaria spp.* and *Gracilaria salicornia*. Low values of H' and J were observed in *Sargassum densifolium* and *Digenia simplex*.

Table 3.9 Shannon-Wiener diversity index (H'), Evenness index (J) and number of species (S) of amphipods for 4 algal categories collected by the quadrat method at Trou aux Biches (TAB).

Algal category	H'	S	J
Gracilaria salicornia	1.22	9	0.56
Centroceras clavulatum	1.08	9	0.49
Ulva lactuca	0.88	7	0.45
Boodlea composita	0.83	10	0.36

A similar trend was observed at Trou aux Biches, with *Gracilaria salicornia* having higher H' and J values as compared to the other algae.

3.3.6.2 Mean total abundance of amphipods on algae

3.3.6.2.1 Algal categories

The mean total number of amphipods was not significantly different among the 12 algal categories compared at Souillac (SOU) ($F_{(11, 56)} = 1.88$, $p_{\text{randomised}} = 0.059$; Figure 3.48). There was also no significant difference in the mean total number of amphipods on the four algae studied at Trou aux Biches (TAB) ($F_{(3, 29)} = 0.46$, $p_{\text{randomised}} = 0.715$; Figure 3.49).

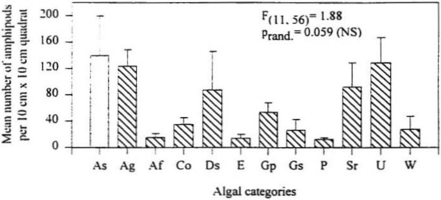

Figure 3.48 Mean total number of amphipods in 12 algal categories at Souillac (SOU)
(NS: no significant difference; Vertical lines indicate standard error)

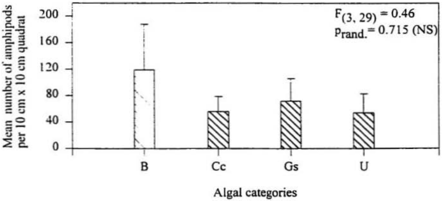

Figure 3.49 Mean total number of amphipods in 4 algal categories at Trou aux Biches (TAB)
(NS: no significant difference; Vertical lines indicate standard error)

3.3.6.2.2 Algal morphological groups

The mean total number of amphipods was not significantly different among the three morphological groups (filamentous, foliose and branched) at Souilllac (SOU) ($F_{(2, 65)} = 1.84$, $p_{randomised} = 0.209$; Figure 3.50). No significance difference was observed among the morphological groups at TAB ($F_{(2, 30)} = 0.46$, $p_{randomised} > 0.999$; Figure 3.51).

3.3.6.2.3 Algal toughness groups

The mean total number of amphipods was not significantly different among algal toughness categories tested at SOU ($F_{(2, 65)} = 0.81$, $p_{randomised} = 0.579$; Figure 3.52)

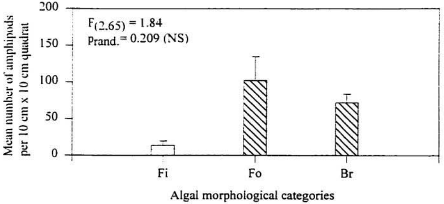

Figure 3.50 Mean number of amphipods in algal morphological categories at SOU. (Fi: Filamentous; Fo: Foliose; Br: Branched); (NS : no significant difference; Vertical lines: standard error)

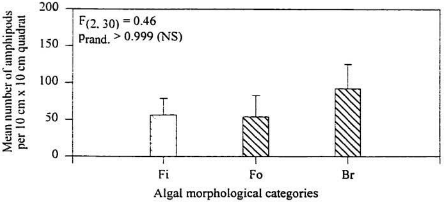

Figure 3.51 Mean number of amphipods in algal morphological categories at TAB. (Fi: Filamentous; Fo: foliose; Br : Branched); (NS: no significant difference; Vertical lines: standard error)

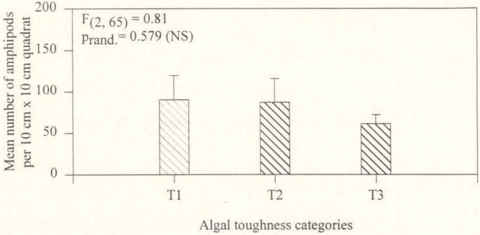

Figure 3.52 **Mean number of amphipods per quadrat in algal toughness categories at SOU. (Toughness: T1: low; T2: intermediate; T3: high); (NS: no significant difference; Vertical lines: standard error)**

3.3.6.3 Amphipod assemblage at sites of different wave exposure

The amphipod fauna on *Ulva lactuca* at two sites (Souillac and Trou aux Biches) of different wave exposures was compared. Although *Gracilaria salicornia* occurred at both sites, no comparison of the fauna on this alga was attempted as adequate numbers of quadrat samples were not taken. The rarefaction curves (using data from both quadrat and non-quadrat samples) indicate that similar numbers of species are expected for the same number of individuals on this alga at the two sites (Figure 3.53).

3.3.6.3.1 Mean total abundance of amphipods per quadrat samples on *Ulva lactuca*

The mean total abundance of amphipods in *Ulva lactuca* was not significantly different at the two sites [Trou aux Biches (protected) and Souillac (exposed) ;

($F_{(1, 19)} = 2.45$, $p_{\text{randomised}} = 0.184$; Figure 3.54].

3.3.6.3.2 Species richness

The expected number of species on *Ulva lactuca* was computed for the two sites using the rarefaction method. For this analysis, non-quadrat *Ulva* samples were also included in computing the total number of amphipods in *Ulva lactuca*, and number of amphipods per species in *Ulva lactuca* at each site.

For the same number of individuals the expected number of species on *Ulva lactuca* was higher at Souillac (SOU) than at Trou aux Biches (TAB) (Figure 3.55).

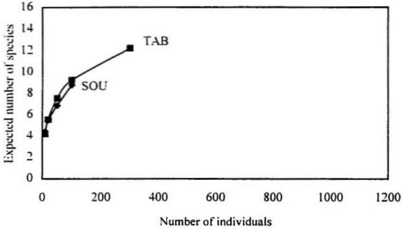

Figure 3.53 Rarefaction curves showing the expected number of amphipod species on *Gracilaria salicornia* at Souillac (SOU) and Trou aux Biches (TAB)

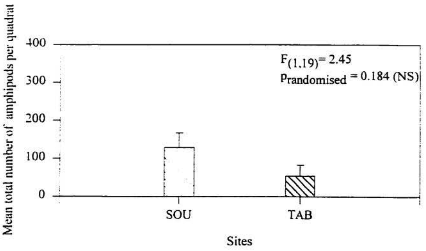

Figure 3.54 Mean total number of amphipods per quadrat for *Ulva lactuca* at Trou aux Biches (TAB) and Souillac (SOU) (NS: no significant difference; Vertical lines: standard error)

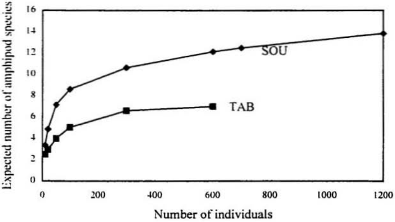

Figure 3.55 Rarefaction curves showing expected number of amphipod species on *Ulva lactuca* at Souillac (SOU) and Trou aux Biches (TAB)

3.3.6.3.3 Species heterogeneity

In order to compute the Shannon-Wiener diversity index and evenness index, the quadrat samples were pooled for *Ulva lactuca* at each site (SOU and TAB). The Shannon-Wiener diversity index in this alga at SOU was 0.99 while its was 0.88 at TAB, the evenness index was 0.43 and 0.45 at Souillac (SOU) and Trou aux Biches (TAB) respectively.

3.3.6.3.4 Relative abundance of amphipod species

The relative abundance of amphipod species in *Ulva lactuca* quadrat samples for the two sites was significantly different (two-way ANOVA interaction term [(species * sites) significant with $F_{(12, 247)} = 4.59$, $p < 0.0004$; Figure 3.56]). Further analysis of the relative abundance of amphipods per quadrat for 4 species which were abundant at either of these sites, showed a significant difference in the mean number of amphipods per quadrat for *Hyale grandicornis* ($F_{(1, 19)} = 7.45$; $p_{randomised} < 0.0004$) but not for *Hyale ayeli* ($F_{(1,19)} = 1.35$, $p_{randomised} = 0.447$), *Mallacoota subcarinata* ($F_{(1, 19)} = 0.81$, $p_{randomised} = 0.744$) and *Grandidierella grossimana* ($F_{(1,19)} = 1.54$, $p_{randomised} = 0.305$).

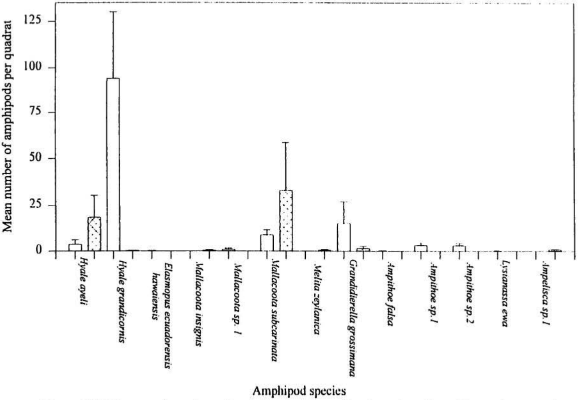

Figure 3.56 Mean number of amphipods for the 13 amphipod species collected in quadrat samples of *Ulva lactuca* at Trou aux Biches and Souillac (unhatched bars : SOU; hatched bars: TAB; Vertical lines: standard error)

3.3.6.3.5 Cluster analysis

A dendrogram of the cluster analysis on presence and absence data of amphipod species using the Jaccard similarity measure and average linkage between groups is shown in Figure 3.57. Exposed sites (A) clustered separately from moderately exposed and protected sites (B) .

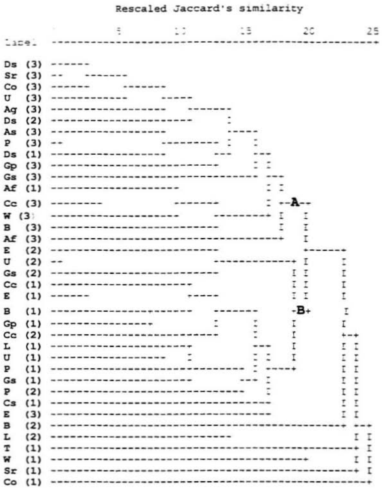

Figure 3.57 Dendogram for cluster analysis of algal categories from different exposures using average linkage (between groups) based on the Jaccard's Coefficient of similarity.
[refer to Table 2.4 for full names of algal taxa; Number in brackets indicates the site exposure categories: 1: Sheltered, 2: Moderately exposed, 3 : Exposed; A and B : cluster of algal categories from exposed and sheltered/moderately exposed sites respectively]

4.0 DISCUSSION

4.1 Amphipod fauna of Mauritius

This study adds 41 species to the known gammaridean amphipod fauna of Mauritius. The other 28 species collected during the study were reported by Ledoyer (1978) and are mostly species of the families Leucothoidae, Lysianassidae, Sebidae, Dexaminidae, Anamixidae, Melitidae and a few species of the family Ampithoidae. The main reasons for the large number of additional species found in my study were the types of substrates sampled and the depth at which samples were collected. Ledoyer (1978) examined mostly coral rubble and cavitary substrates from the subtidal zones. Only 10 of his samples were taken from depths of less than 2 m. With a few exceptions, my sampling was restricted to the intertidal and shallow-subtidal zones (< 0.5 m below low water) and the majority of samples were from algal substrates. In the present work, samples were collected from sites around the island which varied in wave exposure. The present study together with that of Ledoyer (1978) provide a good representation of the intertidal and shallow subtidal amphipod fauna of Mauritius.

4.2 Biogeography of the amphipods of Mauritius

Mauritius is an isolated volcanic island formed during the early Pliocene about 7.8 million years ago (McDougall and Chamalaun, 1969) and amphipods must have colonized the island by 'jump dispersal', a process which involves the movement of propagules across uninhabitable regions (Myers and Giller, 1988). Amphipods lack a pelagic larval stage and brood their young in ventral brood pouches. Dispersal is thus confined to adult-like stages and can be expected to be slow.

Biogeographical studies on marine organisms of Mauritius are sparse. The paper by Michel (1974) is among the few. He concluded that the marine organisms of Mauritius consist mostly of species widespread in the Indo-pacific. Gherardi and Mclaughlin's (1994) study of the hermit crabs of Mauritius supported this view. They concluded that the hermit crabs of Mauritius have broad distributions in the western Indian Ocean. However, this group has pelagic larvae which are readily dispersed.

Many of the Mauritian amphipod species show similar biogeographical patterns. Some are known to be cosmopolitan, for example, *Corophium acherusicum* and *Ampithoe ramondi* while others such as *Stenothoe gallensis, Elasmopus pectenicrus, Melita appendiculata, Cymadusa filosa, Gammaropsis atlantica, Erichthonius brasiliensis* and *Ventojassa ventosa* are known to be circumtropical (Barnard, 1970 and Ledoyer, 1978). *Eusiroides diplonyx, Hyale ayeli, Elasmopus spinidactylus, Paragrubia vorax* and *Gammaropsis afra* are species which occur widely in the Indo-pacific (Barnard, 1970).

The fact that more than 50% of the amphipods reported from Mauritius are shared with Madagascar may indicate that many amphipods of the island originated from Madagascar. According to Peyrot-Clausade (1979), 58 % of Mauritian polychaetes are also common to Madagascar. Peyrot-Clausade (1979) also pointed out that 77 % of anomuran and brachyuran decapods occurring in Mauritius and Reunion are shared with

Madagascar. A likely reason for the similarity between these two faunas is that Madagascar is the closest large land mass and organisms would have to move a relatively short distance (800 km) to reach Mauritius. However, some amphipods likely reached Mauritius from distant places like India or other Indo-pacific regions, their transport being influenced by ocean currents both present and past, and their ability to survive adverse conditions while traveling long distances.

Rafting on marine plants (Myers, 1991, 1993; Highsmith, 1985), debris or logs (Barnard, 1976) may be the means by which some amphipods reached the island. Barnard (1970) suggested that the amphipods of Hawaii reached there by these mechanisms. Amphipods that are domicolous (tube-builders) especially on plants, for example the ampithoids, corophiids, isaeids and ischyrocerids (Bousfield, 1973) are good candidates for dispersal by rafting. Inquilinous species and inquilinous nestling species (dexaminids, leucothoids, amphilochids and stenothoids) that usually associate with sponges, ascidians and hydroids attached to algae may also have been transported in this way. Barnard (1976) pointed out that inquilinous amphipods can be transported in their hosts attached to rafting material. Nestlers associated with algae, for example hyalids and melitids, are likely to have reached the island by rafting. Hyalids can travel long distances on algal flotsam like *Sargassum* (Barnard, 1970); melitids can also be dispersed by floating macroalgal mats (Myers, 1994). Transportation on the hulls of ship (Biernbaum, 1996) may also be an important method of dispersal for some species.

Corophium acherusicum builds tubes on ships and may thus be transported across long distances (Barnard, 1970).

Amphipod species richness in Mauritius (130 species) is much lower than that of Madagascar [287 species, Ledoyer, 1982, 1986 (cited from Barnard and Karaman, 1991)]. One of the possible reasons for the difference may be the depths at which samples were taken; Madagascar, 0-50 m, (Ledoyer 1982, 1986) as cited from Barnard and Karaman, 1991) and Mauritius, 0 -25 m, (Ledoyer, 1978 and present study). However, although one cannot say that the list of species from Mauritius is complete, based on the present work it is unlikely that Mauritius has as many species as Madagascar. There are at least three reasons for this : Mauritius is much smaller in size, younger in age and is more isolated. The theory of island biogeography (McArthur and Wilson, 1963, 1967) predicts that the number of species found on islands will depend on immigration rates and extinction rates, and small islands are expected to have fewer species as there is a greater probability of extinction due to ecological and genetic accidents (Schoener, 1988). Thus species may reach an island through dispersal but colonisation and establishment can only occur provided that the habitat is suitable and interspecific interactions do not drive the colonist to extinction through predation or competition (Myers and Giller, 1988; Myers, 1997).

Ecological biogeography deals largely with extant species and tries to explain distribution patterns in terms of interactions between organisms and their physical and biotic environment at present and during the recent past. As proposed by Myers and

Giller (1988), ecological phenomena can explain the great parallels between the community structure of different continental areas of similar climate and topography. In this context it is interesting that the numbers of known amphipod species in several families in Mauritius, Hawaii and Fiji are comparable, possibly indicating that these islands have undergone similar colonization patterns. The fact that Fiji and Mauritius, both of volcanic origin formed around the same period about 10 and 7.8 million years ago respectively, may also explain similarities in the amphipod faunas of the two islands.

Myers (1985) pointed out that island fauna, may be characterized by species flocks resulting from adaptive radiation of primary colonizers. However, in his review of the amphipod fauna of five Indo-pacific archipelagoes [Fiji, Hawaii, Mauritius (data from Ledoyer, 1978), Moluccas and Ifaluk], he concluded that explosive radiation is lacking in these tropical islands, and he commented that only the Leucothoidae in Mauritius and the Aoridae and Hyalidae in Hawaii show hyperradiation. Comparison of the number of species in families compiled in the present study (Table 3.4) supports this view.

Isolation on both a temporal scale (the greater the age of isolation, the greater the time for speciation) and a spatial scale (the greater the distance between gene pools the lower the genetic interchange) are important in producing endemics (Myers and Giller, 1988). The species which appear to be endemic to Mauritius have similar morphologies to species from Madagascar and India, suggesting that the species have not been isolated for a long time. Nevertheless, isolation on both temporal and spatial scales have contributed to the high number of endemics (about 32%) among Mauritian amphipods. This is a higher degree of endemism than seen in Mauritian brachyurans, about 10% according to Michel (1964) and a probable reason for this is that amphipods lack the pelagic larval stages found in brachyurans. Biernbaum (1996) made similar observations when comparing the percentage endemicity in amphipods and other marine animals on Ascension Island. Similarly, Brusca (1987) suggested that a relatively high proportion of endemics among the amphipods, isopods and pycnogonids of the Galapagos was due to their lack of a pelagic dispersal stage.

Comparable degrees of endemism in amphipods have been reported from Fiji (41%; Myers, 1985) and Hawaii (46%; Barnard, 1970). However, it is probable, given the poor state of amphipod taxonomy, that some of the apparently endemic species of Mauritius will be reported from other regions of the Indo-pacific as more taxonomic effort is put into the region. This has occurred in Hawaii where many of the amphipod species which were originally reported to be endemic (Barnard, 1970) have now been reported from other regions (Myers, 1985). Biernbaum (1996) put forward a similar caution in discussing the apparently high degree of endemism of the amphipods of Ascension Island.

4.3 Ecology

As Myers (1985) pointed out very little is known about the ecology of the Indo-pacific amphipods. Barnard (1976) and Myers (1985) both noted that ecological knowledge of tropical amphipods rests on information concerning their sites of collection and usually what is stated in the literature is inferred by extrapolation from what is known about their congeners in temperate waters.

Ledoyer (1978) briefly noted aspects of the ecology of subtidal Mauritian amphipods and presented data on the distribution of species collected from cavitary substrates as a function of depth. The present work is the first study dealing with aspects of the distribution of Mauritian intertidal/shallow-subtidal marine gammaridean amphipods on different substrates, with an emphasis on algal substrates, collected from sites of different wave exposure.

Barnard (1976) divided tropical amphipods into eight types: nestlers, domicoles, inquilines, substrate burrowers and inhabitants of neritic, strand, estuarine and anchialine habitats. The first five categories are related to the species' lifestyle in terms of abode and feeding while the last three are concerned mostly with location and ionic balance. Clearly, overlaps exist in these categories. For example, nestlers can occur in estuaries. In the present study the emphasis has been mainly on the use of substrates by nestlers and domicolous species (associated mostly with algae).

Amphipods that are nestlers swim or crawl freely between the crevices formed by plant interstices or coralline particles. Domicolous species, on the other hand, live in domiciliary tubes. These tubes are spun from secretions of the third and fourth pairs of thoracic legs and are attached to substrates, either hard or soft (Barnard, 1976; Dixon and Moore, 1997). Soft substrates include algae, rhizomes and seagrasses and external surface of sessile invertebrates. Some domicolous species, for example the ampeliscids, build tubes on soft bottom sediments.

4.3.1 The generalist and specialist amphipods

Analysis of the occurrence of amphipods in sand, coral rubble, debris, algae and seagrass showed that some species occurred only in one substrate (specialists) whereas others were more widespread among the substrates (generalists).

An example of a specialist is *Orchestia anomala* which was confined to debris (dead algae, seagrass and wood pieces) deposited on the shore by high tides. This talitrid can be placed in the "strand" category proposed by Barnard (1976). He pointed out that amphipods in this category are semi-terrestrial with individuals congregating at the moist interface between sand and decaying vegetation. Spicer et al. (1987) in a review of the physiological ecology of land invasion by talitrid amphipods suggests that beach hoppers (for example, *Orchestia gammarellus* found on British shores) possess physiological adaptations (as regards their mode of respiration, ability or inability to survive prolonged immersion and good ionic and osmotic regulation) for surviving in semi-terrestrial habitats. Moore et al. (1995) describe *Orchestia scutigerula* as being adapted to tolerate varying extremes of temperature and salinity. They also found that these amphipods fed mainly on debris composed of grass and green algae. Thus *Orchestia anomala* can be described as a specialist with adaptations to live in the semi-terrestrial habitat.

Among other species considered to be specialists are those that had high percentage frequencies of occurrence on plant substrates. These include species of the Families Eusiridae, Hyalidae, Melitidae, Ampithoidae, Isaeidae, Ischyroceridae, Aoridae and Corophiidae. *Ampelisca sp. 1* was also found to have a high percentage frequency of occurrence on plant substrates but was probably collected together with the sand or soft sediment in which ampeliscids build tubes (Bousfield, 1973).

Hadzia dentifera appears to be another specialist as it had a high percentage frequency of occurrence on sand and coral rubble. Barnard and Barnard (1983) noted that most hadziids are blind and this is true for the present species.

In contrast, some of the amphipod species occurred in a variety of substrates and can be considered generalists. These include some species of the Family Hyalidae, Melitidae, Ampithoidae and Aoridae. *Maera serrata* and *Mallacoota subcarinata*, belonging to the family Melitidae occurred on sand, coral rubble and algae. This indicates that the species are not selective of the types of substrates. Barnard (1976) pointed out that species of these genera occupy many substrates. The occurrence of the aorid, *Grandidierella grossimana* on sand, seagrass and algae may indicate that it can use different substrates to build tubes as Bousfield (1973) has reported for other aorids that build tubes in sand, seagrasses and algae.

4.3.2 Nestlers and domicolous species

Among the species occurring on algae and for which the occurrence on 17 algal taxa was computed, some species occurred on only a few algal types while others were more widespread. *Ampithoe kulafi*, for example, occurred only on a few algae while *Hyale grandicornis* occurred on a large number. Truchot (1963) in a study of the ecology of intertidal amphipods also observed that some amphipod species preferred to live on specific algae. The reasons for these varying patterns of distribution are not clear at present. One can speculate that some algae may be the preferred biotope because they provide the best conditions with regard to food, shelter, protection against predators and reduced competition with congeners. An alga may, on the other hand be a preferred biotope because it grows under the ionic, exposure, and/or turbidity conditions preferred by the amphipod.

Some species of the genera *Hyale, Elasmopus, Maera* and *Mallacoota* occurred on almost all algal taxa. These results are not surprising and can be explained from what is known about the lifestyle of their congeners. These genera as reported by Barnard (1976) can nestle freely among many types of substrates.

Some patterns of occurrence of the domicolous species on algal taxa possibly reflect their ability to utilise the alga as a place to build their tubes. The tube builders belong to the Families Ampithoidae (Skutch, 1926; Just, 1977; Nelson, 1979; Lewis and Kensley, 1982), Aoridae, Isaeidae, Ischyroceridae (Ultrich et al., 1995) and Corophiidae

(Crawford, 1937; Sheader, 1978; Ultrich et al., 1995). Among the tube building genera encountered in this study are *Lembos, Gammaropsis, Ampithoe, Cymadusa, Grandidierella* and *Corophium.*

Amphipod species may occur on specific algae because these conform to their lifestyle, structure of mouthparts and nutritional requirement (Nicotri, 1980; Buschmann, 1990). If an amphipod species consumes the algal substrate it lives on, then the toughness of the algal tissue may be an important factor in determining what alga it is found on. There was a significant difference in the mean number of *Mallacoota subcarinata* and *Hyale grandicornis* among algal toughness categories at Souillac, with the highest mean abundance occurring on algae of low and intermediate toughness, respectively. The significantly high abundance of *Hyale grandicornis* on the lowest toughness algae (*Ulva lactuca* and *Enteromorpha flexuosa*) may indicate that it is feeding directly on them. A congener, *Hyale rupicola,* has been demonstrated to feed on macroalgae like *Ulva sp.* (McGrouther, 1983) and another congener, *Hyale nilssoni*, consumes *Enteromorpha intestinalis* (cf. Mcbane and Croker, 1983). None of the other amphipod species at Souillac showed a significant difference in abundance among algal toughness categories. This may suggest that these species do not feed directly on the algae but are microphagous, feeding on particulate detritus and epiphytic diatoms that accumulate on the plants (Zimmerman et al., 1979). Dixon and Moore (1997) noted that corophioid species (except *Ampithoe* species) feed on suspended or deposited particles including microflora and detritus.

Structural habitat complexity often reduces predatory efficiency by reducing prey capture rates (Crowder and Cooper, 1982; Coull and Wells, 1983; Russo, 1987). Hacker and Steneck (1990) concluded both from field and laboratory experiments that higher densities of amphipods are observed on algae with branched and filamentous morphologies than on those with foliose morphologies. In the present study the mean number of amphipods on three algal morphological categories at Souillac was significantly different only for *Hyale grandicornis*, with the highest mean number on the foliose type. These results suggest that the association between density of amphipods and algal morphological complexity may not be direct. Holmund et al. (1990) showed that some amphipods are more subject to predation by fish when living on highly branched seaweeds than when living on sheetlike algae like *Padina gymnospora* or *Ulva sp*. They concluded that susceptibility of amphipods to predation by ominvorous fish may be affected by both host-plant morphology and host-plant palatability to fish.

Some amphipod species may also be associated with specific algae because these algae produce chemicals that deter their predators, especially fish (Duffy and Hay, 1991, 1994; Hay et al., 1987; Hay et al., 1990). As regards algae in the present study, *Caulerpa racemosa*, is known to contain caulerpenyne which has ichthyotoxic and herbivore deterrent properties (Paul and Hay, 1986). One species, *Mallacoota sp. 1*, did have a high percentage frequency of occurrence and a high abundance on this alga, but whether this is related to the chemical properties of the alga requires further investigation.

Some amphipod species may be found on just a few algal taxa possibly because of interspecific competition. Edgar (1983d) in a study of the factors affecting the distribution of ampithoid amphipods among algae observed that adult amphipods were partitioned among different algal species. Lancellotti and Trucco (1993) in a study of six *Hyale* species occurring on an exposed intertidal shore in Chile, concluded that interspecific competition was the main factor influencing their distribution and coexistence patterns. The three *Hyale* species collected at Souillac had the highest abundance on different algal taxa. *Hyale ayeli* was abundant on *Digenia simplex*, *Hyale chevreuxi* on *Sargassum densifolium* and *Hyale grandicornis* on *Ulva lactuca*. This partitioning of species among algal taxa was also observed in the genera *Mallacoota*, *Elasmopus* and *Ampithoe*.

A possible interpretation is that there is interspecific competition within each genus for resources. The segregation of species to different specific substrates may reduce competition for food and space. Fenchel and Kolding (1979) suggested that habitat divergence in *Gammarus* species may be a result of selection against interspecific precopula formation leading to sterile mating. Edgar (1983d) suggested that partitioning of ampithoids on different algae may be the result of selection that occurred to avoid sterile matings. Based on the distribution patterns of species, this mechanism could be operating in four genera, *Hyale*, *Mallacoota*, *Elasmopus* and *Ampithoe*, at Souillac. However, this needs to be further investigated as the biology of the species in question is not known.

The nature of the environment also affects the occurrence of amphipod species. Some amphipods may have a high frequency of occurrence on specific algae because the algae grow under their preferred salinity, turbidity and/or wave exposure conditions. The occurrence of *Grandidierella bonnieri*, *Grandidierella grossimana* and *Corophium acherusicum* on *Enteromorpha flexuosa*, *Boodlea composita* and *Ulva lactuca* may be such examples. Their associated algae grow under estuarine-nutrient enriched conditions (Raffaelli et al., 1991) and amphipod species of the genera *Grandidierella* and *Corophium* are known to occur in such habitats (Barnard, 1976).

4.3.3 Amphipod assemblages among algae

The mean total number of amphipods was not significantly different among 12 algal categories at Souillac or four algal categories at Trou aux Biches, showing that these algae support similar total numbers of amphipods. That the mean number of amphipods was not significantly different among algal morphological categories differs from the observations made by Sarma and Ganapathi (1970), who concluded that more individuals are found on branched algae. However, Russo (1990), in a study of epiphytal amphipod abundance among algae of different morphologies in Hawaii, also found no direct relationship between amphipod abundance and algal complexity (surface area to biomass ratio). In a study of faunal abundance among macrophytes in Apalachee Bay (Florida, USA), Lewis (1987) observed that the highest number of amphipods was on unbranched rather than branched algae.

These studies together with the present one indicate that the relationship between algal complexity and abundance of amphipods is not a simple one. Edgar (1983a) pointed out that if the total numbers of amphipods are not significantly different among algal taxa, biological characteristics such as body size need to be considered. Edgar (1983a) observed that small amphipods were more likely to occur on filamentous algae than on plants with wider thalli, while larger amphipods showed the opposite response. Hacker and Steneck (1990) also pointed out that higher densities of small amphipods are found on algae with smaller interstitial spaces and thinner branches, whereas medium or large amphipods occurred in highest densities on algae with large interstitial spaces and wider branches. Such distribution mechanisms may be operating in the community presently studied, but further study is required to investigate possible size-dependent habitat selection.

The mean number of amphipods was also not significantly different among algal toughness categories. This may be a reflection of the feeding habits of the amphipods. They may not be consuming the algae but rather feeding on detrital material or other organisms associated with the algae.

According to the theory of spatial heterogeneity a more complex environment will support more species (cf. Heck and Wetstone, 1977) because it contains more resources capable of sustaining large numbers of species than a less complex environment. Abele (1974) indicated that the number of decapod species in shallow water increases as substrate complexity increases. The fact that increased microhabitat complexity resulted in a linear increase in species number among algae was observed by Hicks (1980) in a study of phytal harpacticoid species. Although one must take into account sampling bias, it is not surprising that the algal substrates in this study have a much higher diversity of amphipods than, for example, sand. This may be the result of the fact that algae represent a complex habitat containing more resources such as habitable space and provide better protection from predators (cf. Heck and Wetstone, 1977).

At the algal species level, amphipod species richness based on rarefaction curves was higher on *Amansia glomerata* and *Gracilaria spp.* as compared to *Sargassum densifolium*, *Acanthophora spicifera* and *Enteromorpha flexuosa* at Souillac. At Trou aux Biches a high number of amphipod species is expected on *Gracilaria salicornia* as compared to the other algae. The Shannon-Wiener diversity index was also highest in the case of *Gracilaria* samples both at Souillac and Trou aux Biches.

Russo (1990) in a study of the role of algal morphological complexity in structuring Hawaiian epiphytal amphipod communities ranked the alga *Amansia glomerata* as having the highest complexity and he observed from rarefaction curves that the expected number of species in this alga was highest as compared to other algae. This was the case in the present study. *Amansia glomerata* has a rosette-like morphology, with the tips of the thallus having marginal teeth (Jaasund, 1976). The alga was observed to be strongly attached to rock substrates with many epiphytic algae (*Jania adherens* Lamouroux) attached to it. *Gracilaria spp.* (*G. millardetti, G.crassa, G. corticata*) also form mats on rock surfaces at Souillac. The thallus consists of divided blades and, in the case of *Gracilaria crassa*, are well secured by basal discs and bundles of rhizoids to the substratum (Jaasund, 1976). *Amansia glomerata* and *Gracilaria spp*. both provide complex habitable space, shelter and protection from predation and wave shock for a variety of amphipod species both for the nestling and tube-dwelling species and this may explain why a high number of species occur on them.

The expected number of amphipod species on *Gracilaria salicornia* was also high both at Trou aux Biches and Souillac. This alga forms dense tubular mats attached to rock surfaces. Like *Amansia glomerata* and *Gracilaria spp*., it may provide protection from wave shock and predation, although not to the same extent because it has a more open structure. An interesting observation made on inspecting the species that occur in this alga was the occurrence of species like *Anamixis pottsii*, *Paranamixis bocki* and *Leucothoe madrasana*, genera which are usually associated with sponges. This alga tends to harbour epiphytic sponges and its high species richness is probably due to the additional microhabitats it provides. A similar observation was made by Edgar (1983c) who found that the alga *Thamnoclonium clariferum* had high species richness because it was colonized by epiphytic sponges and bryozoans, which harboured a number of amphipod species.

The Shannon-Wiener diversity index was highest in *Gracilaria spp*. and *Amansia glomerata* at Souillac. The evenness index was fairly high for these two algae, implying that the species tend to be equally abundant on each alga. Possible reasons for this pattern could be that *Gracilaria spp.* and *Amansia glomerata* are morphologically complex and offer more resources to sustain a high number of equally abundant species.

The lower than expected number of amphipod species on *Sargassum* than on *Amansia glomerata, Gracilaria sp.* or *Gracilaria salicornia* at Souillac may be because it has a more open three dimensional structure. The Shannon-Wiener index and the evenness index were low for this alga because of the dominance of *Hyale ayeli.* One of the possible reasons for the low diversity on this alga may be because it was found attached to rocks on the most exposed regions within the site at Souillac and only amphipod species that can resist strong wave action are likely to colonize it.

Competition among amphipod species and also with other organisms can influence the community structure found on different plant substrates (cf. Russo, 1990; Coen et al., 1981). Presence of dominant competitors may cause a decrease in species diversity in amphipod communities in algae.

4.3.4 Amphipod assemblages and environmental variables

The total abundance of amphipods on *Ulva lactuca* was not significantly different at the sheltered site (Trou aux Biches) and the wave exposed site (Souillac). These results contrast with those of Fenwick (1976) who found that the abundance of amphipods in *Caulerpa brownii* in New Zealand was higher at a wave-exposed site compared to a sheltered site.

In terms of the number of species, however, Souillac had a higher expected number of species on *Ulva lactuca* than Trou aux Biches. Moreover, the Shannon-

Wiener index was higher on *Ulva lactuca* at Souillac than Trou aux Biches. The evenness index was low at both sites. These results tend to agree with those of Wakabara et al., (1983) who observed a higher amphipod diversity on *Sargassum* on an exposed shore than on a sheltered shore in Brazil. Possible reasons for a higher diversity at exposed sites are that there is more suspended food and less deposited sediment.

Although the results obtained in the present study do not agree with those of Fenwick (1976), some of the trends in the lifestyle of the species he observed are similar to those observed in the present work. Fenwick (1976) noted that nestlers were equally common on shores of different wave exposure; tube dwellers however were more abundant in exposed conditions. He also suggested that the high incidence of tube-dwelling forms at exposed sites may reflect an adaptation for avoiding displacement by mechanical drag imposed by water movement. Inspection of the species composition on *Ulva lactuca* at the two sites showed that *Ampithoe sp. 1* , *Ampithoe sp. 2* and *Ampithoe falsa*, belonging to a genus of tube-dwellers, only occurred at Souillac. These species possess a pair of hooks at the tips of the third uropods, enabling them to remain attached to their tubes which help overcome the mechanical drag imposed by wave action.

In a study of the distribution patterns of *Hyale* species on the intertidal rocky shores in Chile, Lancellotti and Trucco (1993) observed that *Hyale grandicornis* tends to predominate in the wave exposed intertidal. They attributed the distribution of this species, along with a few other *Hyale* species, to their morphological attributes. They possess strong gnathopods and armed pereiopods as adaptations to withstand waves. In the present study there was also a significantly higher number of *Hyale grandicornis* in *Ulva lactuca* at the exposed site (Souillac) as compared to the sheltered site (Trou aux Biches).

The fact that exposure and possibly macroscopic characteristics of the environment have a strong influence on amphipod communities was apparent from the cluster analysis which indicated that amphipod assemblages at sites with the same exposure were very similar. One reason for this similarity was that some amphipod species were found only at wave exposed sites. For example, on the widely distributed algae, *Boodlea composita, Digenia simplex* and *Gracilaria salicornia, Elasmopus spinidactylus* was collected only at the exposed sites. This species may be adapted to living in exposed conditions as the dactyl has several projections (as the name implies) which may help it to hold tightly to algae. *Jassa sp. 2* is an example of another species that occurred only at the exposed sites. A congener of this species, *Jassa falcata* has a high frequency of occurrence at exposed sites (Wakabara et al., 1983; Tararam and Wakabara, 1981; Krapp-Shickel and Krapp, 1975). Species of this genus are tube-dwellers and can live in rough hydrodynamic environments.

Some species occurred only in moderately exposed and sheltered sites. For example, when considering the algae *Boodlea composita, Centroceras clavulatum, Padina spp., Gracilaria salicornia* and *Ulva lactuca* from which collections were available for all exposure site groups, *Elasmopus pectenicrus* occurred only in moderately exposed and sheltered sites.

Similarly, inspection of *Gracilaria salicornia, Padina spp., Turbinaria ornata* and *Ulva lactuca* samples collected from different exposures showed that *Erichthonius brasiliensis* occurred only at sheltered sites. This observation agrees with what has been reported by Tararam and Wakabara (1981) who observed a high frequency of occurrence of *Erichthonius brasiliensis* on sheltered shores.

4.4 Future work

The results of this study offer fertile ground for future work. The study provides a good representation of the amphipods of the intertidal/shallow-subtidal in general but substrates where inquiline species or burrowing species live need to be further investigated.

The ecology of the amphipod species is far from clear and many factors such as lifestyle, structure of mouthparts, nutritional requirements, competition with other species and protection from predators need to be considered. The characteristics of the plant habitats such as morphology and production of secondary metabolites need to be investigated to better understand why species associate with particular substrates. In the present work, few algae were present within some of the morphological or toughness categories, and association of amphipods with these categories may reflect preference for specific algae rather than the morphological or toughness attributes. In such studies the use of both algae and their mimics (Hacker and Steneck, 1990) need to be considered.

The same factors must also be considered when dealing with amphipod communities. The distribution of amphipod species and communities have been studied in relation to the nature of the substrate and the wave exposure of sites. However, further studies need to be done on the macroscopic physical and chemical parameters of the environment such as wave exposure (water movement) and/or turbidity (Hicks, 1980; Moore, 1972, 1973, 1978), amount of detritus (Dahl, 1948), salinity (Dahl, 1948, Skadsheim, 1983) and degree of pollution (Jones, 1973; Sheppard et al., 1980). Bellan-Santini (1981) in a study on phytal amphipods observed that pollution can cause a decrease in species diversity, a change in the balance of the species in a community favouring species which are detritus and suspension feeders. Jones (1973) in a study of invertebrate communities in polluted kelp forests made similar observations. The fact that some of the sites in Mauritius are polluted cannot be ignored (Fagoonee, 1990; Gendre et al., 1994) and this possible influence on the amphipod community requires further investigation.

5.0 SUMMARY

Sixty-nine gammaridean amphipod species were collected in the present study from the intertidal and shallow subtidal zones from 34 sites in Mauritius. Forty-one of these species are first records for the island; 19 species are undescribed. Together with the work of Ledoyer (1978), 130 species are now known from Mauritius and 42 are believed to be endemic.

Most of the Mauritian amphipod species are widespread in the Indo-pacific. More than 50% of the species are shared with Madagascar (the closest large land mass). However, a high degree of endemism (32%) is observed, probably due to the isolation of the island.

Amphipod ecology was analyzed with reference to substrates with emphasis on algal substrates. Thirty-five amphipod species occurring predominantly on algae showed varied patterns of occurrence on 17 algal taxa. At Souillac, the mean abundance of *Hyale grandicornis* on foliose algae was significantly higher than on any other algal morphology, and it was significantly higher on the softest algae, while *Mallacoota subcarinata* was significantly more abundant on algae having intermediate toughness.

The mean total number of amphipods and the mean number among morphological categories or toughness categories (Souillac only) were not significantly different among algal taxa at Souillac or Trou aux Biches. Species richness was different among algal taxa with *Amansia glomerata*, *Gracilaria spp.* and *Gracilaria salicornia* having higher expected numbers of species at Souillac and *Gracilaria salicornia* having higher expected numbers of species at Trou aux Biches.

No significant difference in total number of amphipods per quadrat was found in *Ulva lactuca* collected from Souillac and Trou aux Biches. A higher species richness was, however, observed at Souillac (the wave exposed site). Inspection of the species showed that *Ampithoe sp. 1*, *Ampithoe sp. 2* and *Ampithoe falsa* occurred only at Souillac. A comparison of the mean abundance of species showed that *Hyale grandicornis* was significantly more abundant at the wave-exposed site (Souillac) than in the sheltered site (Trou aux Biches).

Cluster analysis of the amphipod assemblages in algae collected from sites of different wave exposure showed that a closer similarity existed between assemblages at the moderately exposed and protected sites as compared to the exposed sites. Some amphipod species for example, *Elasmopus spinidactylus* and *Jassa sp. 2* occurred only at exposed sites while *Elasmopus pectenicrus* and *Erichthonius brasiliensis* occurred only at protected/moderately exposed sites.

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8.0 APPENDICES

Appendix A: Brief description of the 34 sites visited during the sampling programme.
[Wave exposure: Sheltered (S), Moderately exposed (ME), Exposed (E)]

Site number	Name	Location	Date visited	Wave exposure	Water temperature	Salinity	Description
1	Anse la Raie (ALR)	57°37.22′ E 19°59.24′ S	09.05.95 02.06.95 04.07.95	S	27 27	22, 23 21, 28	Sandy beach made up of fine sand with a sparse distribution of basaltic rocks. A small stream flows into the area. Sponges and red algae are common.
2	Grand Gaube (GG)	57°39.70′ E 20°00.16′ S	02.06.95	S		30	Sandy beach with basaltic rocks forming part of an old jetty. Green and red algae are common on the rocks.
3	Pointe des Lascars (PDL)	57°42.02′ E 20°05.00′ S	09.05.95 07.06.95	S	27 27	28 30, 32	Shore made up of a mixture of sand and soil with few basaltic rocks. Small pebbles and silt tending to accumulate in the region close to the mouth of Rempart river. Green algae and a few patches of red algae are common.
4	Roche Noires (RN)	57°44.51′ E 20°06.79′ S	07.06.95	E	27	34.5	Sandy beach made up of coarse sand particles. Beach rocks and a few patches of basaltic rocks are present. Brown and red algae are common.
5	Poste la Fayette (PLF)	57°45.01′ E 20°07.50′ S	20.04.95 17.05.95	E	23	35.5	Rocky shore with a large basaltic platform. As one moves south there is a sheltered sandy region with patches of green algae.
6	Poste la Fayette Fisheries post (PLFF)	57°44.79′ E 20°07.88′ S	17.05.95 07.06.95	ME	25 28	29 21.5	Sandy beach with few patches of loose basaltic rocks. Green algae are common. Mangrove plants are very common as one moves south.

7	Poste de Flacq (PDF)	$57^{0}45.55'$ E $20^{0}09.84'$ S	07.06.95	ME	28	32.5	Shore made up of basaltic rocks which tend to form platforms due to erosion. A more sheltered sandy region is found north of the area. Red algae are common.
8	Belle Mare (BM)	$57^{0}46.24'$ E $20^{0}11.47'$ S	07.06.95	S	28	15	Shore made up of fine sand. Coral rubble and green algae are common.
9	Beau Champ (BC)	$57^{0}46.94'$ E $20^{0}16.52'$ S	17.05.95	ME		24, 29	Shore muddy with sparse distribution of loose basaltic rocks. Debris of seagrasses and brown algae are deposited on the shore.
10	Quatre Soeurs (QS)	$57^{0}46.36'$ E $20^{0}18.15'$ S	07.07.95	ME			Shore made up of a mixture of small pebbles and soil. Large amounts of algal and seagrass debris are deposited on the shore.
11	Mahebourg (MAH)	$57^{0}42.31'$ E $20^{0}24.46'$ S	21.06.95	S	27, 29	19.5, 34.5	Shore made up of basaltic rocks and small pebbles. Sandy region interspersed with basaltic rocks tending to become prominent as one moves south. Green algae are common on rock surfaces.
12	Le Bouchon (BOU)	$57^{0}40.52'$ E $20^{0}27.99'$ S	21.06.95	E	28, 29	17.5, 20.5	Shore made up of sand and widespread boulders of basaltic rocks with a sparse distribution of red, and brown algae and seagrass. A sheltered sandy region with abundant green algal growth is found south of the region.
13	Gris Gris (GRI)	$57^{0}31.39'$ E $20^{0}31.30'$ S	22.05.95	E	28		Solid basaltic rocks from a cliff about 10 m high and a sandy shore made up of coarse sand delineate the site. Beach rock and coral rubbles covered with red, brown and green algae are common.

14	Souillac (SOU)	57°30.81′ E 20°31.03′ S	15.04.95 19.05.95 05.06.95 19.06.95	E	25, 27 25, 26, 27	18,22, 34.5 24,24, 29,34.5	Rocky platform dropping from a basaltic cliff about 15 m high. The rocky region is characterised by tide pools and a diversity of algae. A more sheltered region with basaltic rocks covered mostly with green algae is found north of the rocky area. River Savanne flows into this part of the site.
15	Riambel (RIAM)	57°30.00′ E 20°30.87′ S	22.05.95	S			Shore made up of fine sand. A few patches of coral rubble and green algae are present.
16	Pointe aux Roches (PAR)	57°27.86′ E 20°30.71′ S	22.05.95	E	28		Rocky shore made up of platforms and cliffs of basaltic rocks . A diversity of algae occur in the rock pools.
17	Saint Felix (STF)	57°27.51′ E 20°30.38′ S	15.04.95	S			Shore made up of fine sand. A few patches of brown algae are common.
18	Riviere des Galets	57°26.05′ E 20°30.00′ S	22.05.95	S			Shore consists of fine sand and smooth volcanic rocks. Brown, green and red algae are common.
19	M'ma Conde (MAC)	57°21.91′ E 20°29.24′ S	22.05.95	S			Sandy shore with large amount of wood debris. Mangrove patches are found in the close proximity.
20	Le Morne	57°19.83′ E 20°27.39′ S	05.07.95	S	28	37	Sandy shore made up of fine sand. Few patches of seagrass observed in the intertidal but algal substrates are absent. Large amount of seagrass debris is deposited on the shore.
21	Case Noyale (CN)	57°21.73′ E 20°24.18′ S	15.04.95	S			Muddy shore with few basaltic rocks. Sparse occurrence of green algae.

22	Tamarin (TAM)	57°21.91′ E 20°19.46′ S	23.05.95	S	27	34.5	Sandy shore. Coral rubbles and very few basaltic rocks are present. River Tamarin flows into the area. Brown algae are common but green algae tend to be more prominent towards the river mouth.
23	Wolmar (WOL)	57°21.45′ E 20°17.88′ S	23.05.95	S	28	30	Shore made up of fine sand. Coral rubbles and patches of green algae are present.
24	Flic en Flac (FEF)	57°21.73′ E 20°16.14′ S	08.04.95 11.04.95 13.04.95 20.04.95				Sandy shore with coral rubble and brown algae are common. North of this region is a large basaltic rock platform with rock pools with a diversity of algae.
			18.05.95	S	29,29,29,29	28,28, 28,28	
			16.06.95				
25	Albion (ALB)	57°23.76′ E 20°12.72′ S	23.05.95	S	29.5	30	Sandy shore. Few patches of green and brown algae occur.
26	Pointe aux Caves	57°25.55′ E 20°11.20′ S	03.05.95	E			Rocky basaltic platforms dropping from a cliff about 15 m high. The rock pools contain a diversity of algae.
27	Pointe aux Sables (PAS)	57°26.59′ E 20° 10.00′ S	20.04.95 23.05.95	S	29	24	Sandy shore. Coral debris and few basaltic rocks with green algal patches are prominent.
28	Baie du Tombeau (BDT)	57°29.88′ E 20°06.41′ S	23.05.95	S			Shore made up of a mixture of coarse sand and coral rubbles. Shore appears muddy.
29	Balaclava (BALA)	57°30.23′ E 20°04.73′ S	23.05.95	S	28		Sandy shore with abundant coral rubble. Beach rocks are present and brown algae, especially *Turbinaria ornata*, are abundant.
			20.06.95		27	30	

30	Pointe aux Piments (PAP)	$57^{0}30.75'$ E $20^{0}03.53'$ S	20.04.95	S			Sandy shore. Coral rubbles and a few patches of green algae are common.
31	Trou aux Biches (TAB)	$57^{0}31.85'$ E $20^{0}02.23'$ S	19.04.95				Sandy shore with sparse distribution of basaltic rocks. Green and red algae are abundant.
			26.04.95	S			
			11.05.95			33.5, 33.5, 34.5	
			06.06.95		29,29,29	2.5,6.5,8, 8,13,13,13, 18.5,18.5, 18.5,22,22	
			20.06.95		28	4.5, 9, 15,17.5, 18.5, 19.5, 22, 24	
32	Mon Choisy (MCHOI)	$57^{0}32.72'$ E $20^{0}01.09'$ S	09.05.95	S	26, 27	33.5, 33.5,34.5, 34.5, 34.5	Sandy beach. Few green algal patches present. The most common plant substrates are seagrass beds .
33	Grand Baie (GB)	$57^{0}34.57'$ E $20^{0}00.54'$ S	09.05.95	S	27	33.5, 33.5	Sandy shore. Basaltic rocks and an old jetty present. Green algae are abundant.
			02.06.95				
			04.07.95		27	32.5	
34	La Cuvette (CUV)	$57^{0}34.16'$ E $20^{0}00.33'$ S	20.04.95	S			Sandy shore with loose and firm basaltic boulders. Brown algae and red algae are common.
			02.06.95		27		
			04.07.95		26	30	

Appendix B Representative examples of sampling sites

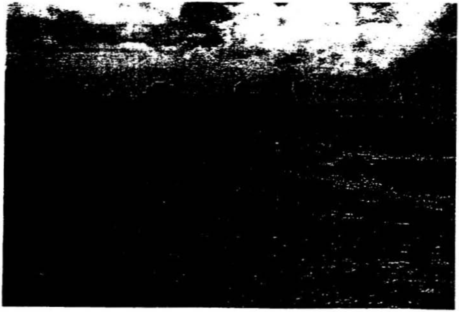

Figure B1 Anse la Raie site (ALR) on the north coast of Mauritius showing the sheltered lagoon with fine sandy region and algal substrates which are uncovered at low tide.

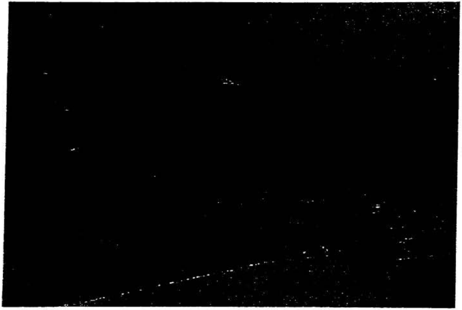

Figure B2 La Cuvette (CUV) site on the north coast of Mauritius showing part of the sandy beach in a sheltered lagoon with patches of brown algae and basaltic rocks covered with green algae.

Figure B3 Pointe aux Roches (PAR) site on the south coast of Mauritius showing the rocky basaltic area covered with a diversity of algae. The site is exposed to heavy wave action.

Appendix C List of amphipods reported by Ledoyer (1978) that have not been found in the present collection (indicated as ** in Table 3.2) (Names have been updated using Barnard and Karaman, 1991).

- Superfamily Eusiroidea
  - Family Eusiridae
    - *Eusiroides diplonyx* Walker, 1909

- Superfamily Oedicerotoidae
  - Family Exoedicerotidae
    - *Kanaloa manoa* J.L. Barnard, 1970

- Superfamily Leucothoidea
  - Family Pleustidae
    - *Tepidopleustes barnardi* (Ledoyer, 1972)
  - Family Amphilochidae
    - *Amphilochella laticarpa* Ledoyer, 1978
    - *Amphilochus neapolitanus* Della Valle, 1893
    - *Gitanopsis pele* J.L. Barnard, 1970

  - Family Cyprodeidae
    - *Cyproidea ornata* Haswell, 1880
    - *Unyapheonoides dabber* J.L. Barnard, 1972
  - Family Leucothoidae
    - *Leucothoe acutilobata* Ledoyer, 1978
    - *Leucothoe angusticoxa* (Ledoyer, 1972)
    - *Leucothoe lihue* J.L. Barnard, 1970
    - *Leucothoe micronesiae* J.L. Barnard, 1965

  - Family Anamixidae
    - *Anamixis grossimana* Ledoyer, 1978
    - *Paranamixis excavatus* Ledoyer, 1978
  - Family Colomastigidae
    - *Colomastix lunalilo* J.L. Barnard, 1970
    - *Colomastix truncatipes* Ledoyer, 1979
  - Family Stenothoidae
    - *Stenothoe gallensis* Walker, 1904
- Superfamily Talitroidea
  - Family Hyalidae
    - *Hyale inermis* Ledoyer, 1979
  - Family Eophliantidae

Ceinina latipes Ledoyer, 1978
Family Phliantidae
Pereionotus alaniphlias J.L. Barnard, 1970
Superfamily Lysianassoidea
Family Lysianassidae
Amaryllis macrophthalma Haswell, 1880
Ensayara angustipes Ledoyer, 1978
? *Paralysianopsis mauritiensis* Ledoyer, 1978
Superfamily Stegocephaloidae
Family Iphimediidae
Iphimedia compacta Ledoyer, 1978
? *Iphimedia sp.* (Ledoyer, 1978)

Superfamily Liljeborgioidea
Family Liljeborgiidae
Liljeborgia heeia J.L. Barnard, 1970
Liljeborgia proxima Chevreux, 1907

Family Sebidae
Seba hirsuta Ledoyer, 1978
Superfamily Dexaminoidea
Family Dexaminidae
Paradexamine indentata Ledoyer, 1978
Superfamily Ampeliscoidae
Family Ampeliscidae
Ampelisca pygmea Schellenberg, 1938
Superfamily Hadzioidea
Family Melitidae
Ceradocus hawaiensis J.L. Barnard, 1970
Elasmopus molokai J.L. Barnard, 1970
Elasmopus pseudoaffinis Schellenberg, 1938
Elasmopus sp. Ledoyer, 1978
Eriopisella dentifera Ledoyer, 1978
? *Maera aequimana* Ledoyer, 1979
Nuuanu amikai J.L. Barnard, 1970
Pseudoelasmopus cheliferus Ledoyer, 1978

Superfamily Corophioidea
Family Biancolinidae
?*Biancolina mauihina* J.L. Barnard, 1970
Family Ampithoidae
Ampithoe pollex Kunkel, 1910
Ampithoe sp. Ledoyer, 1978

?Cymadusa brevidactyla (Chevreux, 1907)

Family Isaiedae
- *Aorcho curvipalma* Ledoyer, 1978
- *Gammaropsis abbotti* (J.L. Barnard, 1965)
- *Gammaropsis afra* Stebbing, 1888
- *Gammaropsis grandimana* Ledoyer, 1978
- *? Gammaropsis holmesi* (Stebbing , 1908)
- *Gammaropsis mauritiensis* Ledoyer, 1978
- *Gammaropsis photissimilis* Ruffo, 1969
- *Gammaropsis pokipoki* J.L. Barnard, 1970

Family Ischyroceridae
- *Ericthonius latimanus* Ledoyer, 1979
- *? Jassa sp*. Ledoyer, 1978
- *Parajassa chilkoa* Griffiths, 1974
- *Parajassa spinipalma* Ledoyer, 1979
- *Ventojassa ventosa* (J.L. Barnard, 1962)

Family Aoridae
- *Bembos pseudopunctatus* (Ledoyer, 1978)
- *Lembos tridens* (Schellenberg, 1938)
- *Ritaumius longicornis* Ledoyer, 1978

Family Podoceridae
- *Laetmatophilus acuticephalus* Ledoyer, 1978
- *Podocerus cristatus* identification of Chilton, 1926
- *Podocerus cf. palinuri* K.H. Barnard, 1916

Appendix D Percentage frequency of occurrence (A_{sub}) for 64 amphipod species

Species	Sand	Coral rubble	Debris	Seagrasses	Algae
Tethpaci	0.00	0	0.00	0	4.23
Perilong	0.00	0	0.00	0	0.56
Amphsp1	0.00	0	0.00	0	0.85
Amphsp2	0.00	0	0.00	0	0.56
Gitasp1	25.00	0	0.00	0	0.85
Leuccren	12.50	0	0.00	0	0.28
Leuchyl	0.00	0	0.00	0	0.28
Leucmadr	0.00	0	0.00	0	0.28
Leucpred	0.00	0	0.00	0	1.13
Leucsp1	0.00	0	0.00	0	0.56
Leucsp2	0.00	0	0.00	0	0.28
Leuebann	0.00	0	0.00	0	0.28
Anampott	0.00	0	0.00	0	2.25
Parabock	0.00	0	0.00	0	1.97
Hyalayel	0.00	0	0.00	4.35	31.83
Hyalchev	0.00	0	0.00	0	15.21
Hyalgran	0.00	12.5	5.00	0	15.49
Parhindi	0.00	0	0.00	0	2.82
Orchanom	0.00	0	100.00	0	0.00
Lysiewa	12.50	0	0.00	4.35	2.82
Lysisp1	0.00	12.5	0.00	0	0.28
Sebatypi	0.00	37.5	0.00	0	0.56
Paraorien	0.00	0	0.00	0	0.28
Ampesp1	0.00	0	0.00	65.2	12.11
Hadzdent	12.50	37.5	0.00	0	0.28
Ceramaha	12.50	0	0.00	0	0.00
Elasecua	25.00	0	0.00	0	10.99
Elashooh	0.00	0	0.00	0	4.23
Elaspect	0.00	0	0.00	0	3.10
Elasspin	0.00	0	0.00	0	3.94
Elassp1	0.00	0	0.00	0	0.56
Maermann	12.50	0	0.00	0	0.85
Maerocto	0.00	0	0.00	0	0.85
Maerpaci	12.50	0	0.00	4.35	5.92
Maerquad	0.00	0	0.00	4.35	1.41
Maerserr	12.50	12.5	5.00	0	1.41
Maersp2	0.00	0	0.00	0	0.28

Appendix D contd.

Species	Sand	Coral rubble	Debris	Seagrasses	Algae
Maertulu	0.00	0	0.00	0	0.28
Melizeyl	0.00	0	0.00	8.7	4.51
Mallinsi	0.00	0	0.00	0	15.21
Mallsp1	0.00	12.5	0.00	0	20.56
Mallsubc	12.50	12.5	0.00	30.4	33.80
Nuuasp1	12.50	0	0.00	4.35	1.41
Ampicavi	12.50	37.5	0.00	8.7	17.75
Ampikula	0.00	0	0.00	4.35	3.38
Ampiramo	0.00	12.5	0.00	0	2.82
Ampisp1	0.00	0	0.00	17.4	5.35
Ampisp2	0.00	0	0.00	4.35	16.62
Cymafilo	0.00	0	0.00	21.7	16.06
Cymamicr	0.00	0	0.00	4.35	10.42
Paramaur	0.00	0	0.00	0	0.28
Paravora	0.00	0	0.00	0	4.51
Perafals	0.00	0	0.00	0	4.23
Gammatla	0.00	0	0.00	8.7	3.10
Ledosp1	37.50	0	0.00	0	0.28
Ericbras	0.00	0	0.00	0	2.25
Jasssp1	0.00	0	0.00	0	11.55
Jasssp2	0.00	0	0.00	0	1.13
bemlwaip	0.00	0	0.00	8.7	2.82
Globindi	0.00	0	0.00	4.35	2.54
Granbonn	0.00	0	0.00	13	6.76
Grangros	25.00	0	0.00	30.4	14.93
lembsp1	0.00	0	0.00	0	0.28
Coroasch	0.00	0	0.00	26.1	9.30

Appendix E Percentage frequency of occurrence (A_{alg}) of 35 amphipod species on algal categories

Species	As	Ag	Af	B	Cs	Co	Cc	Ds
Tethpaci	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.56
Hyalayel	40.00	66.67	83.33	33.33	0.00	28.57	27.59	88.89
Hyalchev	20.00	44.44	0.00	0.00	0.00	42.86	6.90	16.67
Hyalgran	40.00	0.00	0.00	16.67	0.00	0.00	17.24	0.00
Parhindi	0.00	0.00	0.00	0.00	0.00	0.00	3.45	0.00
Elasecua	0.00	33.33	33.33	33.33	0.00	28.57	3.45	11.11
Elashooh	0.00	11.11	0.00	0.00	0.00	0.00	10.34	0.00
Elaspect	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.56
Elasspin	0.00	11.11	0.00	16.67	0.00	0.00	0.00	11.11
Elassp1	0.00	22.22	0.00	0.00	0.00	0.00	0.00	0.00
Maerocto	0.00	0.00	0.00	16.67	0.00	0.00	0.00	0.00
Maerpaci	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Melizeyl	0.00	11.11	0.00	0.00	0.00	0.00	0.00	0.00
Mallinsi	20.00	55.56	0.00	0.00	0.00	28.57	10.34	44.44
Mallsp1	0.00	66.67	66.67	0.00	0.00	71.43	6.90	61.11
Mallsubc	80.00	33.33	16.67	66.67	0.00	0.00	82.76	16.67
Ampicavi	0.00	22.22	0.00	0.00	20.00	0.00	3.45	33.33
Ampikula	0.00	0.00	0.00	0.00	20.00	0.00	0.00	0.00
Ampiramo	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ampisp1	20.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ampisp2	80.00	0.00	16.67	0.00	0.00	28.57	6.90	50.00
Cymafilo	0.00	0.00	0.00	0.00	80.00	0.00	13.79	5.56
Cymamicr	20.00	11.11	0.00	0.00	0.00	0.00	0.00	27.78
Paramaur	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paravora	0.00	22.22	0.00	0.00	0.00	0.00	0.00	0.00
Perafals	0.00	11.11	16.67	0.00	0.00	28.57	0.00	0.00
Gammatla	0.00	0.00	0.00	0.00	0.00	14.29	0.00	11.11
Ericbras	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jasssp1	0.00	55.56	0.00	16.67	0.00	28.57	0.00	16.67
Jasssp2	0.00	11.11	0.00	0.00	0.00	0.00	0.00	0.00
bemlwaip	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Globindi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Granbonn	0.00	0.00	0.00	16.67	40.00	0.00	17.24	0.00
Grangros	0.00	0.00	0.00	33.33	40.00	14.29	37.93	0.00
Coroasch	0.00	0.00	0.00	33.33	40.00	14.29	10.34	0.00

Appendix E contd.

Species	E	Gp	Gs	L	P	Sr	T	U	W
Tethpaci	0.00	0.00	0.00	0.00	20.83	8.33	9.09	11.36	0.00
Hyalayel	4.35	52.94	23.08	25.00	8.33	8.33	0.00	29.55	40.00
Hyalchev	13.04	11.76	11.54	16.67	12.50	91.67	0.00	2.27	0.00
Hyalgran	34.78	23.53	15.38	25.00	8.33	0.00	0.00	38.64	20.00
Parhindi	8.70	11.76	3.85	0.00	0.00	0.00	0.00	0.00	20.00
Elasecua	0.00	0.00	3.85	8.33	4.17	41.67	0.00	11.36	0.00
Elashooh	8.70	0.00	7.69	33.33	0.00	0.00	0.00	0.00	20.00
Elaspect	0.00	0.00	0.00	33.33	4.17	0.00	0.00	2.27	20.00
Elasspin	0.00	11.76	7.69	0.00	0.00	8.33	0.00	0.00	20.00
Elassp1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Maerocto	4.35	0.00	0.00	0.00	0.00	0.00	9.09	0.00	0.00
Maerpaci	0.00	0.00	11.54	8.33	4.17	0.00	45.45	0.00	20.00
Melizeyl	4.35	0.00	3.85	0.00	12.50	0.00	0.00	15.91	0.00
Mallinsi	0.00	5.88	46.15	8.33	4.17	8.33	0.00	6.82	0.00
Mallsp1	4.35	11.76	7.69	33.33	16.67	33.33	0.00	11.36	0.00
Mallsubc	4.35	52.94	30.77	16.67	16.67	33.33	0.00	59.09	20.00
Ampicavi	26.09	0.00	11.54	8.33	41.67	0.00	72.73	2.27	20.00
Ampikula	0.00	0.00	0.00	16.67	0.00	33.33	0.00	0.00	0.00
Ampiramo	0.00	11.76	3.85	0.00	4.17	0.00	45.45	0.00	0.00
Ampisp1	8.70	17.65	0.00	0.00	4.17	0.00	0.00	18.18	0.00
Ampisp2	17.39	17.65	0.00	8.33	4.17	16.67	0.00	22.73	40.00
Cymafilo	26.09	5.88	7.69	25.00	50.00	0.00	27.27	6.82	0.00
Cymamicr	0.00	0.00	7.69	25.00	41.67	0.00	9.09	6.82	0.00
Paramaur	0.00	0.00	0.00	0.00	4.17	0.00	0.00	0.00	0.00
Paravora	0.00	0.00	3.85	0.00	16.67	0.00	36.36	0.00	0.00
Perafals	0.00	0.00	0.00	0.00	0.00	50.00	18.18	2.27	0.00
Gammatla	0.00	0.00	7.69	0.00	8.33	8.33	0.00	0.00	0.00
Ericbras	0.00	0.00	7.69	0.00	4.17	0.00	9.09	2.27	0.00
Jasssp1	0.00	0.00	38.46	25.00	4.17	33.33	9.09	4.55	0.00
Jasssp2	0.00	5.88	0.00	0.00	0.00	16.67	0.00	0.00	0.00
bemlwaip	0.00	0.00	3.85	16.67	4.17	0.00	0.00	0.00	0.00
Globindi	4.35	0.00	0.00	0.00	0.00	0.00	0.00	2.27	0.00
Granbonn	26.09	5.88	3.85	8.33	4.17	0.00	0.00	6.82	0.00
Grangros	17.39	52.94	3.85	16.67	4.17	0.00	0.00	20.45	0.00
Coroasch	34.78	5.88	0.00	50.00	0.00	0.00	0.00	11.36	0.00