Biogeography of Coral Reef Shore Gastropods in the Philippines

Thesis submitted by

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in September 2003

for the degree of Doctor of Philosophy
in Marine Biology
within the School of Marine Biology and Aquaculture
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ABSTRACT

The aim of this thesis is to describe the distribution of coral reef and shore gastropods in the Philippines, using the species rich taxa, *Nerita, Clypeomorus,* Muricidae, Littorinidae, *Conus* and *Oliva.* These taxa represent the major gastropod groups in the intertidal and shallow water ecosystems of the Philippines. This distribution is described with reference to the McManus (1985) basin isolation hypothesis of species diversity in Southeast Asia. I examine species-area relationships, range sizes and shapes, major ecological factors that may affect these relationships and ranges, and a phylogeny of one taxon.

Range shape and orientation is largely determined by geography. Large ranges are typical of mid-intertidal herbivorous species. Triangualar shaped or narrow ranges are typical of carnivorous taxa. Narrow, overlapping distributions are more common in the central Philippines.

The frequency of range sizesin the Philippines has the right skew typical of tropical high diversity systems. This shows that there are many species with small range sizes, and suggests a tendency for these ranges to overlap.

The species area curves are consistent with predictions of basin isolation on species richness. The central Philippine basins (Visayas and, Sibuyan) have a z estimate (a parameter of the Species Area relationship or SPAR) close to unity (0.59-1.30). This contributes to biogeographical provinciality (a measure of faunal uniqueness) in these basins. The basin that is most provincial is the Sibuyan Sea basin. However this provinciality may also be due to a small-area effect or the decoupling of species richness with area as a result of habitat heterogeneity within the basin. Endemicity of taxa is observed mainly in the central, as opposed to the peripheral, oceanic basins.

A regression approach was applied to test the effects of larval duration and habitat availability on range size and species richness of *Conus*. The results suggest that habitat is a more significant factor in determining species ranges and species richness than larval duration. This supports the suggestion from basin isolation for an important effect

of habitat heterogeneity on range size and species richness. . Extinction rate estimates are negative for the Philippines and other areas in the Indo-West pacific (IWP). This suggests that species in the Philippine basins, and the IWP in general, have been accumulating in these areas over the past 18,000 years.

In *Conus*, the mode of speciation was inferred from a published molecular phylogeny, coupled with data on modern ranges. This study also tried to infer *Conus* speciation within the IWP. The relationship of modern ranges and phylogenetic information is not informative, and does not provide inferences on the mode or location of speciation. The ranges and phylogenetic patterns of *Conus* suggest that changes in range extents have been large during the evolution of the genus. This may be due to the long larval duration, that allows for wide dispersal, being largely conserved during *Conus* evolution.

In the sand-dwelling coral reef genus *Oliva,* the ranges and species area curves were similar to those of *Conus*.. The central Philippines basin of the Sibuyan Sea has the highest degree of provinciality. The area of the OGU (geographical regions) affects species richness of *Oliva* significantly This observation is consistent with results of a PCA ordination of the frequency of occurrence of *Oliva*. The presence of sandy habitats affect *Oliva* species richness significantly. The morphological diversity of two widely distributed species of *Oliva* was studied. Monotopic species (species that are found only in a single substrate type) tend to show morphologies that are found only in certain oceanic basins.

Modern ranges suggest basin isolation as an historical process that has maintained and possibly caused the high taxonomic diversity of intertidal and shallow water gastropods in the IWP. There is evidence that high species diversity in IWP is likely related to the existence of numerous habitats. The geological histories of the Philippine oceanic basins may provide important information in future biogeographic studies of patterns of species richness. The evidence is considered with respect to current molecular phylogenetic studies of gastropods. The study highlights the paradox of low endemism in a highly diverse region. Suggestions are made for future research that could provide insight into the nature of endemism and species persistence of marine organisms in the IWP.

ACKNOWLEDGEMENTS

Back in High School and until now, my favourite scientists have always been Galileo Galilei, Albert Einstein and John Steinbeck. You may wonder why John Steinbeck is in the list. While Galileo is rightly known to be the first modern scientist and Einstein flunked his PhD exams twice, Steinbeck is better known as a Nobel Prize winning writer. Steinbeck has only one science publication under his name and this was written with another marine biologist, Ed Ricketts. Steinbeck clearly understood that the impulse to do science and to find meaning in all things is the same.

Nevertheless, Galileo, Einstein, Steinbeck, Ricketts and all the other good scientists did was to take that "bold guess" to conjecture and daringly propose explanations to the inner realities of what the world was all about. While we are unlikely to be that bold in the sense of Karl Popper, I hope that we can try to be like Einstein at times. To this end, I would like to thank the following

My field volunteers whom kept good humour (and prayed!) when the odds were against us on land, at sea and in the air. I also thank the fisherfolk that extended their hospitality to us.

The course of this project was riddled with difficulties. I thank all those who insisted that I conclude this project for it would be a highly significant contribution to understanding the biodiversity of the Philippines. These people are the late Jaime Cabrera of the Philippine National Museum and Professor Fernando Dayrit. I also thank the Philippine National Museum, Australian Museum, Australian Geographic Society and the Delaware Museum of Natural History for travel grants and assistance to do the biogeographical investigation.

I thank the agencies and organisations that provided assistance and information, The Philippine Navy, Philippine Marines, Philippine National Police and the National Mapping and Resource Information Authority and Philippine Atmospheric, Geophysical, Astronomical Authority.

I thank

Professor Howard Choat, Dr John Collins and Associate Professor Garry Russ at JCU
Samantha Itani and Tanya Acheson of the JCU PSA and Student Union respectively

Dr Meryl Williams of the World Fish Centre and Dr John McManus of the University of Miami, Dr Winston Ponder, Dr Peter Middlefart of AMS, Drs Anne Hogget and Lyle Vail of the Lizard Island Research Station and Dr Jean Woods of the DMNH

Professor Edgardo Gomez, Drs Suzanne Licuanan and Perry Aliño of the University of the Philippines, Dr Rhea Samonte of Case Western Reserve University and Dr Al Licuanan of De La Salle University, Professor Toby Dayrit of the Ateneo de Manila University

Reverend Fathers Peter Quilty, Bienvenido Nebres PhD SJ and Daniel McNamara PhD SJ and the Most Reverend Reynaldo de la Paz DSc DD, Orthodox Bishop of Manila, Sister Lucy Kert FDSS, the soon to be Reverend Mel Santos MDiv and the

Jesuit scholastics that always remembered me in their prayers. These are good people who remind us that beyond this there is something more

My mates at the Rotary International House and friends at the Ateneo Law School especially Helen Manzano D of Laws.

Juned Sonido, Punay Caccam in Canberra, Gino and Baby Simpliciano in Melbourne and Bing and Ramon Santos in Sydney

My undergraduate students at the Ateneo de Manila University and the University of the Philippines. I hope that you become better scientists than we are. I hope that in the course of your future studies, you will see much more.

My family.

And the Master for through Him all things were made, all that is seen and unseen.

In the end all can be summarised by the Psalmist

Omnia in opera sapientia fecisti!

Quam multa sunt opera tua Domine

omnia in sapientia fecisti

impleta est terra possessione tua

Hoc mare magnum et latum manibus ibi reptilia innumerabilia animalia parva cum grandibus

Ibi naves pertranseunt Leviathan istum plasmasti ut inluderet ei

How diverse O Lord are your works!

In wisdom you have made them all- the earth full with your creatures

Behold the sea, wide and vast

Teeming with countless creatures

Living things both great and small, a strange world reserved for the ships

For Leviathan, the dragon you made to play with

Psalm 103: 24-26 Latin Vulgate and Revised Standard Version Translation

AD MAJOREM DEI GLORIAM

This work is dedicated to all battlers especially

Brigadier General Benjamin R Vallejo (Armed Forces of the Philippines) (1927-1991)

Jaime J Cabrera (1938-2002)
Curator of Molluscs, National Museum of the Philippines

Professor Fernando Dayrit,
Emeritus Curator of Molluscs, National Museum of the Philippines

Professor Dr Edgardo D Gomez, University of the Philippines

Professor Dr Lilia Rabago, University of the Philippines Integrated School

Reverend Father Dr Bienvenido Nebres SJ, Ateneo de Manila University

My friends and students

And to those who labour for the good of the Philippines and not expect any reward

STATEMENT OF ACCESS

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BENJAMIN VALLEJO JR

31 January 2000
and
19 August 2003

STATEMENT ON SOURCES

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from published and unpublished work of others has been acknowledged in the text and a list of references is given.

BENJAMIN VALLEJO JR

31 January 2000
and
19 August 2003

STATEMENT ON THE CONTRIBUTION OF OTHERS

The following institutions or persons contributed primary and secondary material and or funding in this thesis. The nature of these contributions are indicated

1) **National Museum of the Philippines**- Access to collections and field labels and notes.
2) **Mr Carlos Leobrera, Carfel Seashell Museum, Batangas Philippines** – Museum catalogue
3) **Australian Museum Sydney**- Access to collections and published journals
4) **Delaware Museum of Natural History, United States of America** – Funding support for travel, access to primary and secondary collection material and database.
5) **Lizard Island Research Station, Australia** – Access to primary material
6) **Pontifical University of Santo Tomas, Manila** – Access to Father De Elera's zoological catalogue and holdings of the university museum.
7) **Ateneo de Manila University** – Grants to complete PhD thesis
8) **Australian Geographic Society** – Travel grant
9) **University of the Philippines Marine Science Institute** – Access to Marine Biodiversity Information Center and Museum.
10) **Professor Fernando Dayrit, Quezon City, Philippines –** Access to private malacology collection

Benjamin Vallejo Jr 2 September 2003

APPENDICES

CHAPTER 1.

General Introduction

"Look at the animals. This is what we seem to know about them but the knowledge is not final, and any clear eye and sharp intelligence may see something we have never seen."
-John Steinbeck, Foreword to *Between Pacific Tides* by Edward F. Ricketts and Jack Calvin, 1948

1.1 FACTORS AFFECTING DISTRIBUTION OF BIOTA

1.1.1 Historical Background

In 1859 Charles Darwin posed a question that remains central to biogeography and evolutionary ecology: "Who can explain why one species ranges widely and is very numerous and why another allied species has a narrow range and is rare?" Wallace (1880) suggested a possible answer. He established modern biogeography by suggesting that ranges of species often reflect effects of ancient, long-lasting barriers to their dispersal. Wallace linked evolution, ecology, geological history and geography (Wallace 1880). He maintained that an understanding of evolutionary history is possible only through an understanding of the geological, geographical and ecological history of the region where the species occurs.

Modern biogeography has sought to account for species distributions by borrowing geology's Principle of Uniformitarianism. This states that processes currently operating on earth today are the same processes that operated in geological time (Whittow 1984). Applying this to biology, biogeography assumes that present distributions are a product of past temporal changes (Veron, 1995). This interaction of space and time provides endless possible outcomes. To obtain an understanding of biogeographical patterns, one must measure factors that determine distribution at local and geographic scales. Kohn (1997) classifies these factors as extrinsic (changes in environmental conditions at local and regional spatial scales) and intrinsic (ecological and evolutionary responses of organisms to these factors).

To examine the relative importance of these extrinsic and intrinsic factors, it is necessary to look at several taxa occupying similar habitats. In nature, the effects of these factors are not mutually exclusive (Kohn, 1997). The Indo-Pacific fauna provides an excellent group to examine such questions.

The Indo-Pacific is characterised by island arc complexes on its western rim. On the oceanic Pacific plate, numerous oceanic islands have formed. Others have subsided, and form bases of atolls. These islands have gradients of species composition of marine taxa. The IWP island arc shows the highest number of species. As distance increases from this region, species richness declines. In comparable environments in oceanic islands, some species that are likely to be found in the IWP island arc are missing or replaced by another. These gradients are well known and are caused by factors that select against dispersal by one species and favours dispersal by another (Vermeij 1987). These selective factors are likely related to energetics (Vermeij 1990), geology, geomorphology (Vermeij 1978) and physical oceanography. Those species that were able to cross these dispersal barriers and colonise oceanic islands from the IWP island arc are likely to have undergone subsequent adaptive radiation (Hourigan and Reese 1987; Kay 1990). This is reflected in the high levels of endemicity on these oceanic islands.

Vermeij's studies on molluscs focused on large (ocean-wide) scales. At these scales, barriers to species dispersal are detectable and likely a function of geographical distance. On the scale of the Philippine archipelago, the geographical distance between islands is smaller, and is unlikely to have been an effective barrier to dispersal. An archipelago is a mosaic of island habitats. Marine biota associated with these islands may have different levels of genetic connectivity with each other. In the linear Hawaiian archipelago, there is no distinct island-specific marine invertebrate assemblage (Kay and Palumbi 1987). This implies that dispersal between the islands has been sufficient to maintain genetic connectivity.

Dispersal barriers imply that mollusc faunas on islands and continental landmasses of the Pacific Ocean have different degrees of isolation, and hence different degrees of genetic connectivity. Rosen (1988) reviews current theories of historical marine biogeography. He attempts to explain speciation, endemism and distribution of reef corals. Historical biogeographic hypotheses are framed in terms of (1) distributional change and (2) origin in particular geological strata. These hypotheses are often refered to as:

1. "Centres of origin",
2. Centres of overlap or accumulation

> The centres of origin hypothesis may still be further divided into A. marginal basin isolation and allopatry, B. vicariant allopatry and C. glacial eustatic inhibition of speciation.

None of these hypotheses are mutually exclusive. However, Rosen (1988) suggests that island vicariance, Cainozoic isolation of Pacific plate areas and late Cainozoic convergence of Indo-Pacific biota, have more support than the "centres of origin" hypotheses. One of these hypotheses, with a specific reference to Southeast Asia, and the Philippines, is the basin isolation hypothesis of McManus' (1985).

This thesis examines the patterns of distribution of selected tropical intertidal gastropods. Such organisms are model candidates for studies of biogeography of the IWP. They are relatively easy to collect. Furthermore, their taxonomy and, in some cases, fossil and phylogenetic histories, are reasonably well known.

1.1.2 Local scale distribution of shore gastropods

The local scale distribution and ecology of shore gastropods is well known. The most obvious distribution is the vertical zonation observed on shores. Stephenson and Stephenson (1972) defined three major zones, the supralittoral (high intertidal), midlittoral (mid intertidal), and the infralittoral (low intertidal). This zonation scheme holds for exposed to moderately exposed rocky shores throughout the world. It has been called the "universal zonation" (Stephenson and Stephenson 1949). While it was formerly believed that physical factors (dessication, temperatures) were the major determinants of this zonation, biological factors such as competition and predation can also determine zonation (Connell 1961; Connell 1961; Connell 1972). Both biological and physical factors interact to determine zonation patterns (Rafaelli and Hawkins 1996).

The dominant herbivorous component of these tropical, intertidal gastropod assemblages is *Nerita*. This has its highest diversity in the mid-intertidal. Other components include the patellid and lottiid limpets, the monodont trochids and the siphonariid limpets. The carnivorous component of these assemblages consists of rapanine muricids. Lower on the shore, where habitat heterogeneity is highest, *Conus*, buccinids and other muricid species are dominant. In sandy habitats in the intertidal, *Oliva* are common.

Rocky shores intergrade with coral reefs in the Indo-west Pacific. Tropical rocky shores thus include upper reef and the fringing reef flats, which provide a mosaic of microhabitats including sandy areas. Coral reefs in this study are considered as a special type of rocky shore, peculiar to the tropics (Stephenson and Stephenson 1949; Stephenson and Stephenson 1972).

This study confines itself to exposed and moderately exposed shores with similar geomorphology

1.1.3 Species-area relationships and Biogeography

The species-area relationship (SPAR), the relationship between total area surveyed and the number of species recorded, is one of the fundamental constructs of modern biogeography. The SPAR is used in this thesis to help infer the historical nature of modern distributions, and to delineate biogeographical regions. This approach was first used in terrestrial biogeography. Rosenzweig (1995) discusses the assumptions of inferring aspects of history and biogeography from SPAR. The approach stems from island biogeography (Macarthur and Wilson, 1967).

1.2 BASIN ISOLATION, EAST-WEST ISOLATION AND ARCUATE RANGES

McManus (1985) proposed basin isolation as one hypothesis to explain the high species richness of marine biota in the IWP. Basin isolation was the successive isolation and reconnection of marine faunas, due to changes in sea level. McManus (1985) hypothesized that this facilitated speciation and endemism in Southeast Asia. McManus (1985) showed that East-West isolation (a degree of isolation between Indian and Pacific oceans) was suggested by a common distributional pattern of molluscs in the western Pacific that stretches from southern Japan to the Solomons and the Great Barrier Reef, via Southeast Asia (Figure 1.1). McManus (1985) called such a distribution "arcuate", to emphasize the arc-like shape (Fig. 1.1). This distribution also corresponds with the regions of highest number of marine species. Modern currents and distance are unlikely to cause enough isolation to promote speciation. Thus suggests a mechanism operating in geological time. McManus (1985) suggested basin isolation. Such a model may explain the low rates of endemism in Philippine molluscs, in a region of high species richness (Springsteen and Leobrera 1986).

McManus (1985) defined an arcuate range over a series of islands that essentially follows the subduction zones of continental and oceanic plates in the western Pacific. These islands include the Philippines, Japan, the Ryukyu Islands and the continental island of Taiwan. This area makes up the northern portion of the arc (Fig.1.1). At this scale, he also describes a phenomenon called East-West isolation. East-West isolation is the observable discontinuity in species distribution between the Indian and Pacific Oceans. This can be observed as a sharp regional difference in community similarity and life-form distribution (Uychiaoco et al. 1992; Aliño 1994; Aliño et al. 2002), a disjunction in gene flow and clear population genetic structuring (Endriga 2001), morphological differences in shell shape in widely distributed species (Vallejo 2001) and pairs of species that can be divided into Pacific and Indian Ocean populations (McManus 1985; Bellwood and Wainwright 2002). Many IWP species display this East-West isolation in the northern part of their arcuate ranges. In this thesis, I examine arcuate ranges and east-west isolation within the Philippine archipelago, and explore the possible implications to McManus's original hypothesis.

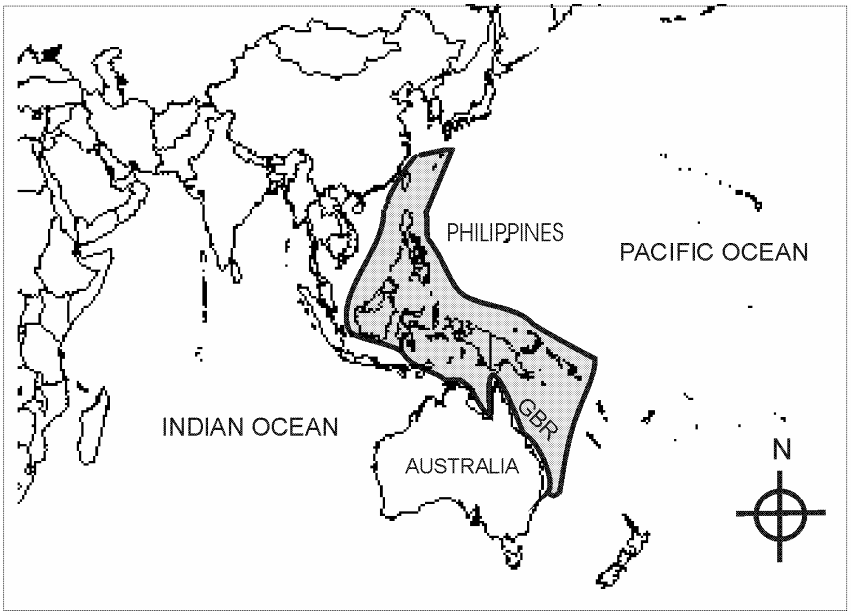


Figure 1.1 The arcuate centre of marine taxonomic diversity in the Indo West Pacific.

Many species of gastropods have arcuate distributions like that shown in Fig. 1.1. Many of these ranges display a good degree of East-West isolation in the Philippine portion of this arcuate distribution. Many other groups of marine taxa conform to this pattern, including corals, reef fish and seagrasses (McManus 1985, Fortes 1986 Uychiaoco *et al* 1992). This pattern of distribution is so common, that it is possible to divide the Philippines into east and west biogeographical regions (DENR and UNEP 1997).

The causes of these biogeographical patterns may be historical, ecological or both. Many of the species in the Philippines that have some degree of east-west separation have wide IWP distributions. A potential criticism of my approach may be that a study of ranges only in the Philippines examines a small part of the arcuate range. However, McManus (1985) framed his hypothesis with Southeast Asia and the Philippines as a primary area of interest. His main question was why this region is species-rich. McManus envisioned that most speciation occurred through vicariance. However he also stressed that ecological factors may account for the high species diversity. The question of effects of ecological factors on species diversity can be examined by looking at ranges within the Philippines. At the time McManus (1985) did not have at his disposal detailed descriptions of distribution of many marine organisms within the Philippines. He did use larger scale patterns obtained from the western Pacific, and also used information on terrestrial biota.

By looking at higher resolution patterns of distribution of marine fauna within the Philippines, collected since McManus first proposed basin isolation in 1985, new hypotheses may be generated. Such hypotheses may provide new understanding of Indo-West Pacific and Philippine biogeography.

1.3 THE SCOPE AND AIM OF THIS THESIS

This is a biogeographical study. The thesis examines distributions of biota in light of McManus' (1985) basin isolation hypothesis. The methods are limited by the nature of the data, and cannot directly test the historical aspects of the basin isolation hypothesis. The methods are inferential tests only of basin isolation. The thesis aims to determine if new data on distributions of marine biota support McManus' (1985) predictions or not. While the data on species distributions are modern, inferences about their history can be made with biogeographical methods such as species-area relationships (Rosenzweig, 1995) and molecular phylogenies (Berlocher 1998; Barraclough et al. 1999).

The gastropods *Nerita, Conus, Oliva, Clypeomorus*, Muricidae, *Oliva* and Littorinidae are common primary material in the Philippine National Museum (PNM), Carfel Seashell Museum, the University of the Philippines, University of Santo Tomas and the Delaware Museum of Natural Museum (DMNH). Other gastropod taxa, such as Buccinidae, Mitridae, Trochidae, Turbinidae, Cerithiidae and Columbellidae are also found in similar environments in the field. However, they are not well represented in collections and an accurate description of their distributions is not possible.

Chapter 2 describes the geological and physical oceanographic environment of the Philippines. This geographic entity is unique, consisting of more than 7000 islands of varying geological ages, but with similar histories. This is due to complex tectonic history. The islands are often fringed with coral reefs. The islands give name to the oceanic basins or archipelagic seas in the country. Chapter 3 details the general methods used in the biogeographical analyses.

Chapter 4 describes the biogeography of rocky shore gastropods in the Philippines, with a focus on *Nerita*. Chapter 5 is a detailed examination of the basin isolation hypothesis, focussing on the most species-rich genus of tropical intertidal gastropods, *Conus*. This genus has been the focus of extensive ecological research since the 1950s (Kohn 1990). More is known about *Conus* palaeontology than any other tropical mollusc (Röckel *et al* 1995). Furthermore, the evolutionary ecology and radiation of *Conus* is linked with the Miocene and Pliocene development of coral reefs in the Pacific (Kohn 1997). The genus can be readily accessed from collections in museums and private collections. In addition, a molecular phylogeny is now available for the genus (Duda and Palumbi 1999).

The archipelagic nature of the Philippines provides an excellent test of the role of oceanic basins in determining species-richness and morphological diversity. What exactly are the roles of these basins in marine biogeography? These hypotheses are examined with reference to the McManus (1985) basin isolation model, and are tested in Chapter 6, with a description of the biogeography of the tropical intertidal gastopod *Oliva*.

In Chapter 7, the possible mode of speciation in *Conus* is inferred, drawing on models of both sympatric and allopatric speciation (Berlocher 1998; Barraclough, Vogler et al. 1999) and upon a molecular phylogeny of *Conus* (Duda and Palumbi 1999; Duda et al. 2001)

Chapter 8 is a general discussion and synthesis of the study, with suggestions for future research. A biogeographical delineation of the Philippines marine fauna is proposed. The final conclusions in this thesis are presented as an hypothesis that can be tested using other species-rich marine taxa.

CHAPTER 2.

Geology, Physical Oceanography and Climate of the Indo West Pacific (IWP)

This chapter describes geography of the Indo West Pacific (IWP). It also describes the recent geomorphology, physical oceanography and climate of the region. The role of monsoons and the El Niño Southern Oscillation are discussed.

2.1 GEOLOGICAL EVOLUTION OF SOUTHEAST ASIA, WITH EMPHASIS ON THE PHILIPPINES

2.1.1 The Philippine Archipelago (Figure 2.1)

With the exception of Palawan, the major islands of the Philippines are volcanic in origin, composed of Cretaceous to Recent oceanic sediments. The islands have geologic sequences composed of ophiolites, basaltic and andesitic lavas, granite intrusions and intercalated coral reef limestones (McCabe and Cole 1989). There is a lack of continental sedimentary influence dating back from the Cretaceous (McCabe and Cole 1989). The only exception is the islands of northern Palawan and the Calamian Group. Northern Palawan and the Calamian Group are displaced continental terranes, derived from the Asian landmass as a result of complex plate spreading that gave rise to the South China Sea (Hutchinson 1989).

The Philippines is thus a complex amalgamation of Cretaceous and younger islands that has been moved to its present position from the southeast by the clockwise rotation of the Philippine Plate (McCabe and Cole 1989).

This rotation of the Philippine plate is of immense biogeographical significance. About 30 MY BP Luzon was separated from the eastern and southern Philippines (present day Bicol peninsula, the Visayan Islands and Mindanao). The eastern and southern Philippines was located a few degrees below the equator, near proto-New Guinea and Australia. Continued clockwise rotation of these islands, and the counter clockwise rotation of Luzon, Palawan, and Borneo, caused the two island groups to meet and thus form the present Philippine archipelago.

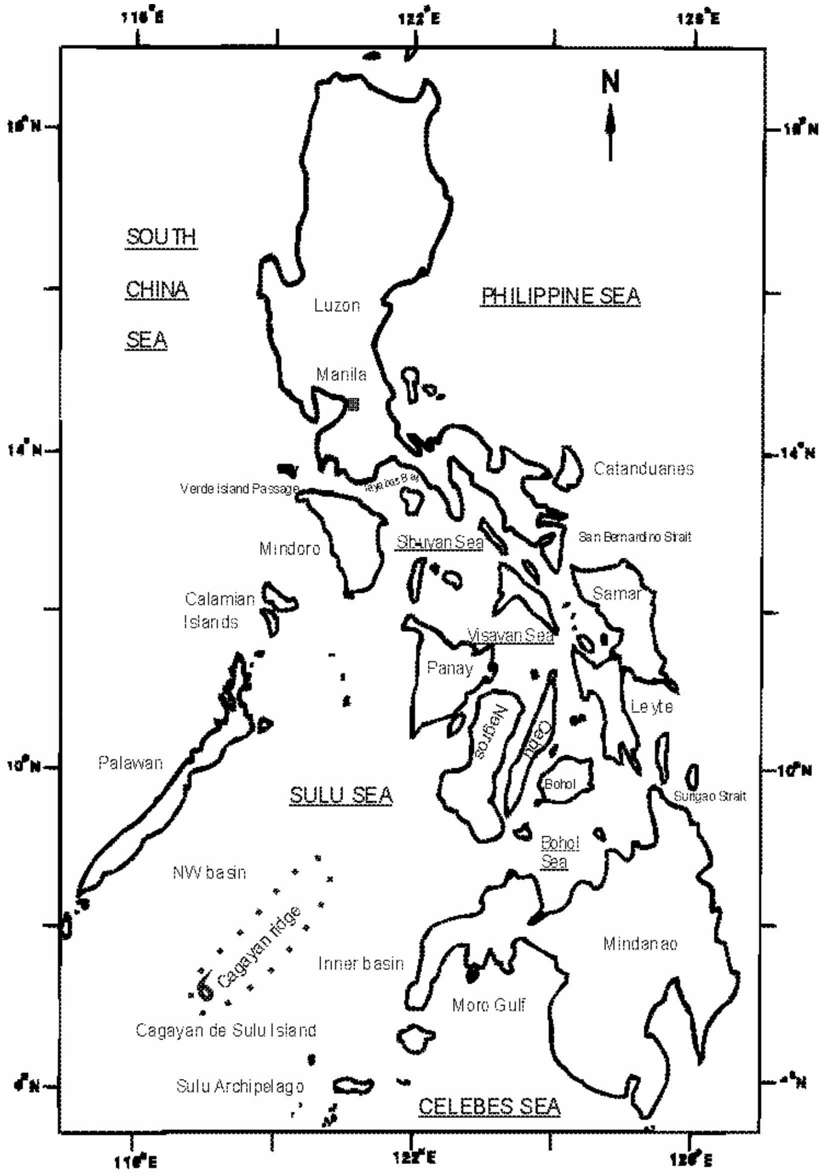


Figure 2.1. The Philippine archipelago. Seven oceanic basins are shown underlined. Basins in uppercase letters are major archipelagic seas whose geological history is fairly known (South China Sea, Sulu Sea, Philippine Sea and Celebes Sea). Basins in lowercase letters are seas whose geological history are poorly described (Sibuyan Sea, Visayan Sea and Bohol Sea). See text for general history of the Sulu Sea.

The Philippine islands have different geological ages. The oldest island is Luzon, where there is evidence of Cretaceous to Paleocene volcanic activity in the north (Karig 1983). Other islands of this age include Marinduque and Cebu. The youngest islands are in the Sulu Archipelago, which is of Tertiary origin (McCabe and Cole 1989). The different ages of the islands have biogeographical significance. It allows the estimation of colonisation and extinction rates of biota (Heaney 1986)

The narrow continental shelves of these islands have provided a suitable environment for coral reef development (Wilson and Rosen 1998). Coral reefs have developed, altering the original shelf base. Thus the shelves now consist of sequences of intercalated reefal limestone. The shorelines of some islands are fringed by non-reef coral communities that have the ecological and functional properties of structural coral reefs (McManus 1988). While these communities may be ephemeral features, they modify the coastlines by reducing exposure to winds and waves, and by contributing carbonate sediments that give volcanic rocky shores greater substrate heterogeneity.

2.1.2 Marginal Oceanic Basins

Oceanic basins on the edges of continental plates (Marginal Oceanic Basins) are one of the most characteristic features of Southeast Asia (Hutchinson 1989). The marginal oceanic basins are associated with continental rifting. The marginal basins of the Indo-West Pacific are separated from the Pacific and Indian Oceans by island arcs (Karig 1971; Karig 1974) and these are described as marginal seas. Marginal basins are often deep and have a seafloor made of oceanic crust. In active basins, there may be active volcanism associated with seafloor spreading (Karig 1971; 1974). In the Philippines four main marginal seas occur. These are the South China Sea, Sulu Sea, Philippine Sea and Celebes Sea basins (Figure 2.1). Several types of marginal basins occur in the Philippines, based on their sedimentary characteristics (Hutchinson, 1989). The major basins are of the wrench and rift type, where new oceanic crust is formed (e.g. in the Sulu Sea).

The histories of these marginal oceanic basins are not well known. It is possible to reconstruct the general history of these marginal basins from paleomagnetic anomaly data. The Sulu Sea basin is the best studied A submerged volcanic ridge called the Cagayan ridge, from which Cagayan de Sulu Island emerges (Figure 2.1), divides the Sulu Sea into a NW and an inner basin (Figure. 2.1) (Hutchinson 1989). The oceanic crust of the inner basin dates from the Eocene (Weissel 1980). The whole Sulu Sea was subsequently isolated by the formation of the Sulu Archipelago in the Tertiary. During the Pleistocene glaciations, it was virtually an enclosed sea. The other basin is the Celebes Sea basin. This is an extinct basin that no longer shows rifting activity. This basin was part of the Tethys Sea (Weissel 1980).

2.1.3 The Ice Age Configuration of the Philippine Archipelago (Figure 2.2)

An important concept in basin isolation is the role of past ice ages in the geography of the Philippines. The changes caused by glacial eustasy had significant biogeographical implications both on land and sea. Glacial lowering of sea level in the Pleistocene repeatedly isolated the marginal oceanic basins in the archipelago. During the last major lowering of sea level (150-200 metre) 20,000 YBP, the archipelago was composed of five major islands. These were Greater Luzon, Greater Palawan, Negros-Panay, Greater Sulu, and Greater Mindanao (Heaney 1986). Other islands with no connection to any larger landmass included Sibuyan, Camiguin and Mindoro. The major islands broke into the modern day islands of Bohol, Samar, Leyte, Negros and Panay during the present inter-glacial. Similarities in terrestrial flora and fauna of the various Philippine islands correspond to the configuration of these larger, ice-age islands, now considered as faunal provinces.

The marginal ocean basins between the terrestrial faunal provinces have acted as dispersal barriers and filters to terrestrial fauna. The degree of isolation correlates positively with endemicity levels of terrestrial mammals in the faunal provinces. For marine fauna, the basins were almost completely isolated from the Pacific and Indian Oceans. Based on the 200-metre isobath, the marginal basins were isolated from the Pacific, with only the San Bernardino Strait linking the central Philippines with the Pacific.

Figure 2.2 The extent of islands and oceanic basins in the Philippines during the maximum Pleistocene sea level regression at 18,000 YBP (150 m) The figure is based on the 150 metre bathymetric line. Islands such as Sibuyan, Mindoro and Camiguin were never connected to any other island. Adapted from Heaney (1985)

2.2 THE PRESENT PHYSICAL OCEANOGRAPHY AND CLIMATE (Figure 2.3)

The islands of the Southeast Asian region and adjacent areas have produced a complex physical oceanography. This oceanography is further complicated by the monsoon climate (Wyrtki 1961). The complex system of islands and basins, coupled with a monsoonal climate, results in spatially and temporally variable biological production in the marine environment (Sharp 1996).

2.2.1 Physical oceanography

The islands of the Philippines and Indonesia are seperated by only a few deep channels that allow for mixing of Pacific and Indian Ocean water. Two of these channels are found in the Philippines, the San Bernardino and Surigao Straits (Figure 2.1). These allow the North equatorial current (Fig 2.3) to reach the eastern and central portions of the archipelago and possibly as far as the northern Sulu Sea. The southern branch of the North equatorial current is deflected by the Sunda shelf (Figure. 2.3) towards the Arafura shelf (Figure. 2.3), between New Guinea and NW Australia (Sharp 1996).

The marginal ocean basins in the region include the Celebes, Sulu, Banda, South China and Java Seas. Only in the deep Makassar Trough (2540 metres) near the Banda Sea can Pacific water pass through to the Indian Ocean (Sharp 1996). The Banda and Flores seas are connected to the Indian Ocean by sills with a depth of 1900 and 2100 metres respectively (Postma and Mook 1988). Thus the Indian and Pacific Oceans are relatively isolated from each other.

The surface and deepwater currents in the marginal ocean basins are not fully understood. However the monsoon is believed to be a major factor. El Niño-Southern Oscillation (ENSO) is likely to be an important influence on oceanography of the region.

2.2.2 Regional Climate

2.2.2.1 The Monsoons and Water Transport

A characteristic of the Southeast Asian region is the two rainy seasons caused by the monsoon. This is typical of the tropics, and results from the interaction between continental high and low pressure cells. (Roy 1996). These pressure systems are relatively stationary, and thus the wind regime is relatively constant, especially over the open ocean. The climate system has a biannual cycle, related to the sun's movement and the earth's inclination on its axis (Roy 1996). This weather system causes rainfall and terrestrial runoff. Such processes affect temperature and density stratification in nearshore and ocean waters (Sharp 1996). During the monsoon season, the upper surface waters inshore are considerably lower in salinity than waters offshore in the Pacific Ocean.

In the northern hemisphere, the summer or southwest monsoon occurs from June to September with a peak in July to August and the winter or northeast monsoon occurs from November to February with a peak in January. These climate phenomena are driven by the interior heating and cooling of continental Asia and Australia. In the northern summer, the formation of the Asian low pressure gradient and the Australian high-pressure gradient drives the southwest monsoon. In the northern winter, the situation is reversed, with a weak Australian low pressure gradient and an Asian high pressure gradient driving the northeast monsoon. The latter also derive partially from the northeast tradewinds. The extent of the northeast monsoon is dependent on the movement of the equatorial low pressure system that lies over northern Australia in January.

Water masses are advected by the monsoons. The northeast monsoon causes north to south transport of surface waters that deflect southeast at the equator. The southwest monsoon causes a westward transport of surface water, but the net transport of water is northward. These monsoon seasons are the major climatic features affecting the nearshore marine environment. The substantial sea level difference between the Pacific and Indian Oceans forces a net southward flow, regardless of the monsoon season

(Sharp 1996). Deepwater currents from the Pacific pass westward through the Mindanao and Surigao Straits to the Celebes Sea, and then to the deep Makassar Trough (Postma and Mook 1988).

The two monsoon seasons cause the major currents in the Philippines to reverse (Figure 2.4). This results in almost continuous mixing in the first 40-50-m in eastern Indonesia (Sharp 1996). Strong northeast monsoons may extend this mixing to 100 m depth. In areas near the shelves, some upwelling occurs during strong monsoons.

2.2.2.2 El Niño Southern Oscillation (ENSO)

ENSO events occur irregularly, at intervals of three to six years. They are also of variable duration. The pressure difference between the eastern and western Pacific affects sea level in the west Pacific. This causes changes in the rates of water flow between the Pacific and Indian Oceans. During an ENSO event, weakening northeast trade winds result in stronger advection of warm water from west to east in the Pacific. This also causes enhanced and deeper mixing of western Pacific waters. During “La Niña” events, the opposite is true. Studies of throughflows from the Pacific to the Indian Ocean during El Niño and La Niña events are lacking (Allan and Pariwono 1990). The interplay of monsoon seasons and ENSO events provide a complex oceanography in Southeast Asia that is not yet fully understood.

2.2.2.3 Tropical cyclones

Tropical cyclones are non-frontal low pressure systems of tropical origin with organised convection (thunderstorm activity) and definite surface cyclonic wind circulation (AOML 2003). They are significant weather systems in the tropics (AOML 2003). In latitudes between 9°-20° N or S, tropical cyclones form over warm ocean water greater than 26.5 ° C, and develop from existing cloud clusters (Puotinen et al. 1998). In the northwestern Pacific, the cyclone season is from May to November, while in the southwest Pacific it is from November to April.

These weather systems are significant for the Philippines. This country receives an average of 21 cyclones (typhoons) a year. Cyclones cause substantial reef damage and massive freshwater runoff (Puotinen et al. 1998).

2.3 ARE PRESENT CLIMATE AND OCEANOGRAPHIC PATTERNS SIMILAR TO THOSE OF THE PAST?

Oceanographic and climatic conditions in the past may help to explain the high species-richness and distribution of marine biota in the western Pacific. Knowledge of past and present climate and oceanography is important to an understanding of the biogeography and dynamics of extinction and colonisation rates of the Pacific islands. Little information is available on past wind and current patterns in the Southeast Asian region. The limited evidence suggests that similar patterns to that of today occurred during the past 30 million years (Houle 1998).

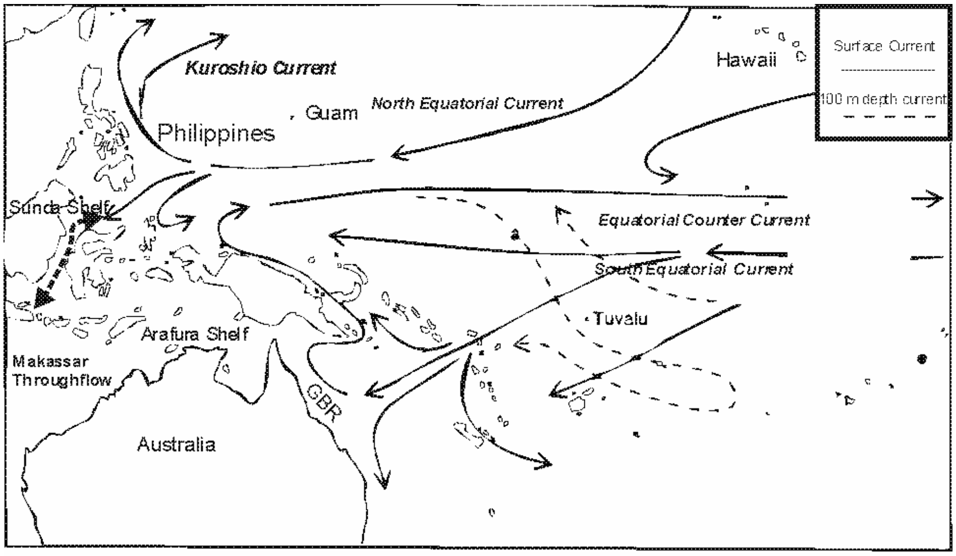


Figure 2.3 Western Pacific current systems. Modified after Benzie (1998)
Double headed arrow represents reversing currents.

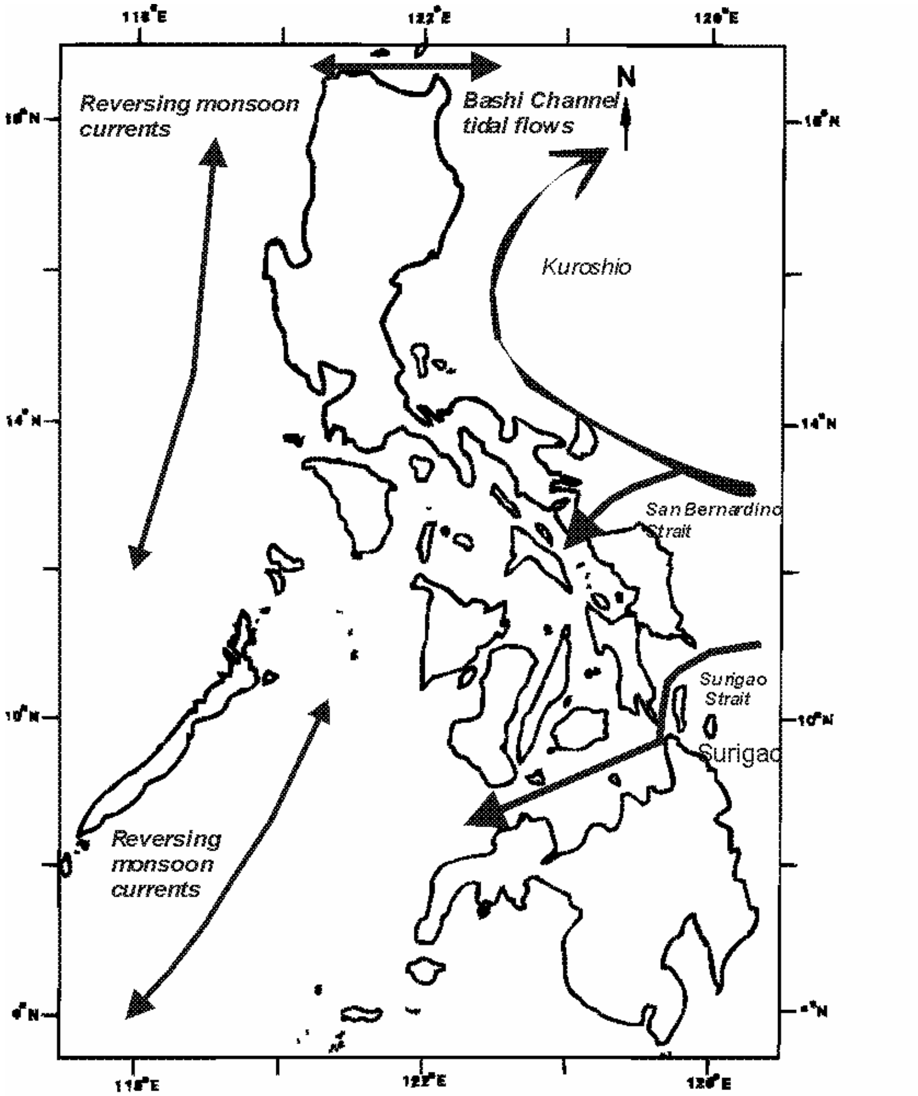


Figure 2.4. Major surface currents within the Philippines. Pacific water enters the marginal basins of the archipelago only through the San Bernardino and Surigao Straits. Off Surigao, the North Equatorial current bifurcates into the Kurushio and southern branch of the North Equatorial current..

The San Bernardino current is derived from the Kuroshio, while the Surigao current is derived from the southern branch of the North Equatorial current. Reversing monsoon currents influence most major basins and embayments The Winter monsoon (northeast) is from November to February and Summer monsoon (southwest) from June to September.

2.4 DISCUSSION

2.4.1 *The Role of Islands in the Biogeography of the IWP*

An understanding of the tectonic history of Southeast Asia is necessary to understand the biogeography of the IWP. The ranges and patterns of distribution of terrestrial plants and animals in the region suggest that biotic exchanges between Australia and Asia were relatively recent. Such exchanges likely resulted from the collision of Australian and Eurasian landmasses in the Miocene to mid-Pliocene. This brought two distinct biotas into contact. This boundary between these two distinct biotas is called Wallace's Line, a boundary essentially determined by plate tectonics (Audley-Charles 1981). While the collision may have allowed filtered dispersal of terrestrial biota between Asia and Australia, the islands in Southeast Asia may have been barriers to dispersal of marine biota between the Indian and Pacific Oceans (Marsh and Marshall 1983; Wallace 1997). The Southeast Asian islands prevent the free exchange of Pacific and Indian Ocean water. Pacific and Indian Ocean water can only exchange through the Sulu Sea and the Makassar Trough. Genetic structure of populations of the asteroid *Linckia laevigata* suggests that present day ocean currents do not facilitate long-distance dispersal through the Indonesian Archipelago (Williams and Benzie 1998; Barber et al. 2000). In mantis shrimps, the geography of genetic differentiation is coincident with Wallace's Line, thus suggesting genetic isolation of populations in Indonesia (Barber et al. 2000).

The presence of Australian biota in the Philippines (e.g. the plants *Eucalyptus, Casuarina, Agathis* and the parrots *Cacatua* and *Loriculus*) is consistent with tectonic history (Hall 1998). Australian biotic affinities in the Philippines are strongest in eastern Mindanao, but also extend to the Visayas and southeastern Luzon. Australian floral affinities are absent in Palawan. Dickerson (1927) hypothesized the diffusion of Australian biota into the Philippines from Sulawesi via New Guinea. However, the absence of recent or ancient land bridge connections from Australia, New Guinea and Sulawesi to southern Philippines does not support this theory. The present distribution of Australian biota in the Philippines is easily accounted for by Hall's tectonic model.

On the other hand, islands may act as stepping-stones for the dispersal of marine species (Williams and Benzie 1998) or act as refuges during sea level changes (Paulay 1990; Leal 1991). This repeated historical isolation of marginal ocean basins may have contributed to the high species-richness of reef corals and molluscs (McManus 1985; Pandolfi 1992). Williams (1998) suggests that the genetic similarity between Western Australian and Philippine *Linckia* populations is due to wide-scale genetic exchange during the Pleistocene, or due to a continuing genetic exchange between the two regions facilitated by island hopping through Indonesia. This suggestion is supported by patterns of distribution of echinoderms in Western Australia (Marsh and Marshall 1983).

The role of islands in biogeography is clearer in terrestrial than marine biotas. There are a number of different views on the role of islands in marine biogeography. These views propose that islands are stepping stones (Williams and Benzie 1998; Zapata and Herrón 2002) or barriers to further dispersal, and thus promote population isolation even in widely dispersive species (Endriga 2001; Taylor and Hellberg 2003). A potentially fruitful approach would be to apply identical analyses to different marine taxa. Genetic data suggests that populations on islands often experience strong variations in population size. This reduces genetic variation (e.g. heterozygosity) and increases susceptibility to extinction (Palumbi 1997; Benzie 1998). Thus, remote islands often have lower species-richness. However, life history and ecological characteristics of the marine taxon must also be considered, in addition to the location, origin and physical conditions of the islands themselves.

2.4.2 *The Role of Physical Oceanography in the Biogeography of the IWP*

The island system in Southeast Asia favours the development of strong surface circulation, as some straits and passages are aligned with the prevailing northeast and southwest monsoons (Wyrtki 1961). Furthermore, since the wind systems are relatively constant, surface circulation is strongly coupled with the monsoons . Monsoon systems are also rain-bearing systems. High rainfall and river runoff causes surface salinity to be less than 34 ppm in wide stretches of inter-island water. The configuration of islands in the region prevents dispersal of low salinity water. This results in extremely variable physical conditions of surface waters. In areas where tidal amplitudes and currents are low, these low salinity conditions may persist until the next monsoon.

2.4.3 *The role of The Monsoons in the Biogeography of the IWP*

The monsoon is the major climatic factor of ecological significance in the region (Sharp 1996). Monsoons are a major influence on the distribution and community structure of corals and other benthic life (Uychiaoco et al. 1992). The reversing wind and current systems generally are a greater influence on biota than ENSO events (Roy 1996).

2.4.4 *Arcuate distributions, tectonics, paleooceanography and paleoclimate.*

The Philippines is at the centre of taxonomic richness in the Indo-Pacific. Was this caused by oceanographic patterns in the past, tectonic history, or both?

Both are responsible for the pattern (Hall 1998). The importance of tectonics is far from clear, however (Hall 1998). A more important question is why this pattern has been maintained, since modern conditions seem suitable for species to extend their ranges to the west, beyond the IWP. Habitat availiablity may maintain the pattern (McManus 1985). However, further biogeographic evidence may improve understanding of what maintains the high species richness in the IWP. This thesis attempts to provide such evidence.

2.5 CONCLUSION

The factors maintaining high species richness of marine biota in Southeast Asia have been reviewed many times (Endean et al. 1956a; 1956b; Vermeij 1978; Pielou 1979; Radovsky, Raven et al. 1984; McManus 1985; Briggs 1987; Rosen 1988; Heads 1990; Hengeveld 1990; Kay 1990; Kohn 1990; Wallace 1991; Briggs 1992; Pandolfi 1992; Kohn and Perron 1994; Veron 1995; Stevens 1996; Palumbi 1997; Johansson 1998; Williams and Benzie 1998). A variety of historical and ecological hypotheses have been proposed to account for present distributions of marine taxa. None of these hypotheses are mutually exclusive. Topography and the unique archipelagic configuration of the region have provided an environment that allows for rapid species diversification and persistence. Habitat heterogeneity, resulting from complex topography, geological history and climate is likely to be a major factor maintaining high species richness in the IWP.

CHAPTER 3

Materials and Methods of Biogeographical Analyses

This chapter presents materials and methods applicable to range and distributional analyses in Chapters 4 to 7.

3.1 MATERIAL

3.1.1 NATURE OF BIOGEOGRAPHICAL DATA

This study uses two kinds of data. Primary data refers to original field observations, collections and studies by the author, and information from museum material that I consulted. This data is used primarily for taxonomic and biogeographic analyses. This data permits direct and detailed comparisons of species assemblages between geographic regions. The data is recorded as presence/ absence or frequency of occurrence. This permits statistical analyses of distributions, assemblages and ranges.

Secondary or reference data are from studies by other systematicists and taxonomists on taxa under study in the Indo-Pacific. These are in the published literature, in printed or electronic form, and are cited. These studies are used to determine species distributions, ecological characteristics, and presence/absence, if the study had this kind of information. If the information concerning occurrence can be referenced to actual material in a publicly accessible museum collection, the presence or absence information was included for statistical analyses.

3.1.2 *Primary Material*

The distributions of recent *Nerita, Clypeomorus,* Littorinidae, rapanine and ergalataxine Muricidae in the Philippines were determined by consulting records and lots deposited at the Philippine National Museum (PNM) in Manila, and the University of the Philippines (UP). In addition, field collections were made between December 1997 and June 1998. Philippine National Museum records for the taxa under investigation consisted of 2595 lots. These lots were collected between 1947 and 1998 from 250 sampling locations. The location of these collection sites ranged from 21° to 4° N and 117° to 126° E. This effectively covers the length and breadth of the Philippine archipelago (Figure 3.1).

Private collections belonging to the Pontifical University of Santo Tomas in Manila were consulted to validate distribution records collected during the Spanish colonial period from 1758-1896.

Conus

Seven hundred and sixty two records of occurrence of shallow water *Conus* belonging to 180 species, were obtained from the collections of the Philippine National Museum (PNM), the University of Santo Tomas (UST) and the University of the Philippines (UP). Secondary material consisting of 363 records was obtained from Cabrera (1984), Springsteen and Leobrera (1986) and Kohn and Perron (1994). These records were collected from 1898-1998. The locations where the specimens were collected were plotted on a map.

Oliva

Only primary material deposited at the Delaware Museum of Natural History, Wilmington, DE USA was used. Five hundred ninety seven (597) lots of Philippine *Oliva,* belonging to 29 species, were examined for this study.

3.1.3 *Secondary Material*

Secondary data sources were used to create a more detailed picture of general distribution and range. While published shell catalogues were initially consulted for distribution analysis, their utility was limited in most cases, since the authors often did not state explicitly the collection site for the figured types in the catalogues. At best these catalogues gave a general regional distribution of the gastropod species. Other more useful sources of secondary data were published taxonomic monographs and

Ph.D. theses that included ecological and field descriptions of the species under investigation.

Secondary data sources assisted in estimates of geographical range. Knowledge of the species composition of molluscan assemblages in the archipelago is due largely to extensive collection during the first 20 years (1898-1918) of United States sovereignty in the country. Types were deposited in the United States National Museum of Natural History and the PNM. The PNM collection was destroyed in World War II. Most of the types were lost. This study therefore, derives primary and secondary material from 100 years of sampling effort.

3.1.4 *Maps*

Published distribution maps, that used occurrence information, were used to help confirm data from primary and secondary material.

3.2 METHODS

3.2.1 *General Assumptions about Sampling Effort*

A major assumption of this thesis is that effort made collecting primary and secondary material in the Philippines is comparable among the different geographical units. However, analysis of sampling effort reveals that the eastern Philippine (Figure 3.1) and southern Mindanao bioregions have been poorly sampled. Operating geographical units (OGU), or bioregions, with less than 5 collection sites were not included in analyses.

3.2.2. *Definition of species richness*

Species richness is defined as the number of species in a given region (Lincoln et al. 1998).

3.2.3 *Definition of Operating Geographical Units and their properties*

Operating geographical units (OGU) were defined as coastlines between 100 to 300 kilometres in length for the large Philippine islands, and between 60 to 99 kilometres in length for the smaller Philippine islands. Each OGU had 5 or more sampling locations. Appendix 2.1 details the characteristics of each OGU.

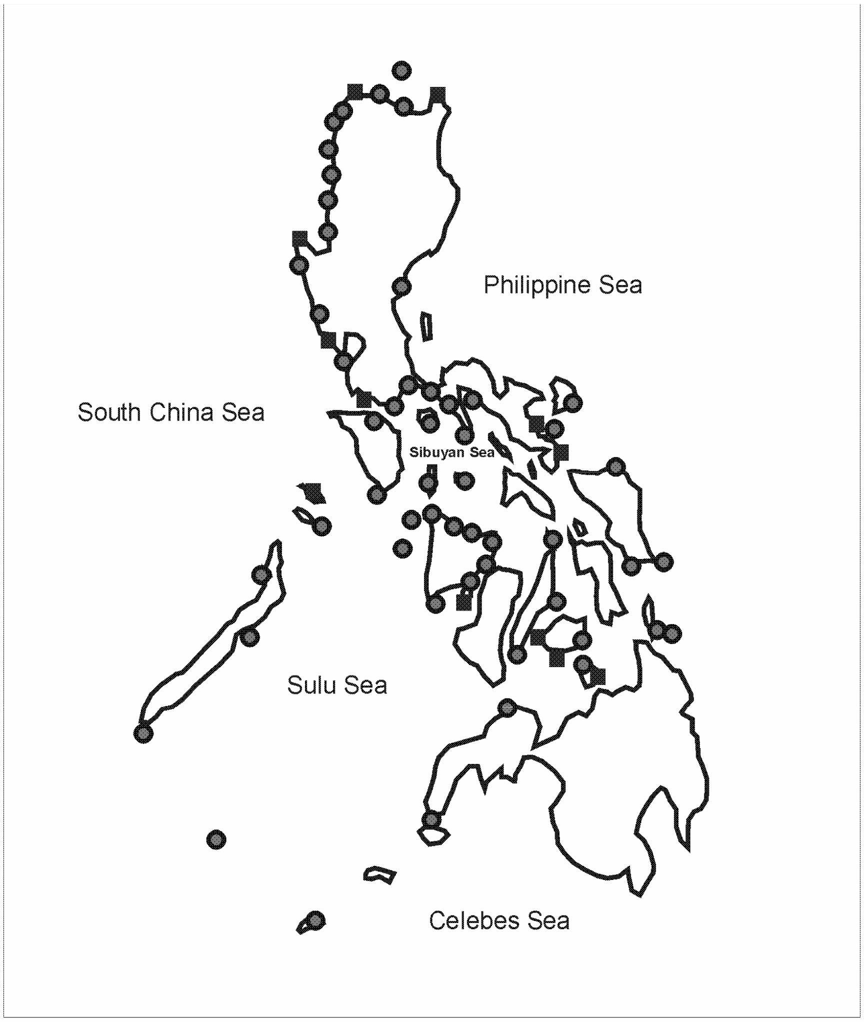


Figure 3.1 Sites within the Philippines where gastropod lots were collected. Squares indicate sites visited by the author in 1997 and 1998

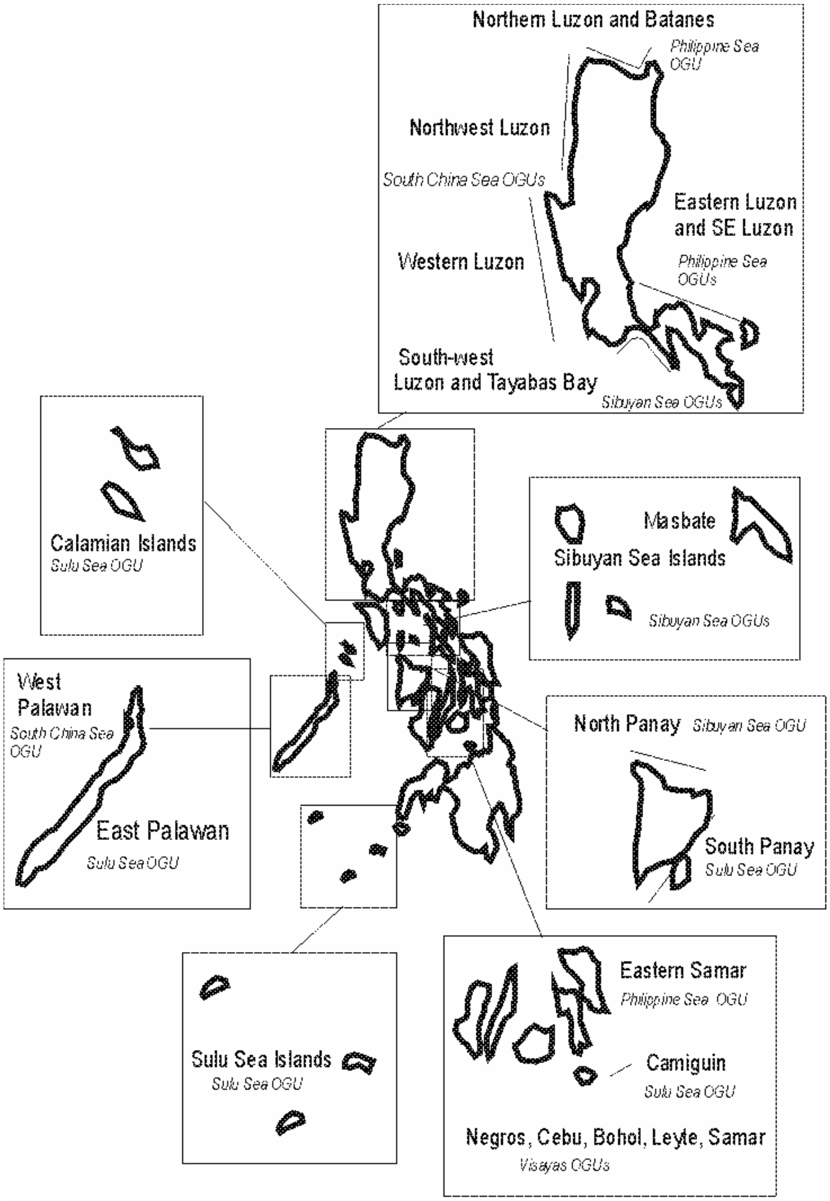


Figure 3.2. Operating geographic units (OGU) used in biogeographic analysis. The oceanic basin of each OGU is labelled in italics. Southern and Eastern Mindanao geographical regions are insufficiently surveyed and not included in analysis.

3.2.4 *Properties of OGU assemblages*

Each OGU had records of species occurrences. The composition of these occurrences was defined as an assemblage.

3.2.5 *Frequency of occurrence*

The frequency of occurrence of each species records the number of times the species was collected or recorded from an OGU. This is not a measure of abundance. Occurrence frequency may partially reflect abundance. Species with large ranges tend to have higher abundances, and thus higher frequencies of occurrence (Brown 1995), if it is assumed that species have equal access to resources (Maurer 1999).

Frequencies of occurrence are important in subsequent ordination methods. It is highly probable that sites will have different occurrence frequencies, due to varying ecological conditions. Suitable environments that enhance species persistence can vary over a geographic range of a species (Maurer 1999).

3.2.6 *Relational Databases*

Occurrence records were entered into a relational database. The database *Range* was used for Philippine upper and mid intertidal taxa. The databases were used to organise information for biogeographic analyses**.**

The database *PhilCone* was created to organise information for biogeographical analyses of Philippine *Conus* species. A printed copy of the database is provided in the thesis in Appendix 5.

3.2.7 *Areography: range shape, size and characteristics*

This study focuses on the geometry and areal extent of a species range. The study of geometry and size of the species range with respect to ecological factors is areography (Rapoport 1982) Species occurrences from primary and secondary sources were mapped. These were queried from records in the relational databases**.**

3.2.7.1 Total Area of the Philippines

The total area of the Philippine archipelago was defined by its political boundaries, omitting the Kalayaan Islands. The Kalayaan Islands were not included for the following reasons

1. From 1900-1965, when most of the primary and secondary data used in this thesis were collected, the Kalayaan Islands were not formally considered part of the Philippines. They were thus not sampled by United States surveys, and the surveys of the Philippine National Museum.
2. The Kalayaan Islands are a geographic unit distinct from the main Philippine archipelago, and are not high islands.

3.2.7.2 Measurement of range area (Figure 3.3)

Occurrence records were plotted on maps to estimate range within the Philippines. A range is defined as a shape determined by at least 2 occurrences. Thus in the most simple case, a range is a line. In other cases, the range is a complex polygon. Since a line has no second dimension, a linear range is defined as the number of grids (0.5 cm^2, 1:5,563,432) it intersects on a map, expressed in square kilometres. It may be considered as a narrow polygon of one grid width. For disjunct distributions, each range is treated as a separate range for analysis. To determine the shape and size of the range, the mean maximum north-south and east-west axes were measured in kilometres. These values were then log transformed and plotted.

A shape index for each range was defined. This was:

$$SI = E/N \qquad \text{Equation 3.1}$$

where SI is the shape index, E is the mean maximum east-west axis length, and N is the mean maximum north-south axis length. An index of less than 1 indicates a primarily north-south orientation of the range. An index of greater than 1 indicates a primarily E-W orientation

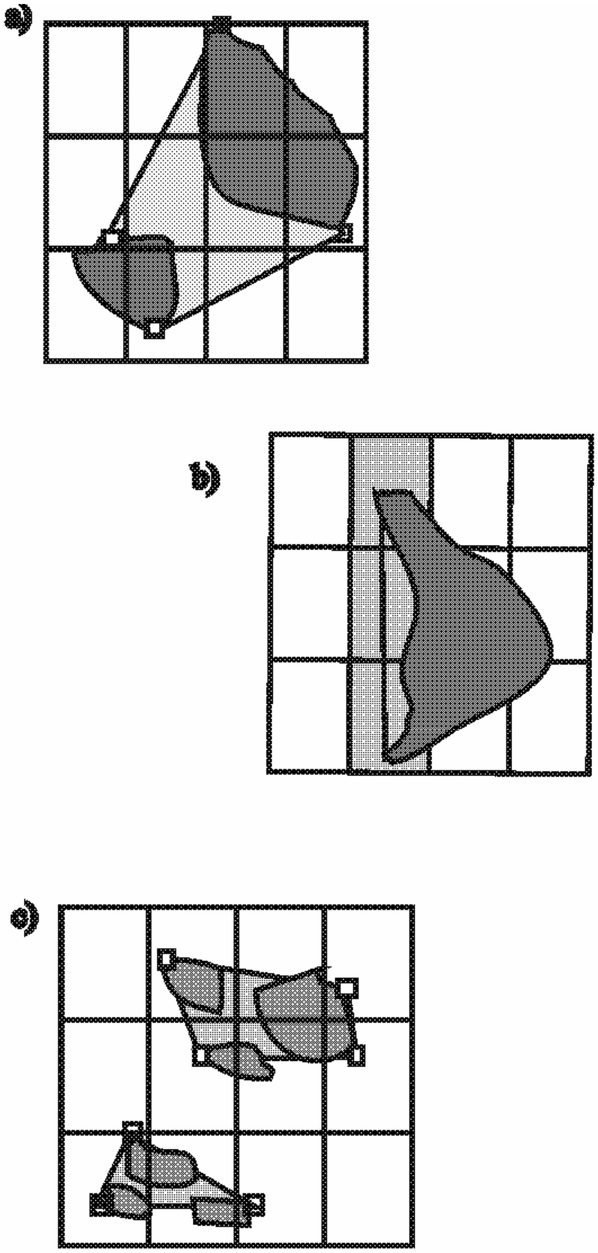


Figure 3.3 Areography of a) polygonal, b) linear and c) disjunct ranges. The disjunct ranges c) have a predominantly E-W orientation while linear range b) has a predominantly N-S orientation.

3.2.7 ***Measures of landscape topography:***

3.2.7.1 Coastal length, area and index of coastal complexity

The coastline was quantified in terms of both length and complexity. Coastal length (km) was measured from digitised equal area projection maps. Coastal complexity is a function of coastal length and the number of embayments along the coastline. An embayment is an indentation of the coastline defined by two headlands. This is an important property of each OGU, as it likely relates to habitat complexity. The number of embayments along a coast was quantified from published maps. The complexity index is given by the equation:

$$C = E/L \qquad \text{Equation 3.2}$$

where C is complexity, L is coastal length based on an equal area map projection (1:5,562,432) and E = number of embayments. An embayment is defined as an indention the coastline, defined by at least two headlands.

One major limitation of defining coastal area of the Philippine coastline is the lack of information from digitised maps. Digitised maps provided by the Philippine National Mapping and Resource Information Authority (NAMRIA 1998) measure only coastal length. Calculations of coastal area were not available. Since there is no coastal area estimates for Philippine OGU based on digitised maps, an assumption was made. The coastal length multiplied by 1 km as measured from the shore was used to represent coastal area. In the very few cases where coastal area estimates were available, these were used. This assumption is a major limitation since 1) areal coverage of intertidal environments was not available 2) it is safe to assume that in most cases, rocky intertidal environments do not extend more than 1 km from shore. Thus, this may overestimate coastal area.

3.2.7.2 Island topography

Estimates of island areas and coastal length in kilometres were gathered from the National Mapping Resource Agency and the Philippine Coast and Geodetic Survey.

Where area estimates are given in Imperial measures, these were converted into square kilometres. Additional information on islands was collected from the United States Coast Pilot, and charts of the Philippine Navy

.3.2.7.3 Distribution of coral reefs

In view of the lack of detailed estimates of coral reef area in any country (ReefBase 1998), linear estimates of coral reef area were made from published maps in the Philippines, provided by the World Conservation Monitoring Centre (WCMC) (Burke et al. 2002). These maps are one of the utilities in the ReefBase 3.0 database. Estimates are presented as a percent of the OGU coastline.

3.2.8 *Ecological relationships: ordination and correlation analyses*

Principal components analysis (PCA) was used to examine distribution patterns in ordination space. PCA allows for capturing the general pattern of groupings based on frequency of occurrence without the assumption of *a priori* groups**.** Correlation analysis was also used to examine the significance of ecological factors (see below) on species-richness. The PCA measured the properties of sites (OGU). Each site has an assemblage of species with differing occurrence frequencies.

The geographical and ecological factors used in the ordinations and correlations were latitude (degrees), longitude (degrees), annual rainfall (mm), island and mainland landform, cyclone frequency (number/year), dry season (presence or absence), wet season (presence or absence) coastal length (km), coral reef area (percent of OGU coastal length), coastal complexity index, tidal amplitude (m) and sea surface temperature (°C). These data were collected from publicly accessible databases and published material of the Philippine National Mapping and Resource Information Authority (NAMRIA 1998), Philippine Atmospheric and Geophysical, Astronomical Sciences Authority (PAGASA 1992; PAGASA 1998), the Philippine Navy, the World Conservation and Monitoring Centre (WCMC) and ReefBase (ReefBase 1998). All data were transformed as z scores to remove the effects of scale. Z-scores normalize each observation with reference to the population mean. Thus the effects of scale are removed.

3.2.9 *Species-area analysis: provinciality and homogeneity*

Species-area relationships can be used to infer a variety of biogeographical processes (Rosenzweig 1995) at different temporal or spatial scales. In this study, species-area relationships were used to infer present isolation of marginal oceanic basins. The partitioning of a biotic area into two or more isolated regions consequently results in a smaller area. Isolation promotes speciation. Since the basin isolation hypothesis predicts increased rates of speciation, reconnection of the basins may result in species loss (McKinney 1998). This species loss will be observed as biotic homogenisation and consequent loss of provinciality. Rosenzweig (1995) suggests that geographical isolation can be predicted from the parameters of the species-area curve

$$S= cA^z \qquad \text{Equation 3.4}$$

where S is the measured species richness, A is area occupied by the species, c is a constant and z the exponent of the curve The parameters of the species-area curve were estimated using the power function routine in Microsoft Excel.

Using parameters estimated from the species-area curve, Rosenzweig's provinciality or geographic index of isolation (McKinney 1998) was used to measure differences in gastropod assemblages in the Philippine marginal oceanic basins. The index is:

$$P = (A^z + B^z)/D^z \qquad \text{Equation 3.5}$$

where A and B are the coastal areas of adjacent OGU, and D is the total coastal area of the regions sampled within the Philippines. Z is the exponent of the inter-oceanic basin species-area curves**.** It is also possible to calculate basin provinciality by comparing the SPAR properties of a basin with that of the whole Philippines:

$$Pb = B^z/D^z \qquad \text{Equation 3.6}$$

where B^z is the basin area and D is the total coastal area of the regions sampled within the Philippines. In comparing basin provinciality, Equation 3.6 was used.

To get a measure of biotic homogenisation (H), the inverse of P (in eqn 3.6) was calculated. If biotic isolation is observed, then the resulting biotic homogeneity indices will be low. P estimates greater than 1 suggest provinciality.

The species-area curves in each oceanic basin incorporate evolutionary isolation, diversification, or the presence of relict species. Thus z differences between basins suggest that the basins have been isolated. This is tested by ANCOVA, with basin effect as the fixed factor, and coastal area as the covariate. ANCOVA tests the homogeneity of regressions and determines if there are significant differences in slopes (z) and intercepts of regressions.

3.3 INTRODUCTION TO THE GASTROPOD TAXA INVESTIGATED

3.3.1 *Herbivorous Taxa*

3.3.1.1 The Nerites – *Nerita* (Neritidae*)*

The Neritidae is a family of intertidal, marine, mainly tropical, neritopsoid gastropods. They are characterised by a globose, porcellaneous shell, with a moderately elevated to flat spire. Sculpturing varies from heavy cords to none. The columellar deck is flat and strongly to weakly dentate. It may be pustulose to smooth. The lip may be strong to weakly dentate. The operculum is calcareous, granulate in all subgenera except *Linnerita*, and has a distinct appendage or peg that enables the animal to close its aperture to prevent desiccation and thermal stress.

The taxonomic unity of the Neritidae is well established (Vermeij, 1984). However, the present subgeneric classification is not widely accepted (Krijnen 1997). Vermeij (1984) reviewed the taxonomy to the subgeneric level, and erected a new subgenus, *Linnerita*, characterised by a smooth operculum and the absence of a heavy sculpturing on the shell. Vermeij proposed that this subgenus was a specialised clade that had a short fossil record and unusual behavioural characteristics (Vermeij 1984).

Partitioning of resources in space and in time enable sympatric species of nerites to co-occur on rocky shores. Clustering, a common behaviour, reduces emersion stress and mortality rates (Vanini and Chellazi 1978; Garrity 1984; Blasini 1968) Clustering thus reduces energetic costs over a tidal cycle (Chellazzi et al. 1985). Size selective feeding and differential movement patterns allow different size classes to minimise competition. Space is often partitioned with respect to exposure and tides, with several species occupying distinct shore positions. Vertical distributions can vary seasonally. Such temporal variation is called "dynamic zonation" and is particularly obvious on tropical shores with strong monsoonal influences (Ruwa and Jaccarini 1986).

Scott (1998) reviewed the reproductive anatomy of the Neritidae. Reproduction in nerites is poorly known. Early studies focused on reproductive anatomy (Govindan 1974; Miskiewicz 1980). Indo-west Pacific species are planktotrophic, with one lecithotrophic species (Knudsen 1997). Some Atlantic species may have lecithotrophic development (Leal 1991).

Gradients of exposure and habitat heterogeneity can influence species distribution on a local scale. Some species can occupy sheltered shores with mangroves. Mangrove areas and protected shores have the greatest species richness of neritids. These environments are heterogeneous, with varying salinity. These habitats may have provided greater resources for nerites to undergo adaptive radiation, and to colonise vacant niches in adjacent freshwater environments. *Neritina, Neritodryas , Septaria* and *Clithon* are representative genera of the family in these environments (Springsteen and Leobrera 1986).

The Neritidae is an ancient family, with a fossil record dating back to the Triassic (Scott 1998). However, since the rocky intertidal is not a depositional environment, the fossil record is unclear. There is fossil evidence that the modern subgenera *Ritena* and *Amphinerita* have existed from the Cretaceous, and that their ecological characteristics are similar to that of today. The existence of nerites in paleontological facies is thought to indicate the presence of tropical climates (Saul and Squires 1997).

3.3.1.2 Rock-creepers – *Clypeomorus* (Cerithiidae)

The rock-creepers are an endemic Indo-Pacific genus within the family Cerithiidae. Houbrick (1985) reviewed the taxonomic status, distribution and general ecology of these gastropods. He identified 12 extant species, with 3 subspecies. The external shell features of *Clypeomorus* resemble the features of other cerithiid genera. The diagnostic character is the operculum.

Many present day rock-creepers stem from a major Miocene-Pliocene adaptive radiation of the cerithiid family to a rocky intertidal habitat. The ancestral stock was likely to be *Cerithium*, an extant genus dating back to the Cretaceous and found in sandy to muddy intertidal substrates. *Clypeomorus* is found in the mid or high intertidal, where it is a microphagous herbivore (Houbrick 1985).

3.3.1.3 Tropical Periwinkles – *Littoraria, Nodilittorina, Echininus* and *Tectarius* (Littornidae)

Littorinidae are found worldwide on rocky shores of all exposures. Shells are small to medium, turbinate or trochoidal, spirally grooved and variable in colour (Reid 1989; 1996) Because of their abundance and ease of collection, the ecology, behaviour, vertical distribution and genetics of the family, especially of the temperate species, has been well studied. Reid (1986) revised the *L. scabra* complex in *Littoraria*. All littorinids are herbivores.

Common tropical genera include *Littoraria, Nodilittorina* and *Tectarius*. *Littoraria* and *Tectarius* are found on shores of all exposures, and are particularly common on mangrove and sheltered shores. *Littoraria* has achieved substantial evolutionary radiation in mangroves, with twenty species recorded (Reid 1986). These genera have varied life histories, with both planktotrophy and non-planktotrophy observed in *Littoraria*. Planktotrophy and non-planktotrophy are also likely in *Tectarius* and *Nodilittorina* (Rosewater 1970a; Rosewater 1970b). Shell morphology is relatively constant in both oviparous and ovoviviparous *Littoraria*. There is no correlation between size of geographic range and life history strategy (Reid 1986). However even for widely distributed species, considerable character differences can be observed, thus suggesting population isolation due with distance.

3.4.2 Carnivorous Taxa (Caenogastropoda)

3.4.2.1 Rock-shells and whelks – *Morula, Cronia, Ergalatax, Muricodrupa, Thais, Manicinella, Purpura, Drupa* (Muricoidea: Muricidae subfam. Rapaninae and Ergalataxinae)

The Muricidae, and members of its superfamily Muricoidea, are the dominant group of carnivorous molluscs on rocky shores. A large and diverse marine group, the muricoideans are typically elongate, fusiform to ovate, with an elongate spire and an anterior siphonal canal (Ponder 1998). The larval phase is variable, ranging from planktonic to intracapsular development. Consequently the protoconch structure is diverse.

The intertida taxa of Rapaninae (=Thaidinae or Thaidididae) are treated in this study as a subfamily (Kool 1993; Ponder 1998). Earlier authors have given this group full family status. Ponder (1998) considers the group to differ from the rest of the muricids in only minor ways.

The ecological positions of the Rapaninae and Ergalataxinae are similar in all environments. As obligate carnivores, they feed on bivalve molluscs, gastropods, barnacles, limpets, polychaetes, and in the case of *Drupella*, scleractinian coral tissue. Some species, such as *Drupella cornus*, are specialist feeders. However many intertidal genera are generalists, feeding on the dominant food resource available.

3.4.2.2 Cone shells - *Conus* (Caenogastropoda: Conidae)

Conus is an obligate carnivorous taxon of lower tropical rocky shores. It is often related closely to the presence of coral reefs. The majority of the estimated 200 species of tropical Indo-Pacific *Conus* range from intertidal to 30 m depth, and are associated with coral reefs. Species distributions within the genus range from island endemism to Indo-Pacific. Information is available on the life history characteristics of the wide ranging and common coral reef associated species (Kohn and Perron. 1994).

3.4.2.3 Olive shells - *Oliva* (Caenogastropoda: Olividae)

The Olive shell genus *Oliva* has 74 recognized species. 35 are found in the Philippines (Tursch and Greifeneder 2001). *Oliva* is exclusively carnivorous and sand dwelling. A majority of species live from 0 to 30 meters depth (Tursch and Greifeneder 2001) and are associated with coral reefs. Tursch and Greifeneder (2001) report that number of species generally decreases with distance from the Philippine archipelago.

Observations on the occurrences of *Oliva* in the Philippines suggest localised distributions, possibly associated with ocean basins (Springsteen and Leobrera 1986). More studies on how their distribution, local ecology, and life histories influence shell shape may help to explain this observation. Intrapopulation variability in shell shape, colour and general physiognomy has resulted in a confused taxonomy (Tursch 1994; Tursch 1998; Tursch and Greifeneder 2001).

CHAPTER 4.

Range and Distribution of Rocky Shore Gastropods in the Philippines

"*Despite formidable obstacles, much has been gleaned over the years, and slowly but surely, a clearer picture of the distribution characteristics and the biological habitats of molluscs is starting to emerge"* – F.J. Springsteen and F.M Leobrera (1986) "Shells of the Philippines"

This chapter describes the range and distribution of some mid to high intertidal rocky shore gastropod taxa. These taxa are the Neritidae: *Nerita,* the Cerithiidae: *Clypeomorus,* the Littorinidae: *Littoraria, Echininus* and *Tectarius* and the Muricidae: Rapaninae and Erglataxinae, in the Philippines. The species ranges are described and correlated with ecological factors. These distributions and ranges are examined with reference to the McManus (1985) basin isolation hypothesis.

4.1 INTRODUCTION

4.1.1 *The nature of species ranges*

The central aim of biogeography is to understand the causes of patterns of distribution in space and historical time. Geographical ranges are determined by the response of species to environmental conditions. This is known as ecological tolerance (Maurer 1999). Range size and shape are relatively easy to measure.

Ranges can be viewed as response surfaces (Hengeveld 1993), reflecting responses to varying environmental conditions. The risk of extinction, and thus absence, is greatest at the edges of the range, and much less at the centre. Highest abundance is often near the centre of a range. Thus, susceptibility to extinction is a function of range size (Maurer 1999). Changes in abiotic or biotic factors across the range may result in a gradient in the frequency distribution of occurrences or abundance.

Analyses of these gradients on a biogeographic scale may allow for the generation of hypotheses that help explain species presence or absence, and perhaps resistance to extinction.

4.1.2 *Basin isolation*

Basin isolation (McManus 1985) is a biogeographical hypothesis that seeks to explain high marine species richness in Southeast Asia. This hypothesis suggests that repeated isolation and reconnection of oceanic basins in Southeast Asia, as a result of changes in sea level, favoured rapid speciation in shallow water marine biota.

An aspect of the hypothesis relates to the nature and patterns of species distributions and ranges in Southeast Asia, which McManus (1985) described as arcuate (arc-shaped) and overlapping. These distributions are particularly unique to the region. McManus lists several factors potentially causing such distributions. These include geological history, habitat heterogeneity, landform configuration, and the prevailing climate system. An examination of species distributions and ranges in the Philippines may help evaluate the hypothesis.

4.1.3 *The Philippines as a geographic unit in which to test biogeographic hypotheses*

The Philippines, the centre of terrestrial and marine biotic species diversity, is a unique environment in which to test biogeographic and evolutionary hypotheses. The country is the only archipelago with a N-S orientation in the Southeast Asian region. The country is shaped like a triangle. The geologic evolution of the Philipiines, especially the different ages of the islands and the different degrees of isolation of the oceanic basins in the arhipelago (see Chapter 2), are unique properties. These properties have been used to assess species diversification in terrestrial mammals across islands of different geological ages (Heaney 1986).

The major climatic and oceanographic systems, the monsoon and its consequent reversing current systems, are believed to be major factors affecting the distribution of shallow water marine biota. The monsoons and reversing current systems are further complicated by the presence of topographically complex islands and coastlines. These factors are investigated in detail, using a primarily exploratory approach, to determine patterns of species occurrence and occurrence frequencies in different intertidal rocky shore gastropod assemblages.

In the past, researchers have treated the Philippines as one geographic unit in biogeographical investigations of a larger region (e.g. Indo-West Pacific). This study describes patterns of distribution of gastropods within the island and regional groups of the Philippines. This approach hopefully will enable a clearer understanding of the nature of marine species richness in the Philippines.

4.2 MATERIAL

The selection of primary and secondary material, including maps of the location of collection sites used in this biogeographic analysis is described in Chapter 3. The material is based on museum record collections and secondary material in published papers, books and monographs. Each record makes up an occurrence. A geographical region may have several occurrences of a species and this is defined as a frequency of occurrence.

4.3 METHODS

The methods for this chapter are described in Chapter 3. These include methods of determining the size and shape of species ranges, description of ecological factors correlated to range sizes and shapes, analyses of species–area relationships, and provinciality. The main method of data analysis was principal components analysis ordination

In general, the geographic range of each species was defined on an equal-area map from frequency of occurrence information. The size and shape of the range was determined using areographical methods (Rapoport 1982) Species-area relationships of the various taxa were plotted by fitting the data using the power function in

Microsoft Excel. The species-area parameters were used to calculate provinciality, that is, a measure of faunal uniqueness. Principal components analysis was used to determine if there are patterns and relationships in the frequency of occurrences and geographical ecological factors.

4.4 RESULTS

4.4.1 Ranges

Figures 4.1a-h show the ranges of representative taxa within the Philippines. The ranges generally follow the shape of the archipelago. There are species that are found only along the western side of the Philippines (*Clypeomorus nympha* (Figure 4.1a) *C. irrorata* (Figure 4.1b) *Nerita picea* (Figure 4.1c), *Cronia auriantiaca* (Figure 4.1f) and *Echininus cumingi spinulosus* (Figure 4.1h)

There are species that are restricted to the central Philippines. (*Clypeomorus adunca, Nerita antiquata, Nerita n. sp. Morula musiva* and *Thais armigera*). Other species have disjunct distributions (*Nerita exuvia, Nodilittorina leucosticta biangulata* and the two subspecies of *Echininus cumingi*) With the exception of *N. exuvia*, these species are not found the central Philippines. The other species investigated have pan-Philippine distributions.

Most of these ranges are triangular and follow the general orientation of the archipelago. The ranges that are restricted to the central Philippines follow the coastline of the islands or embayments where they have been recorded. Species that have mainly western Philippines distribution show a curved range that also follows the general orientation of the islands.

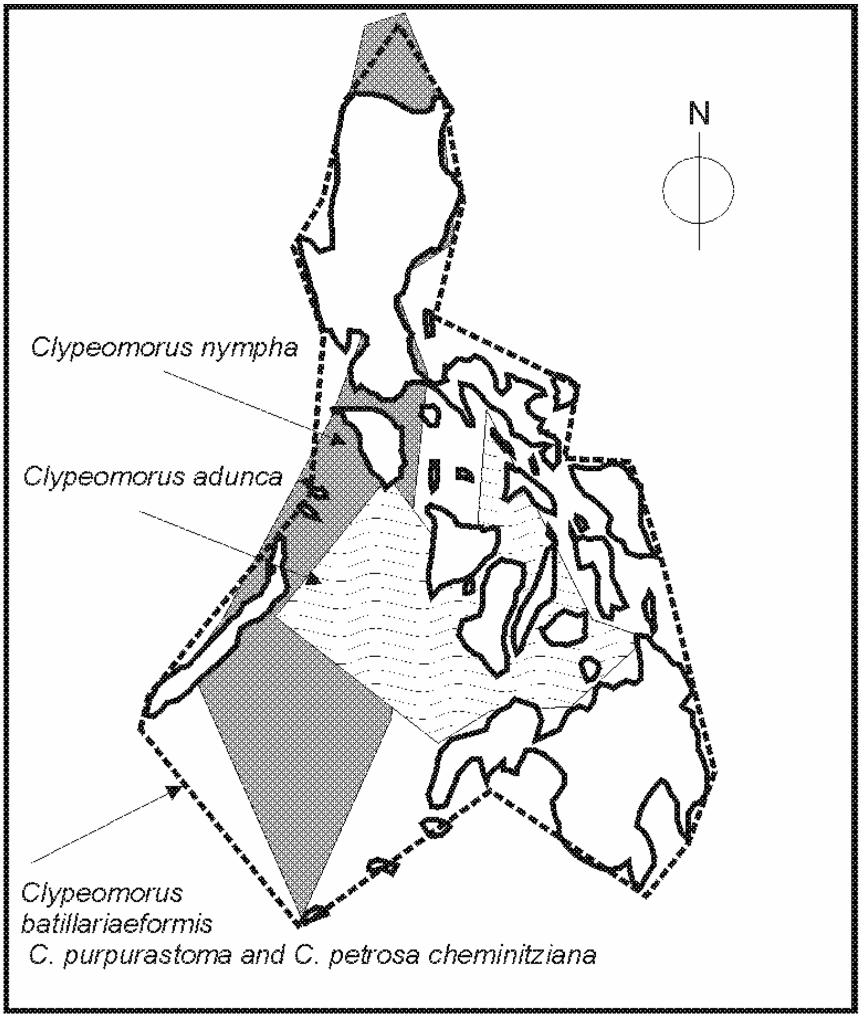


Figure 4.1 a *Clypeomorus batillariaeformis, C. purpurastoma, C. petrosa cheminitziana* have pan-Philippine distributions. *C. adunca* is restricted to central Philippine basins of Sibuyan and Visayan-Camotes, Bohol and the northern Sulu Sea. *C. nympha* has a western range.

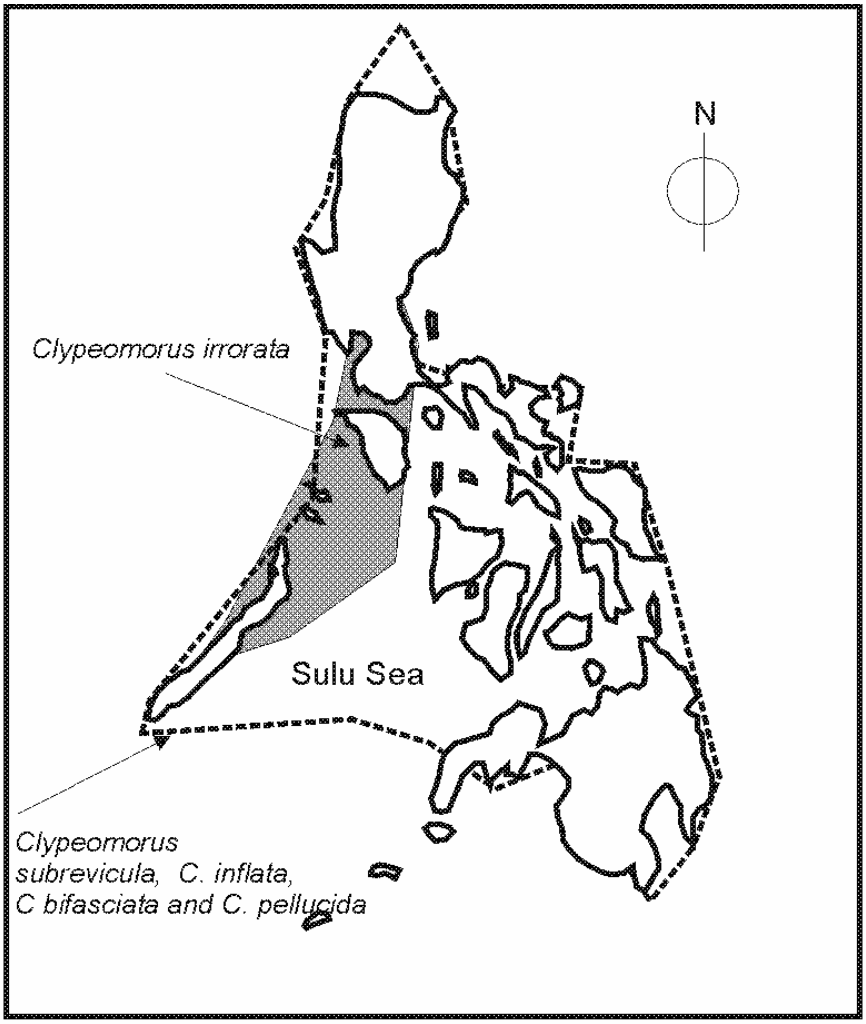


Figure 4.1 b Range maps of *Clypeomorus* without recorded occurrences in the southern Sulu Sea. *Clypeomorus irrorata* in the Philippines seems to be restricted to the South China Sea and Northern Sulu Sea. This species exhibits a curved range. *C. subrevicula, C. inflata, C. bifaciata* and *C. Pellucida* have not been recorded from the southern Sulu Sea.

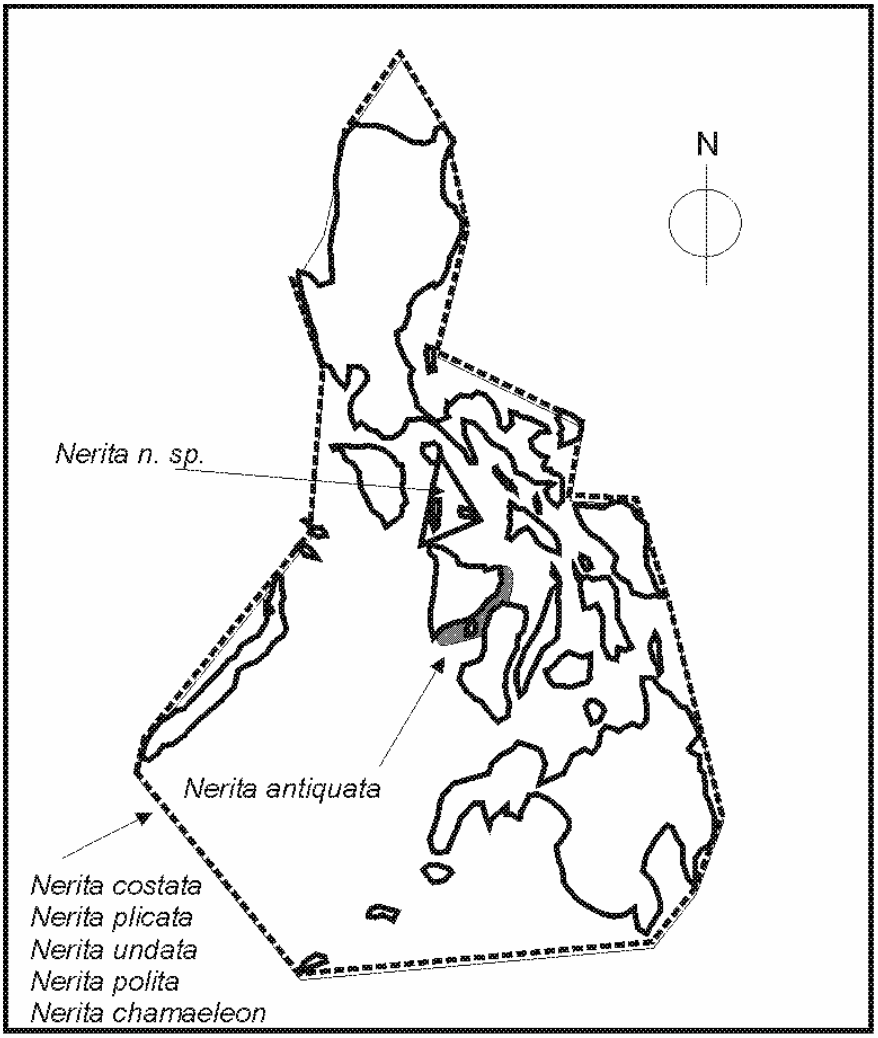


Figure 4.1 c Distribution of *Nerita* in the Philippines. *N. undata, N. costata, N. polita N. chamaeleon* and *N. plicata* have pan-Philippine distributions. The possibly endemic *N. antiquata* and *Nerita n. sp.* are restricted to the central Philippine basins.

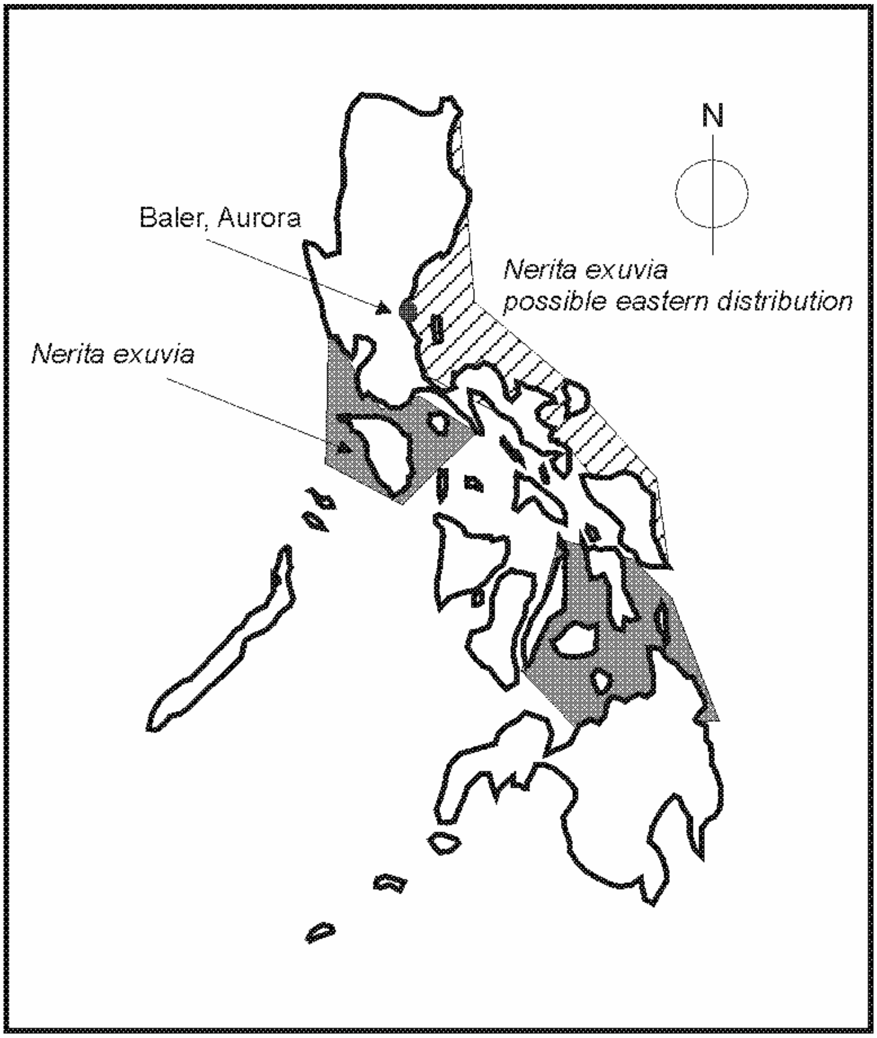


Figure 4.1 d Disjunct distribution in Philippine *Nerita*. *N. exuvia* has a known northern and southern distribution. The only known eastern Luzon record was collected in Baler, Aurora in 1947
The species may have an eastern distribution shown in hatch since eastern Mindanao specimens have been collected..

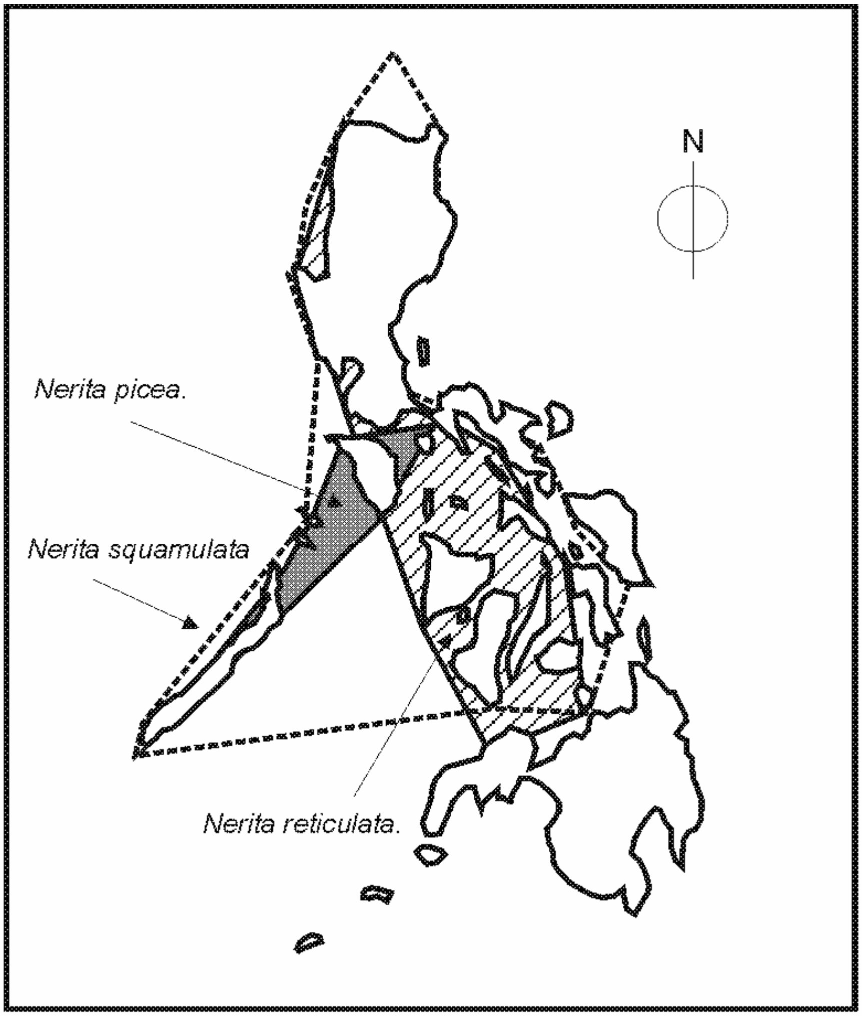


Figure 4.1 e Distribution of uncommon *Nerita* in the Philippines. *N. squamulata* has a wide but mainly west-central distribution. The non-planktotrophic *N. reticulata* is found mainly in the central Philippines basins of Sibuyan and Visayan Seas. *N. picea* has only been recorded from Tayabas Bay and the western margins of the Sulu Sea.

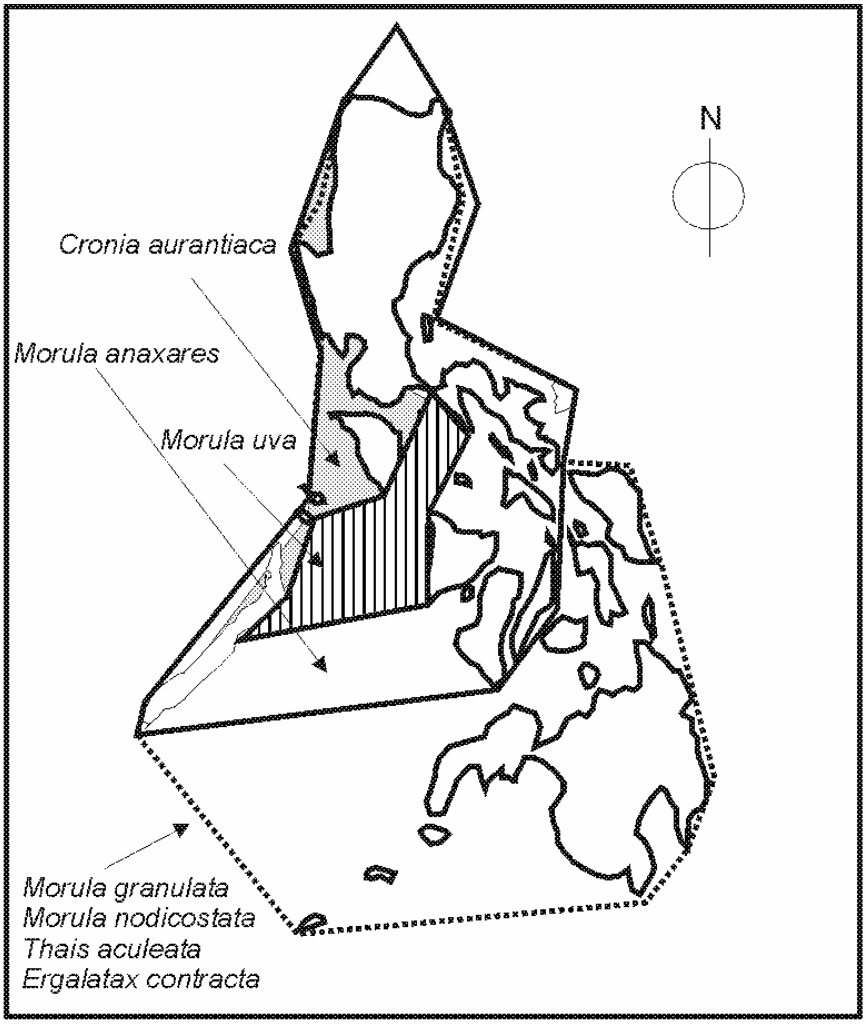


Figure 4.1 f Distributions of rocky shore muricids in the Philippines. *Cronia aurantiaca* shows a western curved distribution. *M. anaxares* has a wider distribution but largely confined on the western coast of the Philippines. The other species have pan-Philippine distributions.

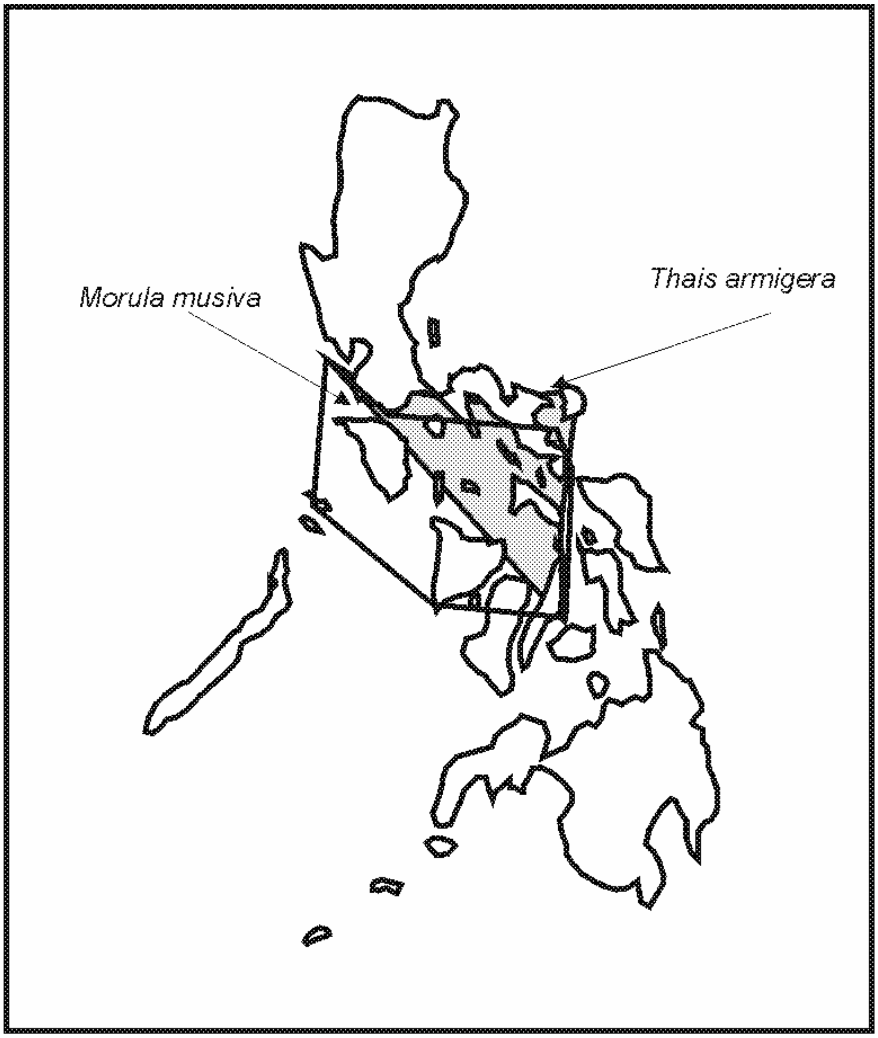


Figure 4.1g Distributions of rocky shore muricids with restricted ranges *Morula musiva* and *Thais armigera* are mainly restricted to the Sibuyan Sea.

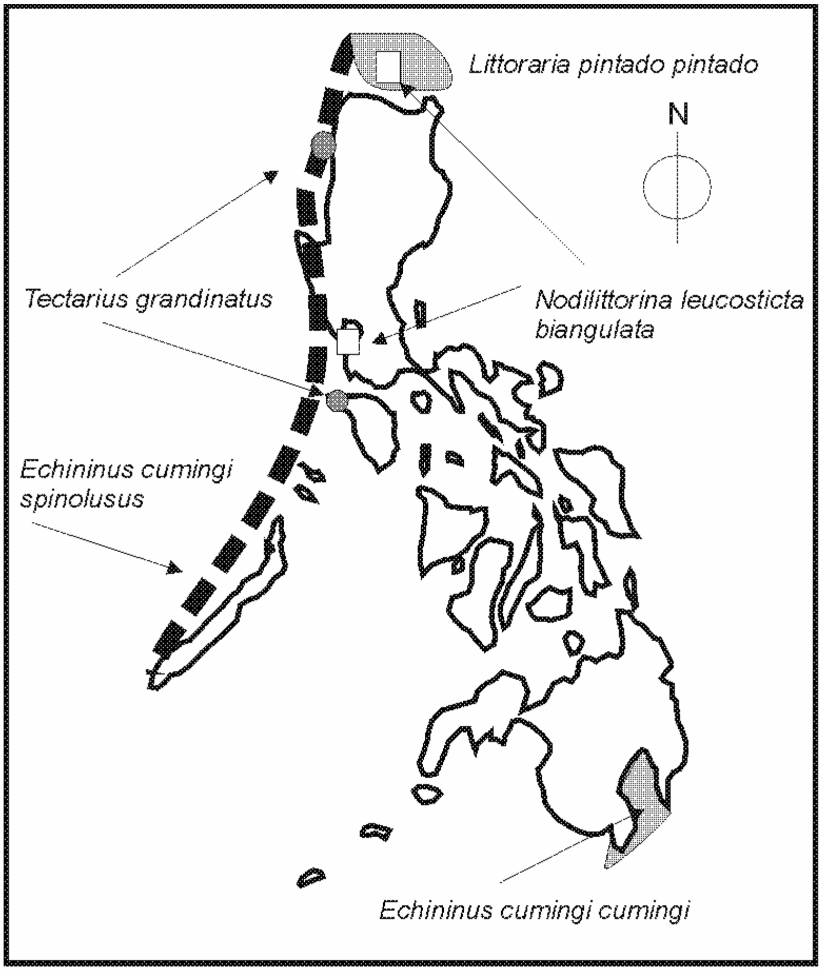


Figure 4.1 h Littorinids with restricted distribution in the Philippines. *Littoraria pintado pintado* has been recorded only from Batanes and Babuyan Islands. The two subspecies of *Echninus cumingi* show a disjunct distribution with *E. cumingi spinolosus* restricted to the western coast of the Philippines and the South China Sea basin. *Tectarius grandinatus* has only been recorded on two sites in Ilocos and Occidental Mindoro both on the South China Sea coastline. *Nodilittorina leucosticta biangulata* has been recorded only from Batanes and Manila Bay.

4.4.2. *Ecological corrrelates of ranges*

4.4.2.1 Ordination analysis

Tables 4.1 a-d show results of the principal component analyses for 5 taxa. Many of the principal axes account for relatively small amounts of variance in the data (eg 27-35% for axis 1). Table 4.1e shows the Pearson and Kendall correlations of OGU assemblages with ecological factors. For the Littorinidae, latitude is the main ecological correlate with frequency of occurrence (Figure 4.2). *Nerita* frequency of occurrence is correlated with longitude and on the 3rd and 2nd principal components, with dry and wet seasons (Figure 4.3 a-c). *Clypeomorus* has reef distribution, tidal amplitude and latitude as major correlates of frequency of occurrence (Figure 4.4). The upper and mid-intertidal Muricidae has sea temperature and tidal amplitude as major correlates (Figure 4.5).

Latitude, cyclones and SST differences correlate best with frequency of occurrence of Littorinidae. In *Clypeomorus*, reefs may provide a habitat that determines the species composition of assemblages. Tidal amplitude is also an important correlate that determines frequency of occurrence, but this is strong only in PC axis 2 where its correlation is -0.544 (Table 4.1e). In *Nerita*, tidal amplitude is not an important correlate with frequency of occurrence. Rather, the length and duration of the monsoons, as reflected in the dry and wet season variables and longitude do correlate well with frequency of occurrence. The effects of monsoons in the Philippines are correlated with island landform and tend to be attenuated by longitude. In general, the western coastlines experience the strongest monsoon influence in the summer and the eastern coastlines experience strong monsoons in the winter. The central islands have varying exposures to the winter and summer monsoons.

The PCA axes in the analyses do not account for a large fraction of the variance. The main reason for this is that the ecological correlates represent a mean value for the region (OGU) concerned. There were no ecological data for sites within an OGU. If these were available, then a large part of the variance may have been accounted for, and a more robust PCA would result. This is an unavoidable limitation. However, the main objective of the study was to demonstrate a gradient in species composition, and occurrence frequency in the ordination.

	PC axis					
Geographic unit	1	2	3	4	5	6
Calamian Islands	0.0986	-0.0353	-0.1332	0.0331	0.1100	0.0718
Camiguin	-0.0420	0.1429	0.0543	-0.1122	-0.0999	0.0403
East Cebu	0.0143	-0.3772	0.0367	0.0154	-0.2103	0.1490
East Palawan	0.3452	0.4417	-0.0108	0.0233	-0.0114	0.0759
Eastern Samar	0.3382	-0.1421	0.0815	-0.0673	-0.0803	-0.0161
North Luzon	-0.0765	0.0311	-0.0076	-0.0165	0.0718	-0.0382
North Panay	-0.2818	0.0426	0.1092	-0.0061	0.1176	0.0653
North Bohol	-0.1200	0.1605	0.1079	-0.1025	-0.0706	-0.0589
Northwest Luzon	-0.0622	-0.1022	0.1067	0.0899	-0.0050	-0.1423
Southeast Luzon	0.1761	0.1115	-0.0704	-0.0595	0.0073	-0.0623
Sibuyan Sea Islands	-0.0837	-0.2599	-0.2191	-0.0485	0.1205	0.0101
South Panay	-0.1847	-0.0225	0.0827	-0.0834	0.0718	0.0712
Sulu Sea Islands	0.3467	-0.1387	0.0346	0.0105	0.1417	0.0119
South Bohol	0.0126	-0.1018	0.0631	-0.1070	0.0508	-0.1031
Tayabas Bay	-0.2308	0.1117	0.0727	-0.0423	-0.0093	0.0317
Verde Islands	-0.1508	0.1603	-0.0893	0.2536	-0.0082	0.0492
Western Luzon	-0.1245	0.0526	-0.3083	-0.0561	-0.1519	-0.0809
Western Palawan	0.0255	-0.0751	0.0892	0.2756	-0.0445	-0.0747
Variance explained (%)	29.55	26.82	11.43	9.62	7.67	4.65

Table 4.1a Unit loadings for the various geographic units and axes of the pricncipal components analysis. The PCA was based on frequency of occurrence of *Nerita*.

	PC Axis					
Geographical unit	1	2	3	4	5	6
Batanes Islands	0.3026	0.3518	-0.0173	-0.2438	0.0165	-0.0846
Calamian Islands	-0.0760	-0.1433	-0.0267	-0.1181	0.0417	0.1542
East Cebu	-0.1191	-0.0514	0.0701	0.0505	-0.0887	0.0587
West Cebu	0.2695	-0.5152	0.0450	-0.1365	0.2367	-0.0186
Davao	0.2488	-0.1468	-0.3105	0.1076	0.0013	-0.0018
East Luzon	0.0145	-0.1760	-0.1058	0.0543	0.1199	-0.1731
Eastern Samar	-0.4698	0.1224	0.2431	0.1107	-0.0164	0.0354
Masbate	-0.1657	0.1287	-0.0537	-0.2009	0.0388	0.0434
North Luzon	0.2293	0.0097	0.2880	0.2003	-0.0034	-0.0165
Northwest Luzon	0.3511	0.3740	0.1837	0.0604	0.0633	-0.0015
Ragay Gulf	0.2534	-0.2421	-0.0403	-0.0012	-0.4370	0.0504
Southeast Luzon	0.0582	0.0784	-0.1573	0.1865	0.1465	0.1260
Southern Mindanao	-0.0423	0.0833	-0.0933	0.0547	-0.0390	-0.0157
Southern Palawan	-0.3831	-0.1006	0.1145	-0.0188	-0.0589	-0.1814
South Panay	-0.2480	0.0492	-0.0932	0.0004	-0.0599	-0.0748
Sulu Sea Islands	-0.1944	0.1366	-0.2921	0.1369	0.0255	-0.0251
Southwest Luzon	0.0721	0.0827	0.0788	-0.2651	-0.0451	-0.0065
Southwest Mindanao	-0.2772	-0.0261	-0.0886	0.0193	0.0746	0.1121
Verde Islands	0.1582	0.1664	-0.2603	0.0184	-0.0675	-0.0613
Western Luzon	0.1087	0.0792	0.1798	0.0789	0.0753	0.0056
Western Negros	0.2386	-0.1318	0.2151	0.1286	-0.0244	0.0036
Western Palawan	-0.0521	0.0348	0.0264	-0.1628	-0.0028	0.1169
Samar	-0.2774	-0.1638	0.0944	-0.0603	0.0027	-0.0453
Variance explained (%)	34.02	22.63	16.61	10.58	8.93	4.32

Table 4.1b Unit loadings for the various geographic units and axes of the principal components analysis. The PCA was based on frequency of occurrence of *Clypeomorus*.

	PC Axis					
Geographical unit	1	2	3	4	5	6
Calamian Islands	0.0744	-0.0018	0.1567	-0.1297	0.0950	-0.0334
East Cebu	-0.0188	-0.1845	-0.0364	-0.0790	0.0190	0.0056
East Luzon	0.8900	-0.0080	-0.1072	0.0323	-0.0083	-0.0451
East Palawan	0.0413	0.1140	-0.0430	0.0683	0.1727	0.3501
Eastern Samar	0.0235	-0.3116	0.2086	0.0967	-0.0325	0.0165
North Luzon	-0.1289	0.2636	-0.0184	0.0881	-0.1576	-0.0321
Northwest Luzon	-0.1339	0.3712	-0.0791	0.1861	0.0028	-0.0185
Southeast Luzon	0.0168	0.0219	-0.2083	0.0639	-0.1331	-0.0683
South Panay	-0.1160	0.1212	0.0902	-0.1938	0.1130	0.0105
Sulu Sea Islands	-0.2235	-0.3479	0.0091	0.2593	-0.0634	0.0514
Southwest Bohol	-0.2038	-0.0844	-0.1775	0.0407	0.2829	-0.2258
Tayabas Bay	-0.1256	0.1411	0.2131	-0.0448	-0.0883	-0.0532
Verde Islands	-0.1770	-0.1325	-0.2867	-0.3067	-0.1495	0.0814
Western Luzon	0.0817	0.0379	0.2789	-0.0815	-0.0528	-0.039
Variance explained (%)	35.11	18.85	13.35	10.38	7.51	6.95

Table 4.1c Unit loadings for the various geographic units and axes of the principal components analysis. The PCA was based on frequency of occurrence of selected species of Muricidae.

	PC Axis					
Geographical unit	1	2	3	4	5	6
Batanes Islands	-1.5154	0.0893	0.0250	0.0621	0.0384	0.0423
Calamian Islands	0.1045	-0.1336	-0.0543	-0.0424	0.0694	-0.2325
Camiguin	0.0955	0.1602	-0.0166	0.0200	-0.0138	-0.1423
East Cebu	0.0534	0.3328	-0.7569	-0.4196	-0.0062	0.3133
Davao	0.1598	0.4203	0.5430	-0.3530	0.5479	0.2496
East Luzon	0.1194	0.0576	0.1395	-0.0197	-0.3183	0.1647
East Mindanao	0.1211	0.1042	0.1227	-0.0309	-0.2919	0.1312
East Palawan	0.0955	0.1602	-0.0166	0.0200	-0.0138	-0.1423
East Samar	0.1210	0.1577	-0.0185	0.2093	0.0148	0.0230
Masbate	0.1330	0.0578	-0.1090	0.3212	0.1702	0.0271
North Luzon	-0.0213	-0.7400	-0.1850	-0.2524	0.3848	-0.2527
North Panay	-0.0482	0.1427	0.0139	0.0220	-0.0457	-0.1218
Northwest Luzon	-0.0328	-0.0421	0.0725	-0.1013	-0.1065	-0.1714
Southeast Luzon	0.0996	0.1436	0.0249	-0.0160	-0.0713	-0.1311
Sibuyan Sea Islands	0.0940	0.1530	0.0361	0.0244	-0.0967	-0.0774
Southern Palawan	-0.0515	0.0890	0.0835	0.0376	-0.1550	-0.0234
South Panay	0.1030	-0.1407	-0.0016	-0.0380	-0.0135	-0.1676
Sulu Sea Islands	0.1670	-0.1377	-0.1676	0.6448	0.3013	0.2633
Southwest Mindanao	0.0955	0.1602	-0.0166	0.0200	-0.0138	-0.1423
Verde Islands	0.0124	-0.8890	0.1669	-0.1193	-0.1757	0.3746
Western Luzon	0.0946	-0.1455	0.1149	0.0110	-0.2046	0.0158
Variance explained (%)	27.77	21.18	11.52	10.72	9.85	7.01

Table 4.1d Unit loadings for the various geographic units and axes of the principal components analysis. The PCA was based on frequency of occurrence of selected species of Littorinidae.

Taxon	Axis								
	1			2			3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
OGU: N = 23									
Clypeomorus									
Wet season	0.107	0.011	0.046	0.368	0.135	0.312	0.128	0.016	0.138
Island	-0.379	0.144	-0.291	-0.197	0.039	-0.090	-0.049	0.002	0.011
Cyclones	-0.022	0	0.088	-0.058	0.003	-0.026	0.439	0.193	0.403
Rainfall	-0.318	0.101	-0.207	0.148	0.022	0.016	0.103	0.011	-0.024
Tide	-0.193	0.037	-0.119	**-0.544**	0.296	-0.334	-0.118	0.014	-0.111
Latitude	**0.494**	0.244	0.301	0.402	0.162	0.222	0.417	0.174	0.214
Reef	**-0.493**	0.243	-0.362	-0.067	0.004	0.069	-0.094	0.009	-0.028
Embayment	-0.422	0.178	-0.436	0.172	0.030	0.097	-0.096	0.009	-0.024
Complexity	-0.332	0.11	-0.328	0.080	0.006	0.162	-0.295	0.087	-0.138
OGU: N = 21									
Littorinidae									
Cyclones	-0.349	0.122	0.226	0.085	0.007	0.105	0.293	0.086	0.017
SST	0.336	0.113	-0.102	0.004	0	0.082	-0.012	0	-0.073
Latitude	**-0.451**	0.204	0.140	-0.370	0.137	-0.072	0.186	0.035	-0.092
OGU: N = 14									
Muricidae									
SST	0.220	0.048	0.179	**0.559**	0.312	0.380	-0.261	0.068	-0.201
Tide	**0.493**	0.243	0.221	0.167	0.028	0.088	-0.073	0.005	-0.177
OGU: N = 18									
Nerita									
Island	0.107	0.011	0.120	-0.409	0.168	-0.322	0.135	0.018	0.083
Rainfall	0.396	0.157	0.112	-0.334	0.112	-0.401	0.167	0.028	0.151
Dry season	-0.233	0.054	-0.201	0.298	0.089	0.330	**-0.543**	0.295	-0.410
Wet season	-0.347	0.120	-0.296	0.003	0	0.031	**-0.455**	0.207	-0.187
Longitude	0.122	0.015	0.144	**-0.600**	0.360	-0.420	0.400	0.160	0.289

Table 4.1e Pearson (r) and Kendall (tau) correlations of Philippine rocky shore gastropod assemblages found in OGUs. Figures in bold represent significant correlations that are shown as vectors in PCA plots.

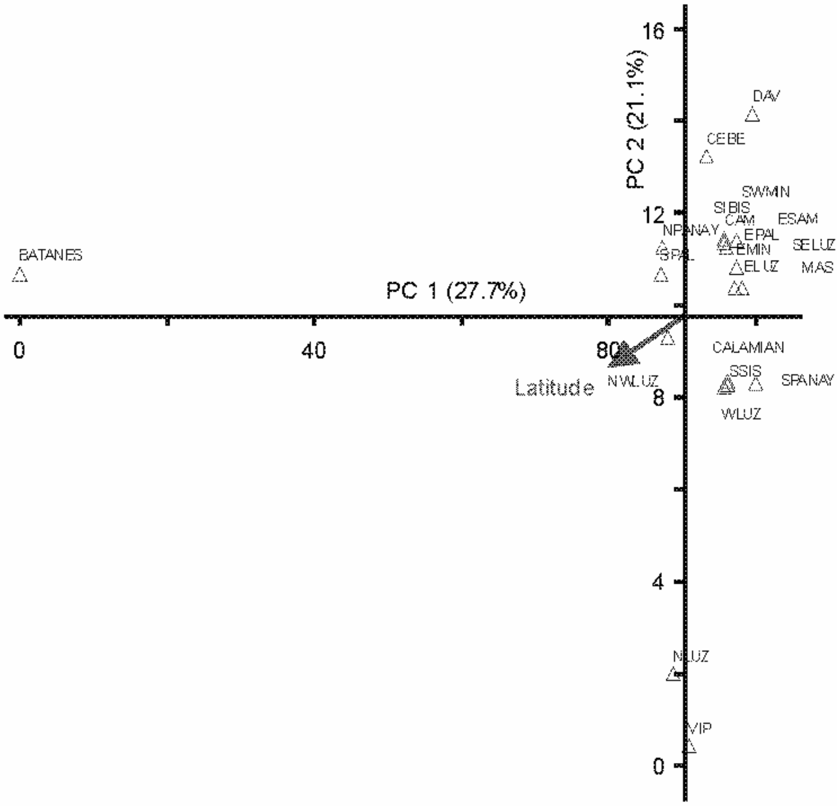


Figure 4.2 PCA bi-plot of macroecological variables
on geographic regions with intertidal and shallow subtidal
Littorinidae assemblages in the Philippines

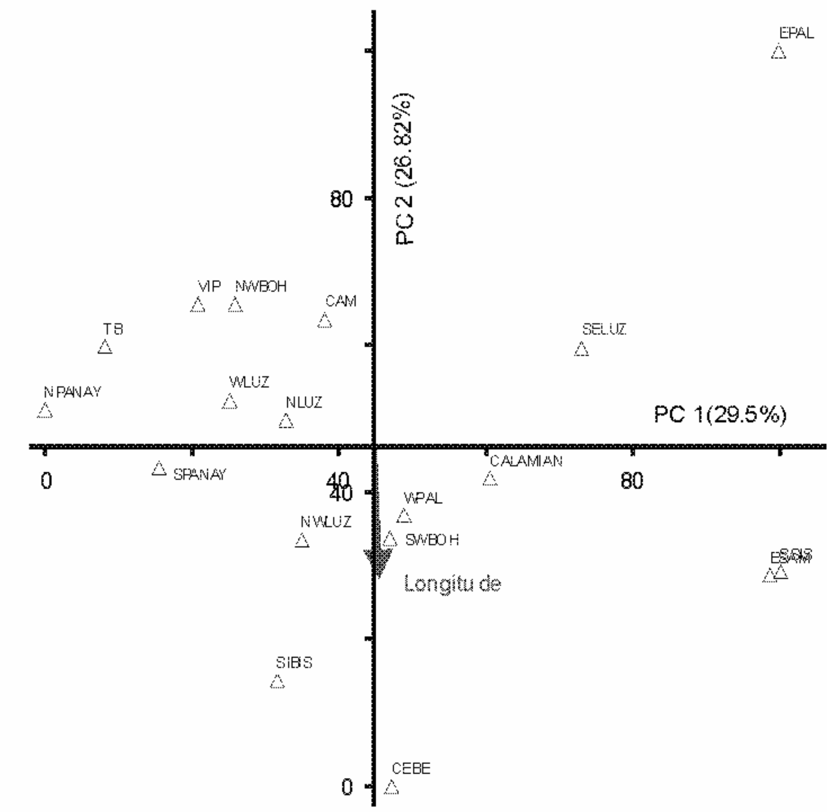


Figure 4.3a. PCA bi-plot of macroecological variables on geographic regions with *Nerita* assemblages in the Philippines

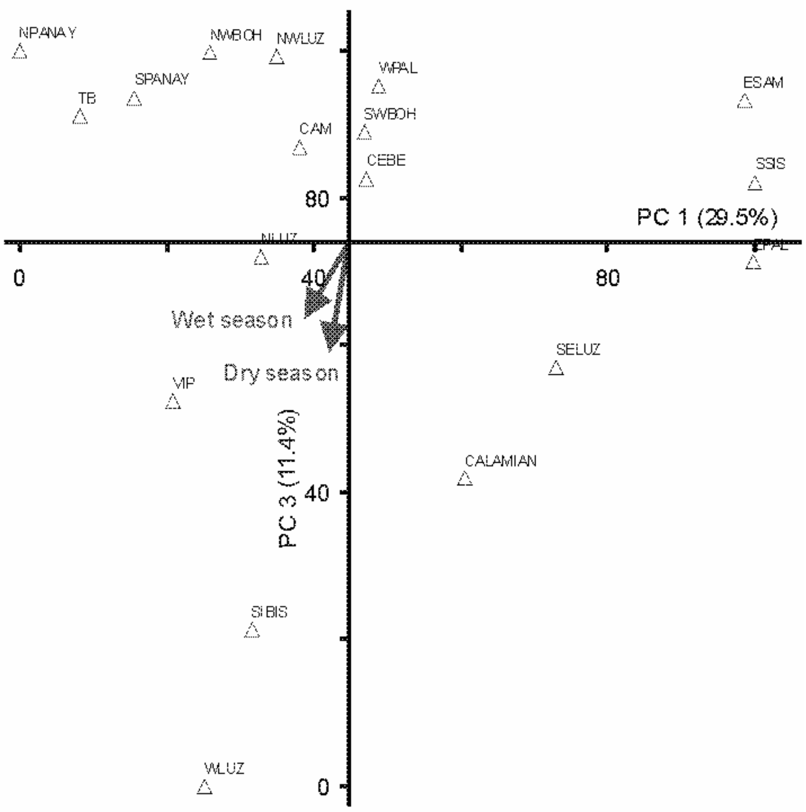


Figure 4.3b. PCA PC 1 and PC 3 bi-plot of macroecological variables on geographic regions with *Nerita* assemblages in the Philippines.

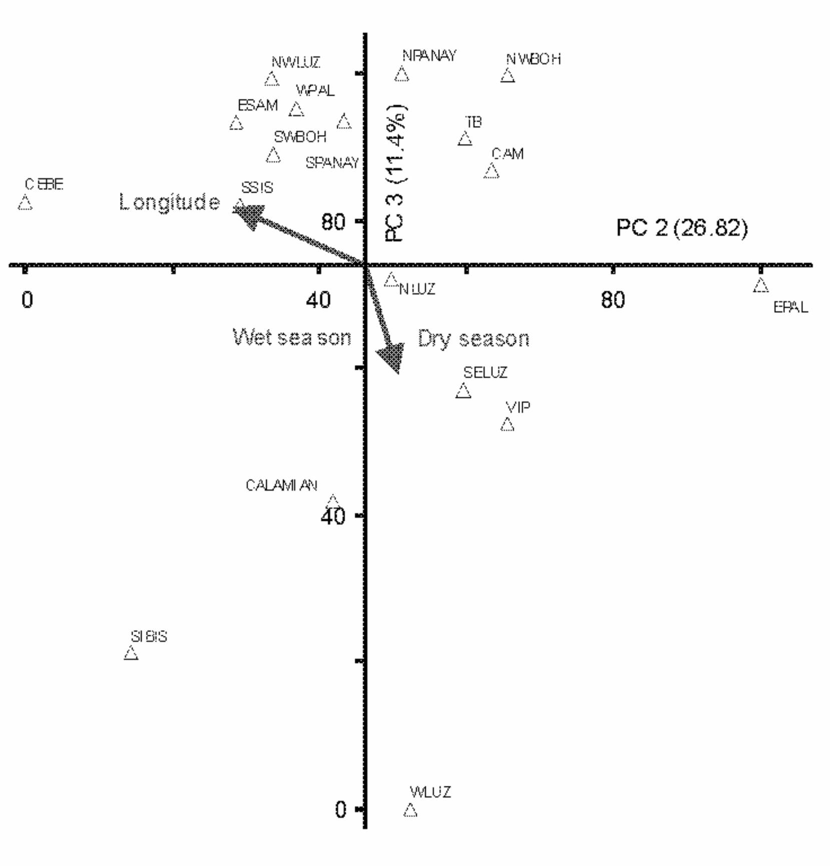


Figure 4.3c PCA PC 2 and PC 3 bi-plot of macroecological variables on geographic regions with *Nerita* assemblages in the Philippines

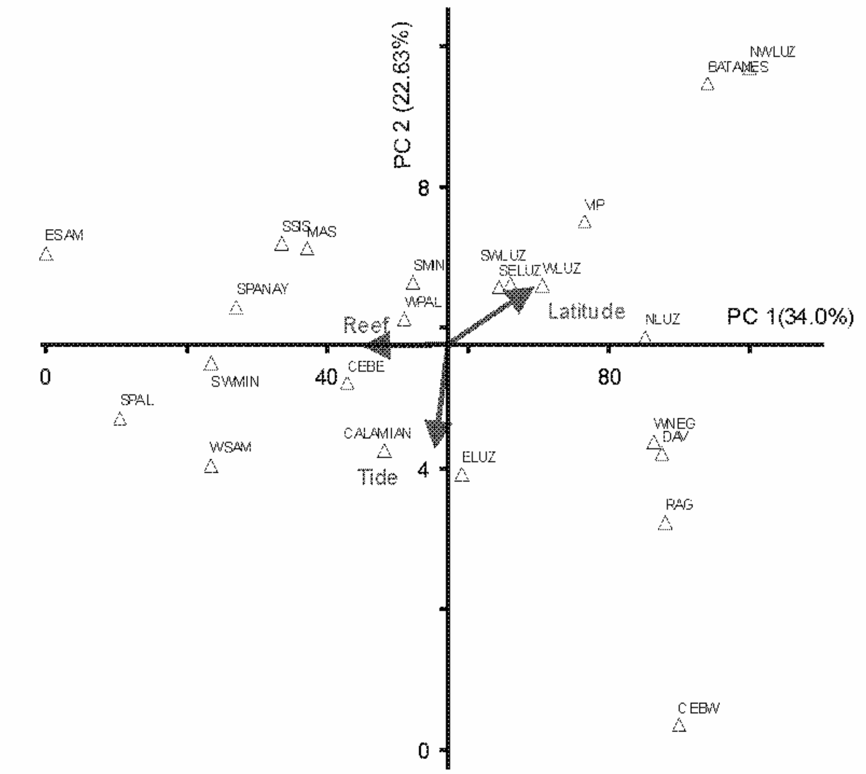


Figure 4.4 PCA bi-plot of macroecological variables on geographic regions with intertidal and shallow subtidal *Clypeomorus* assemblages in
of the Philippines

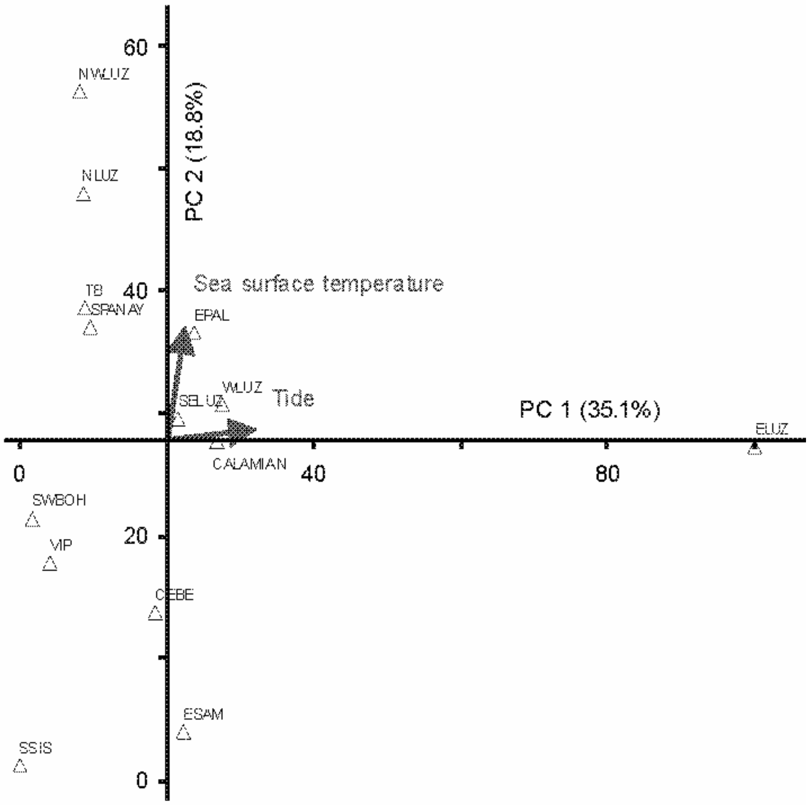


Figure 4.5 PCA bi-plot of macroecological variables on geographic regions with intertidal and shallow subtidal Muricidae assemblages in the Philippines

4.4.2.2 Correlation of species richness and ecological factors (Table 4.1f)

Correlation analysis suggests that area, tides, cyclone frequency and rainfall are significant correlates ($P<0.05$) of species richness of Littorinidae and *Clypeomorus*. In *Nerita*, significant correlates of species richness are area ($P <0.01$), coastal complexity and coral reef distribution ($P<0.05$). In Muricidae, only area has a significant correlation with species richness ($P<0.05$).

	Eecological factor												
Taxon	**Area**	**Lat**	**Long**	**Tide**	**Temperature**	**Cyclones**	**Rainfall**	**Dry season**	**Wet season**	**Island**	**Reef**	**Embayment**	**Complexity**
Clypeomorus	*0.586	0.113	-0.384	-0.448	-0.221	-0.023	*-0.503	0.429	0.479	-0.432	-0.261	-0.212	-0.110
Littorinidae	*0.555	0.370	0.080	-0.363	-0.457	*0.497	0.278	-0.218	0.069	0.183	0.066	-0.106	-0.106
Muricidae	**0.576	0.387	-0.330	0.339	-0.339	0.350	-0.255	0.341	0.241	0.265	0.324	0.241	0.354
Nerita	**0.590	*0.523	0.243	-0.081	-0.319	0.188	-0.383	0.050	0.050	-0.095	*-0.588	*-0.520	*-0.567

Table 4.1f. Pearson correlation co-efficients of ecological factors with species richness of Philippine rocky shore gastropods.
*significant at ($P<0.05$) ** significant at ($P<0.01$)

Group	*Linear*	*Polygonal*	*Percent linear*
By trophic class			
Herbivores	2	29	6.45
Carnivores	14	34	29.1
By taxon			
Clypeomorus	0	8	0
Littorinidae	0	8	0
Nerita	2	13	13
Muricidae	3	12	20

Group	*E-W*	*N-S*	*Percent E-W*
By trophic class			
Herbivores	2	29	6.45
Carnivores	5	40	11.1
By taxon			
Clypeomorus	0	8	0
Littorinidae	0	8	0
Nerita	2	13	13
Muricidae	2	13	13
Total	8	69	

Table 4.2 Summary of range shape and orientation of Philippine rocky shore gastropods.

Taxon	**Number of observations**	**R square**	**P value**
Clypeomorus	11	0.86	0.0007***
Littorinidae	11	0.79	0.0175*
Muricidae	15	0.63	0.0003***
Nerita	14	0.53	0.0030**

Table 4.3 Results of linear regression analysis of frequency of occurrence versus range size in Philippine rocky shore gastropods.

***significant at (P<0.001)

** significant at (P<0.01)

* significant at (P<0.05)

	Clypeomorus						
Basin	Area	SR	C	z	P	H	Sites
Philippine Sea	1294.08	7	0.15	0.56	1.08	0.93	42
Visayan Sea	868.22	8	0.002	1.76	3.80	0.26	48
Sibuyan Sea	751.12	7	0.13	0.69	1.18	0.85	49
Sulu Sea	550.05	6	2.36	0.14	0.66	1.52	70
South China Sea	418.38	8	1.51	0.80	1.23	0.81	61
Philippines	3812.91	13	0.40	0.44	1.00	1.00	270
	Littorinidae						
	Area	SD	C	Z	P	H	Sites
Philippine Sea	561.92	15	0.38	0.11	0.70	1.42	19
Visayan Sea	443.10	3	0.38	1.14	1.89	0.53	91
Sibuyan Sea	693.73	15	1.81	0.60	1.19	0.84	64
Sulu Sea	524.67	11	0.18	0.15	0.73	1.38	47
South China Sea	692.83	7	0.18	0.63	1.24	0.81	31
Philippines	2916.25	15	0.74	0.37	1.00	1.00	252
	Nerita						
	Area	SD	C	Z	P	H	Sites
Philippine Sea	1203.43	8	0.30	0.46	1.00	1.00	35
Visayan Sea	671.33	5	0.29	0.54	1.05	0.95	25
Sibuyan Sea	912.18	7	0.26	0.61	1.16	0.86	25
Sulu Sea	560.32	9	1.06	0.26	0.78	1.28	61
South China Sea	723.48	7	0.08	0.75	1.32	0.76	54
Philippines	4070.74	13	0.55	0.40	1.00	1.00	200
	Muricidae						
	Area	SD	C	Z	P	H	Sites
Philippine Sea	877.08	9	0.01	1.12	1.83	0.55	27
Visayan Sea	404.52	6	0.31	1.07	1.52	0.66	15
Sibuyan Sea	268.56	4	0.51	1.47	2.02	0.50	20
Sulu Sea	442.05	8	0.19	0.82	1.21	0.82	48
South China Sea	767.8	10	1.97	0.17	0.66	1.52	28
Philippines	2684.67	15	0.29	0.49	1.00	1.00	138

Table 4.4 Area (km^2), number of sites, species richness (SR), c and z parameters and provinciality (P) and homogeneity (H) estimates for four rocky shore gastropod taxa in the Philippine oceanic basins.

4.4.3 Shape, size and characteristics of ranges

Figure 4.7 shows the shape, size and characteristics of the ranges of gastropods studied. Ranges can be characterised as linear or polygonal. The graph has four quadrants. Reading the graph clockwise from 12:00, distributions with a primarily N-S distribution are plotted above the diagonal in the 4th quadrant. Species with narrow and short ranges are linear, while those with long and wide ranges are polygonal in the Philippines case, usually triangular.

Carnivorous taxa tend to have a greater percentage of linear ranges than herbivorous taxa (Table 4.2) Twenty-nine percent of the intertidal rapanine muricid ranges are linear. Herbivorous taxa are characterised by large polygonal ranges with a north-south orientation. The majority of the ranges whether linear or polygonal have a typical N-S axis as a result of the geographical orientation of the islands. There are curved ranges with an E-W axis for Muricidae.

Regression analyses indicate a highly significant relationship between frequency of occurrence and range size in all taxa (Table 4.3). The distribution of range size and species number is skewed to the left (Figure 4.8).

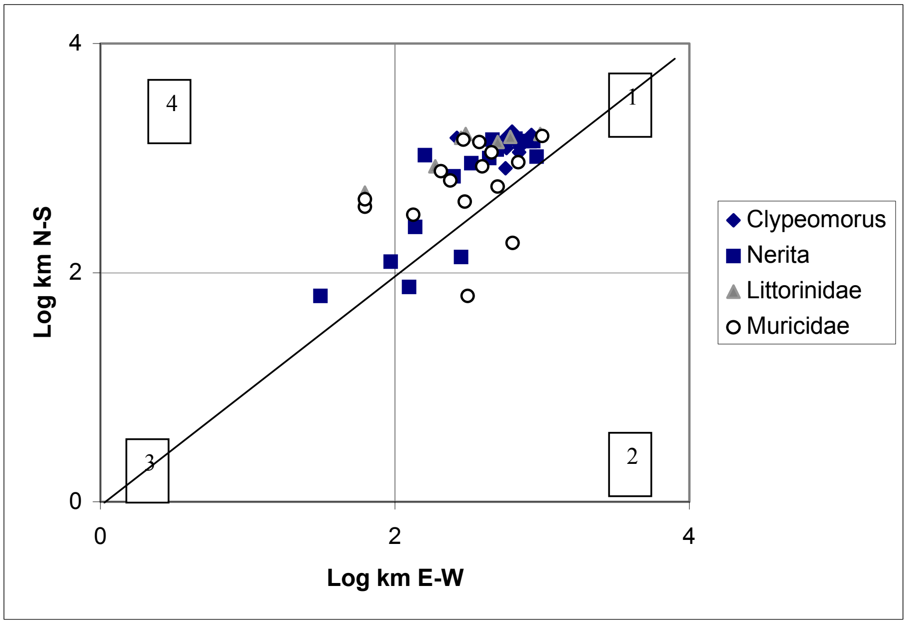


Figure 4.7. Shape of geographical ranges of rocky shore gastropods in the Philippines. A majority of distributions have a polygonal (triangular) N-S orientation. Points above the diagonal in the 4th quadrant are curved shaped with an N-S distribution.

4.4.5 Species-area Relationship: provinciality and homogeneity

Figures 4.9a-d and Table 4.4 show the results of the provinciality (geographic index of isolation and consequent faunal uniqueness) analyses, and the parameters of the species-area curves for the 4 taxa in each oceanic basin. Table 4.5 shows the results of the ANCOVA on basin species richness.

4.4.5.1 *Clypeomorus*: Figure 4.9a

Clypeomorus in the Visayas Sea, Sibuyan Sea and South China Sea have high levels (>1) of provinciality. Provinciality is an index of faunal uniqueness as a possible result of geographic isolation. A provinciality index of greater than 1 implies that the fauna is unique The Basin isolation effect on the z parameter of the species-area function and the covariate area are significant ($P<0.05$)

4.4.5.2 Littorinidae: Figure 4.9b

Littorinidae in the Visayas Sea, Sibuyan Sea and South China Sea show reasonably high levels of provinciality. The Basin isolation effect on the z parameter of the species-area function and the covariate area are significant ($P<0.05$)

4.4.5.3 Rapanine and ergalataxine Muricidae: Figure 4.9c

Muricidae in all the basins had high levels of provinciality, with the exception of the South China Sea. The Basin isolation effect on the z parameter of the species-area function and the covariate area are highly significant ($P<0.001$)

4.4.5.4 *Nerita*: Figure 4.9d

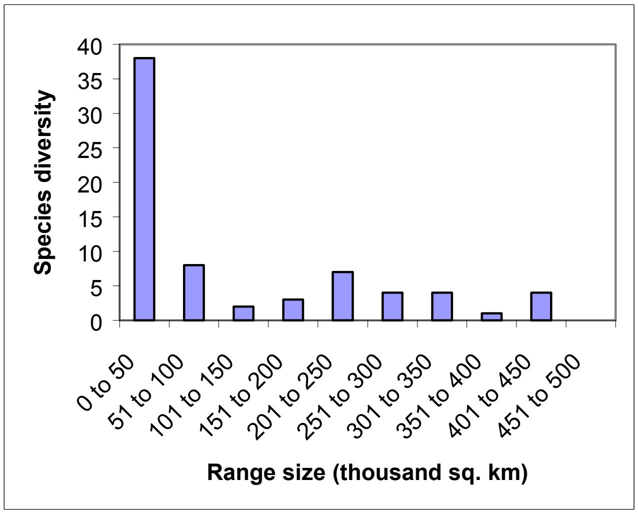
Nerita assemblages in the Sibuyan Sea, South China Sea and the Visayas Basin had lower levels of provinciality compared with the other taxa investigated. The Basin isolation effect on the z parameter of the species-area function and the covariate area are highly significant ($P<0.001$)

Taxon	**Factor**	P from ANCOVA
Clypeomorus	Area	0.012*
	Basin	0.050*
Littorinidae	Area	0.030*
	Basin	0.020*
Muricidae	Area	0.001***
	Basin	0.019*
Nerita	Area	0.000***
	Basin	0.130

Table 4.5 Comparisons of the effects of basin isolation and coastal area of the basins on species richness of Philippine rocky intertidal gastropod taxa. Coastal area is used as a covariate.

*significant at (P<0.05)
***significant at (P<0.001)

a)



b)

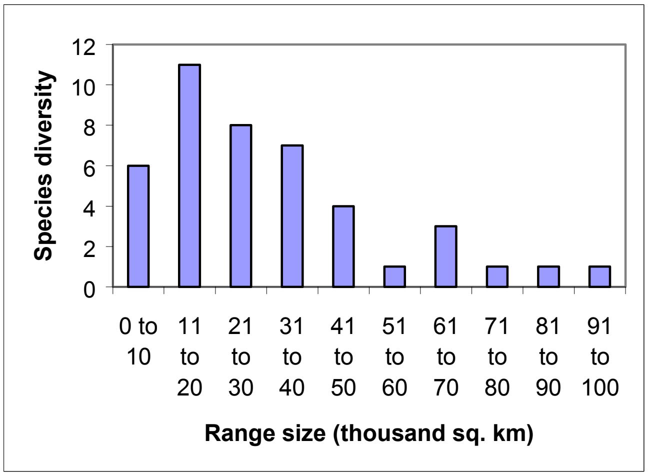


Figure 4.8. Range size frequency distribution and species number of Philippine rocky shore gastropods. a) all range size classes, b) range size classes less than 100,000 sq. km.

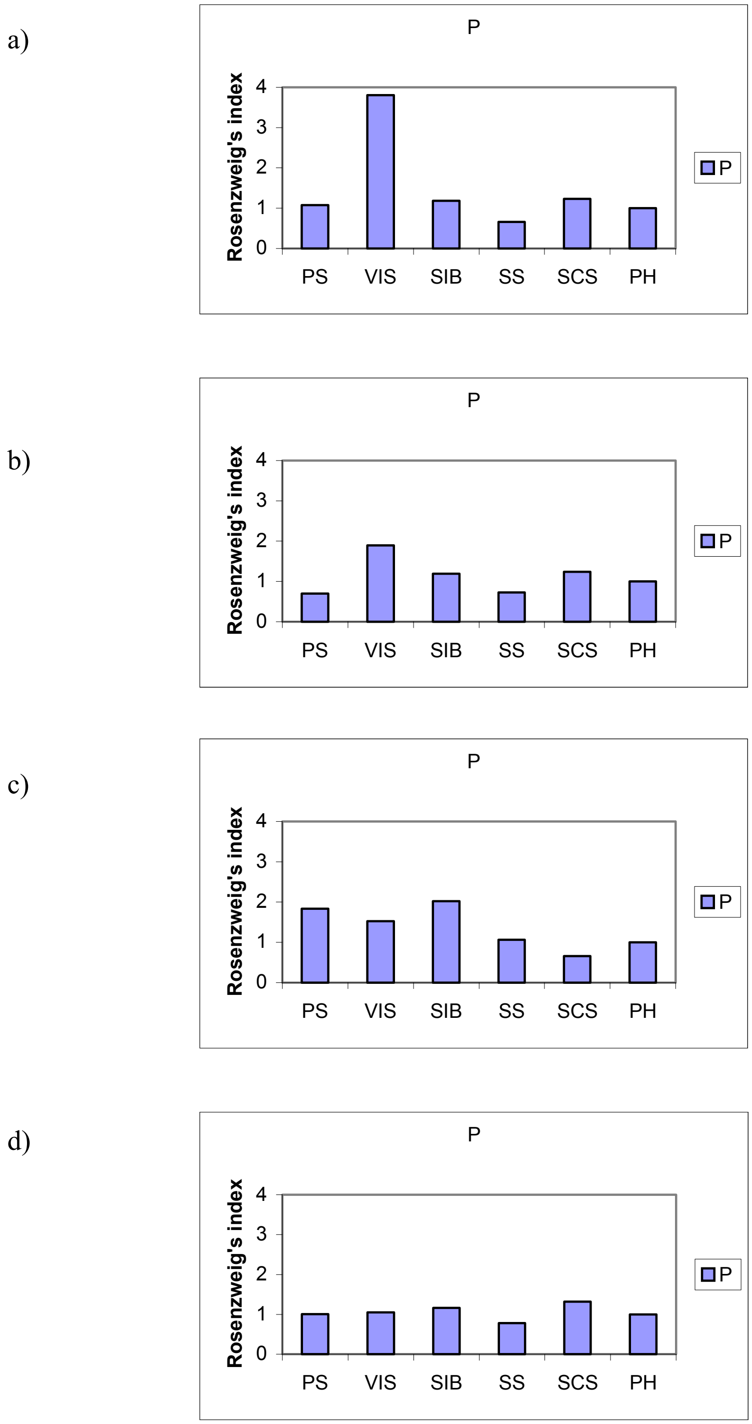


Figure 4.9. Provinciality (P) graphs for a) *Clypeomorus*, b) Littornidae, c) Muricidae and d) *Nerita* from the Philippine marginal ocean basins.

4.6 DISCUSSION

4.6.1 *The modern pattern of distribution: ecological correlates and species richness*

The archipelagic setting of the Philippines presents special challenges for interpreting distribution of shallow water marine biota. As a physical geographic unit, the archipelago is shaped like a triangle, with a predominantly N-S axis. The similarly complex and larger archipelago, Indonesia, has an E-W axis, and straddles the equator. Thus, while the Philippines lies wholly in the tropics, great climate variability on a local scale is often observed, and is the basis for climate-based classification. This variability in climate is a result of the orientation of the islands towards the prevailing climate system, the rain-bearing monsoon.

Rainfall and the presence of a wet season are major correlates of species occurrence and occurrence frequencies of *Nerita*. Rainfall is determined by the longitudinal distribution of the island landforms that determine local climate types (DENR and UNEP 1997). *Clypeomorus* species occurrences are significantly negatively correlated with rainfall. *Clypeomorus* occurrences are also negatively correlated with reef presence, embayment, coastal complexity, island, sea surface temperature and longitude. Thus, the whole suite of assemblages in this taxon may have similar habitat requirements to upper shore dwelling *Nerita* and Littorinidae. The presence of reefs, embayments and high coastal complexity equate to heterogenous habitats that may not favour the occurrence of *Clypeomorus*. Perhaps competition from other species may exclude them from such areas. The distribution of the intertidal Muricidae may be related to the presence of its prey items, such as oysters and bivalves. The distribution of these prey items may be correlated to sea surface temperature (Vermeij 1990). The presence of coral reefs is an important determinant of gastropod occurrence in the intertidal. Coral reefs are common in the central Philippines. These islands provide a large number of habitats suited for colonisation of intertidal taxa.

In this study, the geographical distribution of tidal amplitudes was an important correlate of the distribution of the Muricidae and *Clypeomorus*. Higher tidal amplitudes correlate positively with occurrence and occurrence frequencies of

Muricidae. Higher tidal amplitudes correlate negatively with *Clypeomorus* occurrence and occurrence frequencies (Table 4.1f) This result was not expected for the Philippines, where tidal amplitude is small (< 1 m). Exposure to prevailing winds and cyclones were expected to be major correlates of gastropod occurrence. It is likely that the tidal regime is a significant factor in determining local zonation. This has been observed in similar oceanic island environments in Bermuda (Thomas 1985). It is possible that the distribution of prey items of Muricidae may be determined in large part by tidal amplitudes. For the herbivorous, rock and sandy-rock substrate dwelling, *Clypeomorus*, tidal amplitude may not be significant in determining the distribution of its food items.

Latitudinal correlates of distribution have not been given much attention by earlier Philippine biogeographers. Dickerson (1927) and Springsteen and Leobrera (1986) state that the Philippines is “climatically insulated”. Thus the low variation in sea surface temperatures were thought to preclude the existence of climatically defined marine faunal and floristic assemblages. The whole country can be classified as tropical, with very little variation in species assemblages. However, Cordero (1977), based on a study of the geographic ranges of red algae, proposed that a temperate and subtropical marine floristic province occurs in northern Luzon. It is of interest that in the intertidal taxa in this study, *Clypeomorus*, *Nerita*, *Cypraea*, and Muricidae, have endemics mainly found in the central Philippines.

Environmental correlates of species richness show a consistent pattern. Coastal area is the major correlate of occurrence of each taxon. This is consistent with the hypothesis that larger coastal areas support larger populations. These populations in turn have lower extinction probability (Macarthur and Wilson 1967). Other significant ecological correlates are monsoon climates, cyclones, and rainfall. Coastal complexity and coral reef distributions show significant negative correlations with distribution of *Nerita*. A majority of rocky shore *Nerita*, with the exception of members of the *Linnerita* clade and one member of the *N. chamaeleon* clade, avoid reefal environments. The positive correlation between cyclone frequency and species richness of Littorinidae suggests that shore exposure and rainfall favour this taxon. In *Clypeomorus*, the significant negative correlation of frequency of occurrence with rainfall suggests that the taxon does not tolerate changes in salinities caused by the monsoon climate. The fact that distibution of Muricidae does not correlate significantly with any ecological factors investigated suggests that other factors such as the distribution of prey or life history adaptations may be better predictors of species richness.

Further research is necessary to determine if there are distinct biogeographic breaks in the Philippines, determined by latitude and climate. Increased sampling and surveys in northern Luzon may determine disjunct distributions. Longitudinal correlates of distribution are however well known. These correlates allow for the division of the country into two major marine biotic provinces, the South China Sea and the Philippine Sea provinces. Analysis of seagrass assemblages and distributions support this delineation (Fortes 1986). This biogeographical division is due to the longitudinal distribution of tides, rainfall and the prevailing monsoon driven current system (DENR and UNEP 1997). This is further evidenced by the significant negative correlations of climate factors with longitude (Table 4.5)

4.6.2 *Distribution and ranges*

Basin isolation predicts that the high species richness in the Philippines is due to the overlapping of narrow species ranges. A characteristic narrow distribution range is the “curved” distribution (Figures 4.1a-h). This distribution is common near the western edges of oceanic basins. Such distributions are often associated with boundary currents such as the Kuroshio and the Gulf Stream in the northern hemisphere, and the eastern Australian current in the southern hemisphere. These boundary currents originate from tropical waters, and are thus warm. This enables the range extensions of warm-water taxa such as butterfly fish into regions in which otherwise they would not exist (Allen et al. 1998).

Curved distributions are a property of the geographical orientation of the Philippine archipelago. The majority of the 50 distribution ranges examined in this study had a characteristic N-S axis, co-incident with the orientation of the islands and ocean currents. A few had a polygonal E-W axis, while none had a curved E-W axis. A curved distribution with an E-W axis is usually limited by temperature, and is most apparent when one approaches the Polar Regions. In the tropics, where temperature differences are minimal, this kind of distribution is rare, and the common case is a curved N-S axis, a range coincident with the ocean's western margin and strong boundary currents.

This study has shown that curved distributions occur in the Philippines. These distributions are likely to be determined and maintained by regional oceanographic, climatic or ecological factors and geologic history. Among these factors are the strong monsoon seasons that affected the ordination analyses (Uychiaoco et al. 1992). The monsoon, which is known to force reversing current systems in Southeast Asia and the Indian Ocean, is believed to be an important determinant of the structure of shallow water marine assemblages important to fisheries (Sharp 1996). While Philippine regional oceanography is poorly described, it is likely that at the archipelagic scale, regional oceanographic factors are the main determinants of species distribution, at least in species with weak to moderate capacity for planktonic dispersal.

In an ecological context, the carnivorous intertidal taxa tend to have a greater percentage of narrow linear and curved distributions. The rapanine and ergalataxine muricids are the dominant molluscan carnivorous taxa on the mid to high intertidal of rocky shores. Their life history strategy favours rapid dispersal in the plankton, with long planktonic stages (Middlefart 1997a). Thus it may be inferred that their potential to occupy the widest possible range of habitats in the Philippines is great. However, only three of the 15 species of intertidal muricids in this study have wide ranging polygonal distributions. The distributions imply ecological limitations that may reflect the distribution of favoured prey items.

The hypothesis that prey items may be a major determinant of the distribution of carnivorous gastropods is supported by the observation that the principal prey items of most rapanine and ergalataxine muricids are suspension feeding bivalves characteristic of continental and high island rocky shores. The distribution of these bivalves is correlated with primary productivity (Vermeij 1990) and estuarine conditions that are affected by the monsoons (Wyrtki 1961). Thus, it may be hypothesised that the distribution of these bivalves will show a north-south orientated and curved distribution, since the islands are situated along this geographical axis. This hypothesis may be tested in the future, by plotting the distribution of bivalves in the Philippines.

Generally, herbivorous taxa, the Littorinidae*,* *Nerita* and *Clypeomorus*, have large, wide polygonal (triangular) distributions, with only a few curved linear ranges belonging to ecologically specialised species. This possibly implies a larger capacity of herbivorous taxa to disperse and occupy suitable habitats. Such taxa may only be limited by their tolerance to ecological factors. However, several members of these taxa have small curved or polygonal ranges. These may represent relict distributions, e.g. *Nerita exuvia,* that has a disjunct northern and southern range. *Nerita antiquata* is part of the *Linnerita* clade (Vermeij 1984). Its phylogenetic relationship with the type species *Nerita (Linnerita) polita* is not fully known. However its restricted distribution, and rather primitive shell and aperture features, would suggest that this species is a relict. *Clypeomorus adunca* is a Philippine endemic and may represent an adaptive radiation to coralline substrates, rather than it being a relict (Houbrick 1985). The high-shore Littorinidae, such as *Echininus*, are found only in a few islands in the central Philippines, and very rarely on the shores of large islands. These littorinids are ovoviviparous. This may account for their historical and present rarity (Reid and Geller 1997)**.** Their apparent ecological specialisation on uplifted coral atolls and karstic limestones may explain their absence on the volcanic high islands of the Philippines. In the central Pacific, ovoviviparity has not precluded colonisation over a 6300 km distance (Reid and Geller 1997). It is likely that the species island hopped over coral atolls now submerged, rather than drifted to these widely separated atolls by chance. Another littorinid, *Littoraria coccinea* is widely distributed throughout the Pacific, but is an ecological specialist, being found only on uplifted, highly exposed coral islands.

Curved ranges are a common pattern in shallow water marine biota in the western Indo-Pacific. These distributions closely follow the direction of western boundary ocean currents. In the Philippines, such distributions may follow the margins of oceanic basins and the distribution of the islands within the basins. However the direction of this curvature is opposite to the curve direction of the IWP arcuate distribution that McManus described. The causes of this difference are unclear.

However, curved ranges within the Philippines may demonstrate that geographical ecological factors are significant in determining the distributional limits of marine species within the country, even though these species have otherwise large ranges in the IWP. Ecologically specialised taxa tend to exhibit curved ranges. The maintenance and persistence of these ranges need to be further examined.

4.6.4 *Species-area relationships: provinciality and homogeneity*

The aim here was to infer similarities of faunal assemblages in the marginal oceanic basins. Such similarities (or differences) are a function of the species ranges. The usefulness of this approach is apparent when comparing species diversities over geographic regions. The major limitation of the approach is that it often does not take into account the effect of habitat heterogeneity on distribution, but is based simply on total area occupied by the species. This approach is an ecological approximation, since it is highly difficult to factor out the effects of range area on habitat. The former is auto-correlated with the latter (Rosenzweig 1995).

Z describes the rate of increase in the number of species that occur as the area of the OGU sampled increases. If species are randomly distributed, and all occur in each site, then z will be zero, since there is no net accumulation of species as the OGU is sampled. If an area is devoid of species, then z will approach infinity. Species pools are dynamic and changing with speciation, extinction and the persistence of relicts. While it is difficult to experiment with species pools, natural events that result in isolation and re-connection of faunas change the nature of species pools and consequently the z parameter (McKinney 1998).

The varied species-area curves imply that the total species pool of the taxa in this study in the Philippines is not well mixed. That is, species do not have equal probabilities of being found in suitable communities (Maurer 1999). While truly well mixed species pools rarely occur in nature, well-mixed pools would imply that lottery-type community dynamics is responsible for geographic distributions, and this would therefore be random. This may account for the less tight SPAR predictions that were observed (Rosenzweig 1995).

The importance of this approach is emphasized when the individual species-area relationships of the basins are compared to the species-area relationship of the total Philippine fauna for any particular taxon. This approach is a conceptual experiment in which all the biogeographical barriers to distribution are removed.

If the fauna of a particular basin is homogenous with the total fauna, the z of the particular basin is similar to the z of the total fauna (Rosenzweig 1995). This implies that in terms of the species-area relationship, the basin is not a distinct unit isolated from the total area of the Philippines, but is a subset of that total area (Patterson 1986). If the basin fauna is provincial (that is, has a high index of geographic isolation and faunal uniqueness) relative to the rest of the Philippine fauna, this implies that the z estimate of the basin is different from the z of the total species-area relationship of the Philippines. The more the basins are evolutionarily independent, the higher the z of the total fauna. Evolutionary independence implies that faunal elements have minimal exchange (Rosenzweig 1995).

Rosenzweig's (1995) statement on evolutionary independence in provincial geographical units needs to be taken with a caveat. It is philosophically impossible (from the standpoint of earth history and modern oceanography) to consider the oceanic basins of the world to be completely isolated from each other. Rosenzweig (1995) states that marine provinces are inherently "leaky" because certain ocean currents (e.g. Antarctic circumpolar) to a large extent connect the provinces. Floral and faunal species can theoretically disperse if they have long pelagic larval stages. This caveat supports my position in the succeeding paragraph.

A comparison of species-area patterns in terrestrial ecological systems suggests that areas with high z and high provinciality values have been isolated in the past. However, in the context of the marine system, this isolation is confounded by genetic and recruitment connectivity, and thus the oceanic basins are not true analogues of terrestrial islands in the sense of the Theory of Island Biogeography (Macarthur and Wilson 1967). In this theory, islands derive their species purely from immigration. In terrestrial islands recruitment or immigration is mainly a function of distance from the source of recruits. This selects against organisms with low dispersal ability. In the marine system, connectivity may be largely a function of time that selects against species with short planktonic stages. Thus in many marine molluscs, natural selection has favoured those with long planktonic stages to have large ranges (Kohn and Perron 1994).

Basin isolation predicts that during sea level regressions, speciation will be enhanced. However, constant re-connection at different time scales may account for the low endemism of the total Philippine molluscan fauna, estimated at 3 to 5 percent (Springsteen and Leobrera 1986). Endemic species are largely recorded only from the central Philippines. Near endemics are recorded from adjacent ocean basins. Because the present isolation of marine provinces is mainly a function of the time of planktonic pre-competency and competency, the distances between the Philippine islands are not large enough to prevent dispersal for most planktotrophs. Hawaii is typical of a biotic province isolated by distance. Its fauna is derived from the western Pacific via the north equatorial current that moves eastward past Hawaii. Thus, a high degree of molluscan endemism is observed there among taxa with short planktonic pre-competency. Similarly, the Northern Mariana Islands have a significant degree of endemism in rocky shore molluscs (Vermeij 1987). The Philippines has a prevailing monsoon system. Thus the shore fauna tends to show a gradient in assemblages, with windward sides showing distinct assemblages from the leeward sides. Monsoonal effects are not constant throughout the archipelago. Some areas tend to be more exposed to the winter or summer monsoons (Dickerson, 1927).

Philippine rocky intertidal gastropods have low levels of endemism. Yet the Philippines has the highest species richness of gastropods of any tropical rocky shore assemblage in the world. What accounts for the high species richness of the Philippine shallow water marine biota? Is it that the archipelago “collects” species rather than generates them? Do the different oceanic basins serve as extinction refuges? If the archipelago collects species by serving as an extinction refuge, then this will be reflected in a low gastropod:bivalve ratio, since bivalves are believed to be less resistant to extinction than gastropods (Vermeij 1987). If the archipelago is a truly isolated biota, then the gastropod:bivalve ratio will be high, since there will be a higher extinction risk for the bivalve fauna (Paulay 1990). Paulay does not make inferences on gastropod extinction rates. The Philippines has a gastropod:bivalve ratio of 2:1, which is considered very low (Springsteen and Leobrera 1986). On the other hand, the two million-year-old, distance-isolated Hawaiian Archipelago, has a gastropod:bivalve ratio of 6:1 (Kay and Palumbi 1987). The Philippine ratio suggests that bivalves persisted through major extinction events that decimated species assemblages elsewhere. Extinction in bivalves during periods of low sea level is often due to habitat loss (Paulay 1990) associated with the regression of coral reef habitats. Only regions with suitable geomorphology provided refuges against such extinctions. Paulay (1990) argues that the western Pacific archipelagos were the refuges against extinction, and that the present Holocene bivalve fauna on Pacific islands is derived from the western Pacific.

While species accretion and speciation are not mutually exclusive phenomena, there is no evidence to suggest that under tropical conditions speciation rate is enhanced (Maurer 1999). However there is evidence that species survival and persistence are enhanced (Eldredge 1999). Archipelagos typically have overlapping distributions of marine taxa. This observation is supported by evidence from modelling studies (Patterson 1986) of extinction dynamics in areas that are geographically fragmented. These overlapping distributions, under a random assumption of equal extinction risk, imply that selective extinction and persistence of species may be responsible for the distribution patterns observed. Extinction risk in small islands is greater. While available habitat-area is the main correlate for these patterns, other ecological correlates may be responsible for maintenance of populations that eventually leads to extinction or persistence (Patterson 1986).

The oceanic basins of the Philippines may be viewed as an archipelago of “seas”. If geographic complexity is the insurance policy that covers for qualitative habitat loss and prevents mass extinction in this system during low sea levels, then the Philippines is an area where this hypothesis may be evaluated. The Pliocene to Pleistocene distribution of coral reefs in the country argues against complete loss of reef structures, with many reefs from this period uplifted as modern day coral islands (Romero and Zacher 1981) or submerged as marine terraces in the present interglacial. Areas in southern Cebu and Negros such as Sumilon Island were tectonically uplifted during the Pleistocene, and show evidence of reef development during low sea levels (White 1987). Pleistocene reef development is also observed in the Sulu Sea (Romero and Zacher 1981). Thus it can be argued that similar environments were present during low sea levels that may have served as refuges when extinction happened elsewhere in the Pacific.

Basin isolation predicts rapid speciation. However the evidence from the present ranges of gastropods suggests that the oceanic basins may have served more as extinction refuges than centres of speciation, due to the lack of endemism. This is not to discount totally the role of rapid speciation, for this is likely to happen under isolating conditions. McManus proposed his hypothesis on the basis of numerous species of deepwater fishes in the Sulu Sea basin, and the presence of endemic corals, that suggest that under lowered sea levels, rapid speciation occurred.

The paradoxical low endemism and high species richness has made tests of speciation hypotheses in the IWP problematic. The possible key to unravelling such hypotheses is to determine the phylogenetic histories of the endemics and the near endemics. If the endemic species have pleisomorphic characters, then these species are likely to be relicts. If these species have apomorphic or derived characters, then they are possibly new species. A correlation of these phylogenetic traits and geographical ranges would provide insights into speciation in the region.

Evidence suggests that gradients in allele diversity occur throughout the range of widely distributed taxa such as sea urchins and butterflyfish (Palumbi 1996; Palumbi 1997). These gradients may parallel species or genetic gradients, but both can serve as response variables to test the centre of origin and accumulation hypotheses in Pacific marine biogeography. Benzie (1998) argues that present day genetic evidence suggests peripheral Pacific basin speciation is most likely, rather than speciation in Southeast Asia. Speciation processes and genetic diversification operate at two different time scales. The influence of genetic changes and speciation on a wide geographical area is not fully understood (Palumbi 1994). The key to further examination of this lies in the mapping of calibrated molecular phylogenies over existing geographical range information.

Thus there are two models to account for the high species richness in the IWP region. I present two avenues for further research to test the centre of origin and collection (accumulation) hypotheses. Comparing phylogenetic histories of various taxa from within and bordering the basins could test the nature of speciation. A test of geographic heterochrony, wherein relict assemblages co-exist with modern assemblages occurring within the basins, tests the collection and persistence hypothesis (Petuch 1987). Unlike the centre of origin model, extinction is an integral element of this hypothesis. Geographical heterochrony is in line with Rosenzweig's (1995) predictions that at larger time scale, sink species in a high diversity system do not become extinct due to the presence of refugia where they can persist. Sink species are derived from other areas. Although not explicitly tested in this study, the presence of numerous disjunct occurrences of deepwater *Conus* within the Indo-Pacific centre of species diversity (Röckel *et al* 1995) suggest that relict assemblages have survived in this distribution centre.

Thus is the modern pattern of gastropod distribution, the high provinciality and high z values in the central Philippine basins may be due to differential extinction, survival and speciation as a result of basin isolation. These processes may also be brought upon by ecological factors that allow species to persist. A test of this, using the highly diverse coral shore neo-gastropod *Conus*, is presented in Chapter 5.

4.7 CONCLUSIONS

1. The major ecological correlates of frequency of occurrence are taxon-specific, with high intertidal assemblages affected primarily by the monsoon and its effects on climate and oceanography. Lower intertidal taxa (eg *Clypeomorus*) are correlated with presence of coastal habitats such as coral reefs. These observations tend to support the longitudinal or "East-West" separation of Philippine marine provinces.

2. Latitudinal correlates of frequency of occurrence of species suggest that temperate influences may affect the northern area of the Philippines. The degree of this influence needs to be further assessed through similar studies with other subtidal taxa.

3. Curved and overlapping distributions of gastropods may be observed. Members of the carnivorous taxon Muricidae often have curved distributions.

4. Species-area analysis suggests that gastropods in basins are isolated and show reasonably high levels of Rosenzweig's provinciality. However, the low endemism of gastropod taxa suggests that the provincial characteristics of the ocean basins in the archipelago are a result not of rapid speciation in the past, but of differential extinction and survival of many species.

CHAPTER 5

The biogeography of intertidal and shallow-water *Conus*: environmental heterogeneity and the basin isolation hypothesis

"*McManus' patterns stand in their own right, regardless of whether a suitable geological theory has been found to explain them.*"- B.R. Rosen (1988)

"However, available evidence from the Paleogene and especially Neogene radiations suggest that the strongly and stylishly shelled, Conus is a young, upwardly mobile and progressional genus, albeit at a snail's pace" – A.J. Kohn (1990)

This chapter describes the modern biogeography of Indo-West Pacific *Conus* in the Philippines. As the most species-rich coral reef gastropod genus, the taxon is used as a model to evaluate the basin isolation hypothesis. Modern ranges are examined to estimate potential influences of basin isolation in the Philippines.

5.1 INTRODUCTION

McManus (1985) proposed the basin isolation hypothesis to account for historical patterns of species diversity in Southeast Asia and the western Pacific. This hypothesis predicts that repeated isolation and reconnection of marginal oceanic basins in archipelagic environments as a result of sea level changes favoured rapid diversification and speciation in shallow water (0-30 m) marine biota.

Biogeographic evidence that supports this hypothesis has been both qualitative and phylogenetic. Phylogenetic patterns of species divergence in scleractinian corals and the possible presence of regional endemic species with restricted distribution support the hypothesis (Pandolfi 1992; Wallace 1997). Cluster analysis of presence and absence data has demonstrated dissimilarities in coral composition consistent with the geographical location of major oceanic basins in the Philippines. Cluster analysis, while intuitive and useful in detecting differences in faunal assemblages, does not

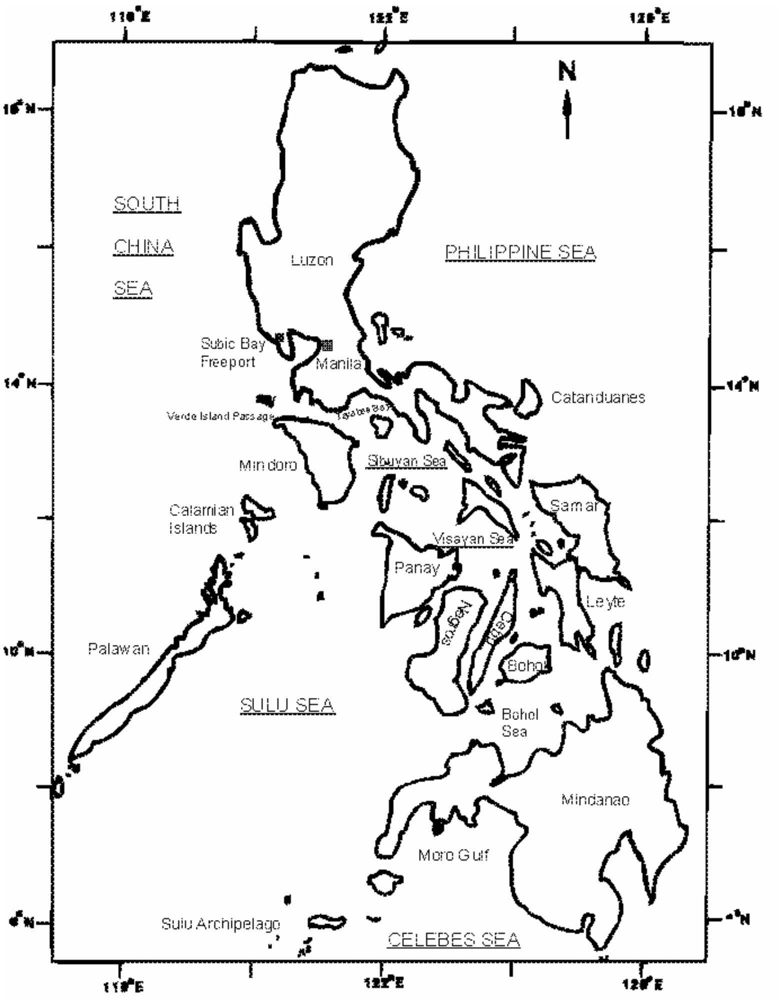


Figure 5.1 The Philippine archipelago. Marginal ocean basins are underlined.

usually account for ecological effects on a geographical scale (Hengeveld 1990).

As a result of its geological evolution, the Philippines is bordered by several oceanic basins, and encloses the Sulu Sea basin (Figure 5.1). These basins are bordered by regional island groups. With the exception of northern Palawan, the islands of the archipelago are of oceanic crustal origin, and have different geological ages. The oldest island is Luzon, where the northern terrane has evidence of Cretaceous to Paleocene volcanic activity (Karig 1983). Other islands dating back from this time include Marinduque and Cebu. The youngest island group is the Sulu Archipelago, which is likely of Tertiary origin (McCabe and Cole 1989).

The species-area curve, a fundamental construct of biogeography (McKinney 1998), is used to examine the nature of basin isolation in the Philippines. Species-area patterns can infer a variety of ecological processes across time and space, and are useful in comparing diversities between geographical regions or between taxa. Furthermore, species-area curves can be used to account for the effects of area on species richness, and thus enable inferences about the effects of other ecological factors on species number (Connor and McCoy 1979). This study uses the concept of biotic homogenisation (Rosenzweig, 1995) in quantitatively testing possible basin isolation in the Philippines. Biotic homogenisation is defined as the mixing of previously isolated biotas that often results in extinction of certain taxa. It is assumed that in an archipelagic environment without barriers to dispersion, or which did not experience historical basin isolation, the homogenisation index will be high, and species with wide ranging distributions are likely to colonise suitable environments over a wide area. Consequently regional endemics will be rare.

The neogastropod genus *Conus* is used here as the study taxon. The genus has an estimated 500 extant species, with 300 species of Indo-Pacific distribution. The Philippines has an estimated 172 species of shallow water *Conus* based on the primary and secondary material consulted in this thesis (Appendices 4, 5, 8). About 45% of the 300 Indo-Pacific species are found in coral reef associated intertidal environments. Many *Conus* species have a wide distributional range, and occupy distinct niches based on their prey items. Habitat characteristics are summarised in

Table 5.1a. The spatial patterns of species diversity observed in the genus are related to reproduction and development, and resource and habitat utilisation (Kohn 1997). In this study, ranges of *Conus* are examined to examine predictions of the basin isolation hypothesis.

5.2 MATERIAL

The selection of primary and secondary material, including maps, used in the biogeographic analysis was subject to criteria given in Chapter 1 of this thesis. The nature of material, sources and their locations are described in Chapter 3. For PC analyses for Philippine data, eighteen OGUs had *Conus* records (Appendices 2, 4), however only 14 OGUs had useful ecological information. These were the only ones used in PC analyses (Table 5.1a).

5.2.1 *Data limitations*

As *Conus* is a species-rich neogastropod genus, there is a possibility that the species number recorded here is an overestimate. Some species have been recorded only once, and their taxonomic validity may be in question. This may overestimate species number in each basin. Species that have been recorded only once, and whose taxonomic validity is in question, were thus not included in the analysis. Species identifications were validated using Röckel *et al* (1995) to increase taxonomic certainty (Table 5.1b).

Code	Geographical Regions	Physical features
CEBE	**Eastern Cebu and Mactan** (includes Olango island)	The coast is composed of low-lying coral limestone islands with an average elevation of 10 metres
EPAL	**Eastern Palawan** (From Calamianes to Balabac)	Embayed coastline. Extensive reef and mangrove development.
ESAM	**Eastern Samar** (Philippine Sea coast of Samar Island)	Narrow insular shelves and steep underwater drop-offs characterize coral reef shorelines
NPANAY	**Northern Panay** (Antique coastline including Sapian Bay)	Heavily embayed with extensive reef and mangrove areas.
NWLUZ	**Northwest Luzon** (Ilocos) (From Lingayen Gulf to Pagudpud, Ilocos Norte)	Embayed coastline fringed by narrow reefs with wide sandy beaches. Northernmost shorelines

		have little reef development
SAM	**Samar** (Visayan Sea coastline of Samar Island)	Embayed coastline with numerous reefs. Some reefs have steep drop-offs
SELUZ	**Southeast Luzon** (Bicol) (Includes Albay, Camarines Norte, Sorsogon and Catanduanes)	Tectonically active coastline with many bays. The coast is bordered by fringing reefs
SIBIS	**Sibuyan Sea Islands** (Boracay, Romblon, Sibuyan, Marinduque)	Volcanic islands that have been isolated from major Philippine islands. Narrow reefs in Sibuyan. Extensive reefs near Boracay
SPANAY	**Southern Panay** (Guimaras and Southeast Iloilo and smaller islands)	Guimaras and eastern Iloilo islands are bordered almost wholly by fringing reefs. Panay Gulf subject to strong tidal flows
SSIS	**Sulu Sea Islands** (Sulu, Tawi Tawi, Tubbataha Atoll, Cuyo and Cagayan de Sulu islands)	Most Sulu islands are volcanic. Submerged platforms support extensive reef development. True atoll development observed in Tubbataha and Cuyo islands.
SWBOH	**Southwest Bohol** (Maribojoc, Loay, Panglao and Pamilacan islands)	Shore is generally sand and rubble with intertidal benches fringed with coral reefs
SWLUZ	**Southwestern Luzon** (Nasugbu to San Juan Batangas including minor islands)	Embayed coastline, tectonically active, narrow reef flats affected by strong tidal flows
TB	**Tayabas Bay** (Laiya Batangas to Bondoc Peninsula)	Diverse coastal features. Wide sandy beaches in eastern part, reef and mangrove development towards Bondoc Peninsula
WLUZ	**Western Luzon** (From Subic Bay, Zambales to Cape Bolinao)	Embayed coastline in the south, extensive reef development in the north. Zambales coastline extensively modified by lahar flows following 1991 Pinatubo eruption

Table 5.1a Attributes of the geographical regions where *Conus* assemblages and their frequency of occurrences were recorded.

Cone ID	Genus	Species	OGU
34	*Conus*	*capitaneus*	Eastern Cebu
36	*Conus*	*mustelinus*	Eastern Cebu
49	*Conus*	*nussatella*	Eastern Cebu
53	*Conus*	*muriculatus*	Eastern Cebu
54	*Conus*	*sulcatus*	Eastern Cebu
57	*Conus*	*mucronatus*	Eastern Cebu
59	*Conus*	*acutangulus*	Eastern Cebu
60	*Conus*	*floridulus*	Eastern Cebu
67	*Conus*	*articulatus*	Eastern Cebu
76	*Conus*	*grangeri*	Eastern Cebu
78	*Conus*	*sulcatus*	Eastern Cebu
93	*Conus*	*circumcisus*	Eastern Cebu
96	*Conus*	*neptunus*	Eastern Cebu
97	*Conus*	*comatosa*	Eastern Cebu
102	*Conus*	*aculeiformis*	Eastern Cebu
104	*Conus*	*dusaveli*	Eastern Cebu
109	*Conus*	*eximius*	Eastern Cebu
114	*Conus*	*generalis*	Eastern Cebu
117	*Conus*	*gloriamaris*	Eastern Cebu
121	*Conus*	*ichinoseana*	Eastern Cebu
122	*Conus*	*ione*	Eastern Cebu
123	*Conus*	*kimioi*	Eastern Cebu
125	*Conus*	*kintoki*	Eastern Cebu
127	*Conus*	*eugrammatus*	Eastern Cebu
130	*Conus*	*lenavati*	Eastern Cebu
132	*Conus*	*leopardus*	Eastern Cebu
134	*Conus*	*luteus*	Eastern Cebu
142	*Conus*	*pertusus*	Eastern Cebu
143	*Conus*	*sulcocastaneus*	Eastern Cebu
148	*Conus*	*viola*	Eastern Cebu
151	*Conus*	*proximus*	Eastern Cebu
153	*Conus*	*molluccensis*	Eastern Cebu
177	*Conus*	*omaria*	Eastern Cebu
178	*Conus*	*praecellens*	Eastern Cebu
180	*Conus*	*memiae*	Eastern Cebu
183	*Conus*	*pseudorbignyi*	Eastern Cebu
185	*Conus*	*vimineus*	Eastern Cebu
187	*Conus*	*scalptus*	Eastern Cebu
189	*Conus*	*polongimarumai*	Eastern Cebu
190	*Conus*	*saecularis*	Eastern Cebu
192	*Conus*	*saecularis*	Eastern Cebu
216	*Conus*	*crocatus*	Eastern Cebu
140	*Conus*	*thomae*	Davao Gulf
191	*Conus*	*sazanka*	Davao Gulf
17	*Conus*	*arenatus*	Eastern Palawan
24	*Conus*	*planorbis*	Eastern Palawan
25	*Conus*	*furvus*	Eastern Palawan
26	*Conus*	*magus*	Eastern Palawan
41	*Conus*	*frigidus*	Eastern Palawan
43	*Conus*	*textile*	Eastern Palawan
44	*Conus*	*telatus*	Eastern Palawan
101	*Conus*	*dayriti*	Eastern Palawan

102	*Conus*	*achatinus*	Eastern Palawan
154	*Conus*	*spectrum*	Eastern Palawan
159	*Conus*	*thalassiarchus*	Eastern Palawan
166	*Conus*	*nobilis*	Eastern Palawan
186	*Conus*	*montillai*	Eastern Palawan
7	*Conus*	*chaldeus*	Eastern Samar
13	*Conus*	*lividus*	Eastern Samar
30	*Conus*	*australis*	Eastern Samar
35	*Conus*	*rattus*	Eastern Samar
37	*Conus*	*miles*	Eastern Samar
40	*Conus*	*flavidus*	Eastern Samar
50	*Conus*	*terebra*	Eastern Samar
69	*Conus*	*aulicus*	Eastern Samar
70	*Conus*	*auratinus*	Eastern Samar
72	*Conus*	*auricomus*	Eastern Samar
106	*Conus*	*episcopatus*	Eastern Samar
129	*Conus*	*legatus*	Eastern Samar
136	*Conus*	*tulipa*	Eastern Samar
137	*Conus*	*obscurus*	Eastern Samar
147	*Conus*	*tenuistriatus*	Eastern Samar
163	*Conus*	*sanguinolentus*	Eastern Samar
165	*Conus*	*retifer*	Eastern Samar
176	*Conus*	*magnificus*	Eastern Samar
209	*Conus*	*zapatosensis*	Sibuyan Sea Islands
2	*Conus*	*imperialis*	Northern Panay
3	*Conus*	*litteratus*	Northern Panay
5	*Conus*	*eburneus*	Northern Panay
7	*Conus*	*chaldeus*	Northern Panay
8	*Conus*	*ebraeus*	Northern Panay
11	*Conus*	*musicus*	Northern Panay
12	*Conus*	*sponsalis*	Northern Panay
13	*Conus*	*lividus*	Northern Panay
15	*Conus*	*distans*	Northern Panay
17	*Conus*	*arenatus*	Northern Panay
21	*Conus*	*catus*	Northern Panay
24	*Conus*	*planorbis*	Northern Panay
26	*Conus*	*magus*	Northern Panay
28	*Conus*	*stramineus*	Northern Panay
31	*Conus*	*radiatus*	Northern Panay
34	*Conus*	*capitaneus*	Northern Panay
35	*Conus*	*rattus*	Northern Panay
36	*Conus*	*mustelinus*	Northern Panay
37	*Conus*	*miles*	Northern Panay
39	*Conus*	*emaciatus*	Northern Panay
47	*Conus*	*striatus*	Northern Panay
51	*Conus*	*glans*	Northern Panay
112	*Conus*	*miliaris*	Northern Panay
114	*Conus*	*generalis*	Northern Panay
132	*Conus*	*leopardus*	Northern Panay
193	*Conus*	*pulicarius*	Northern Panay
2	*Conus*	*imperialis*	Northwest Luzon (Ilocos)
11	*Conus*	*musicus*	Northwest Luzon (Ilocos)

12	*Conus*	*sponsalis*	Northwest Luzon (Ilocos)
13	*Conus*	*lividus*	Northwest Luzon (Ilocos)
14	*Conus*	*moreleti*	Northwest Luzon (Ilocos)
16	*Conus*	*biliosus*	Northwest Luzon (Ilocos)
19	*Conus*	*varius*	Northwest Luzon (Ilocos)
21	*Conus*	*catus*	Northwest Luzon (Ilocos)
23	*Conus*	*planorbis*	Northwest Luzon (Ilocos)
24	*Conus*	*planorbis*	Northwest Luzon (Ilocos)
26	*Conus*	*magus*	Northwest Luzon (Ilocos)
31	*Conus*	*radiatus*	Northwest Luzon (Ilocos)
35	*Conus*	*rattus*	Northwest Luzon (Ilocos)
36	*Conus*	*mustelinus*	Northwest Luzon (Ilocos)
37	*Conus*	*miles*	Northwest Luzon (Ilocos)
44	*Conus*	*telatus*	Northwest Luzon (Ilocos)
46	*Conus*	*quercinus*	Northwest Luzon (Ilocos)
47	*Conus*	*striatus*	Northwest Luzon (Ilocos)
50	*Conus*	*terebra*	Northwest Luzon (Ilocos)
53	*Conus*	*muriculatus*	Northwest Luzon (Ilocos)
112	*Conus*	*miliaris*	Northwest Luzon (Ilocos)
145	*Conus*	*ochroleucus*	Northwest Luzon (Ilocos)
151	*Conus*	*proximus*	Northwest Luzon (Ilocos)
193	*Conus*	*pulicarius*	Northwest Luzon (Ilocos)
194	*Conus*	*litoglyphus*	Northwest Luzon (Ilocos)
197	*Conus*	*vexillum*	Northwest Luzon (Ilocos)
198	*Conus*	*obscurus*	Northwest Luzon (Ilocos)
200	*Conus*	*tulipa*	Northwest Luzon (Ilocos)
201	*Conus*	*suratensis*	Northwest Luzon (Ilocos)
5	*Conus*	*eburneus*	Samar
8	*Conus*	*ebraeus*	Samar
9	*Conus*	*coronatus*	Samar
18	*Conus*	*stercusmuscarum*	Samar
21	*Conus*	*catus*	Samar

22	*Conus*	*striatellus*	Samar
23	*Conus*	*planorbis*	Samar
29	*Conus*	*consors*	Samar
33	*Conus*	*vexillum*	Samar
47	*Conus*	*striatus*	Samar
51	*Conus*	*glans*	Samar
52	*Conus*	*scabriusculus*	Samar
62	*Conus*	*furvus*	Samar
75	*Conus*	*balteatus*	Samar
79	*Conus*	*boeticus*	Samar
82	*Conus*	*bullatus*	Samar
83	*Conus*	*canonicus*	Samar
94	*Conus*	*coccineus*	Samar
100	*Conus*	*cylindraceus*	Samar
110	*Conus*	*fischoederi*	Samar
112	*Conus*	*miliaris*	Samar
133	*Conus*	*litoglyphus*	Samar
150	*Conus*	*mitratus*	Samar
193	*Conus*	*pulicarius*	Samar
216	*Conus*	*crocatus*	Samar
214	*Conus*	*darkini*	Sarangani
1	*Conus*	*marmoreus*	Southeast Luzon (Bicol)
5	*Conus*	*eburneus*	Southeast Luzon (Bicol)
26	*Conus*	*magus*	Southeast Luzon (Bicol)
57	*Conus*	*mucronatus*	Southeast Luzon (Bicol)
69	*Conus*	*aulicus*	Southeast Luzon (Bicol)
115	*Conus*	*geographus*	Southeast Luzon (Bicol)
14	*Conus*	*moreleti*	Sibuyan Sea Islands
16	*Conus*	*biliosus*	Sibuyan Sea Islands
19	*Conus*	*varius*	Sibuyan Sea Islands
20	*Conus*	*achatinus*	Sibuyan Sea Islands
28	*Conus*	*stramineus*	Sibuyan Sea Islands
53	*Conus*	*muriculatus*	Sibuyan Sea Islands
91	*Conus*	*cinereus*	Sibuyan Sea Islands
95	*Conus*	*collisus*	Sibuyan Sea Islands
149	*Conus*	*monachus*	Sibuyan Sea Islands
89	*Conus*	*cervus*	Southern Mindanao
108	*Conus*	*excelsus*	Southern Mindanao
119	*Conus*	*hirasei*	Southern Mindanao
157	*Conus*	*samiae*	Southern Mindanao
2	*Conus*	*imperialis*	Southern Panay
3	*Conus*	*litteratus*	Southern Panay
7	*Conus*	*chaldeus*	Southern Panay
8	*Conus*	*ebraeus*	Southern Panay
11	*Conus*	*musicus*	Southern Panay
12	*Conus*	*sponsalis*	Southern Panay
13	*Conus*	*lividus*	Southern Panay
14	*Conus*	*moreleti*	Southern Panay
17	*Conus*	*arenatus*	Southern Panay

20	*Conus*	*achatinus*	Southern Panay
21	*Conus*	*catus*	Southern Panay
24	*Conus*	*planorbis*	Southern Panay
26	*Conus*	*magus*	Southern Panay
28	*Conus*	*stramineus*	Southern Panay
31	*Conus*	*radiatus*	Southern Panay
34	*Conus*	*capitaneus*	Southern Panay
35	*Conus*	*rattus*	Southern Panay
36	*Conus*	*mustelinus*	Southern Panay
37	*Conus*	*miles*	Southern Panay
40	*Conus*	*flavidus*	Southern Panay
45	*Conus*	*figulinus*	Southern Panay
47	*Conus*	*striatus*	Southern Panay
51	*Conus*	*glans*	Southern Panay
53	*Conus*	*muriculatus*	Southern Panay
79	*Conus*	*boeticus*	Southern Panay
95	*Conus*	*collisus*	Southern Panay
132	*Conus*	*leopardus*	Southern Panay
151	*Conus*	*proximus*	Southern Panay
177	*Conus*	*omaria*	Southern Panay
193	*Conus*	*pulicarius*	Southern Panay
63	*Conus*	*ammiralis*	Sulu Sea Islands
66	*Conus*	*armadillo*	Sulu Sea Islands
73	*Conus*	*aurisiacus*	Sulu Sea Islands
81	*Conus*	*broderippi*	Sulu Sea Islands
91	*Conus*	*cinereus*	Sulu Sea Islands
92	*Conus*	*circumactus*	Sulu Sea Islands
98	*Conus*	*corallinus*	Sulu Sea Islands
111	*Conus*	*floccatus*	Sulu Sea Islands
126	*Conus*	*kuroharai*	Sulu Sea Islands
173	*Conus*	*voluminalis*	Sulu Sea Islands
211	*Conus*	*cordigera*	Sulu Sea Islands
2	*Conus*	*imperialis*	Southwest Bohol
3	*Conus*	*litteratus*	Southwest Bohol
15	*Conus*	*distans*	Southwest Bohol
39	*Conus*	*emaciatus*	Southwest Bohol
64	*Conus*	*aphrodite*	Southwest Bohol
74	*Conus*	*baileyi*	Southwest Bohol
80	*Conus*	*boholensis*	Southwest Bohol
90	*Conus*	*chiangi*	Southwest Bohol
96	*Conus*	*neptunus*	Southwest Bohol
103	*Conus*	*dondani*	Southwest Bohol
124	*Conus*	*kinoshitai*	Southwest Bohol
170	*Conus*	*sugimotonis*	Southwest Bohol
4	*Conus*	*tessulatus*	Southwest Luzon
11	*Conus*	*musicus*	Southwest Luzon
12	*Conus*	*sponsalis*	Southwest Luzon
32	*Conus*	*parius*	Southwest Luzon
46	*Conus*	*quercinus*	Southwest Luzon
112	*Conus*	*miliaris*	Southwest Luzon
145	*Conus*	*ochroleucus*	Southwest Luzon
1	*Conus*	*marmoreus*	Tayabas Bay
2	*Conus*	*imperialis*	Tayabas Bay
3	*Conus*	*litteratus*	Tayabas Bay

4	*Conus*	*tesullatus*	Tayabas Bay
5	*Conus*	*eburneus*	Tayabas Bay
6	*Conus*	*caracteriscus*	Tayabas Bay
7	*Conus*	*chaldeus*	Tayabas Bay
8	*Conus*	*ebreaus*	Tayabas Bay
9	*Conus*	*coronatus*	Tayabas Bay
11	*Conus*	*musicus*	Tayabas Bay
12	*Conus*	*sponsalis*	Tayabas Bay
13	*Conus*	*lividus*	Tayabas Bay
14	*Conus*	*moreleti*	Tayabas Bay
15	*Conus*	*distans*	Tayabas Bay
16	*Conus*	*biliosus*	Tayabas Bay
17	*Conus*	*arenatus*	Tayabas Bay
18	*Conus*	*stercusmuscarum*	Tayabas Bay
19	*Conus*	*varius*	Tayabas Bay
20	*Conus*	*achatinus*	Tayabas Bay
21	*Conus*	*catus*	Tayabas Bay
22	*Conus*	*striatellus*	Tayabas Bay
23	*Conus*	*planorbis*	Tayabas Bay
24	*Conus*	*planorbis*	Tayabas Bay
25	*Conus*	*furvus*	Tayabas Bay
26	*Conus*	*magus*	Tayabas Bay
27	*Conus*	*subulatus*	Tayabas Bay
28	*Conus*	*stramineus*	Tayabas Bay
29	*Conus*	*consors*	Tayabas Bay
30	*Conus*	*australis*	Tayabas Bay
31	*Conus*	*radiatus*	Tayabas Bay
32	*Conus*	*parius*	Tayabas Bay
33	*Conus*	*vexillum*	Tayabas Bay
34	*Conus*	*capitaneus*	Tayabas Bay
35	*Conus*	*rattus*	Tayabas Bay
36	*Conus*	*mustelinus*	Tayabas Bay
37	*Conus*	*miles*	Tayabas Bay
38	*Conus*	*virgo*	Tayabas Bay
39	*Conus*	*emaciatus*	Tayabas Bay
40	*Conus*	*flavidus*	Tayabas Bay
41	*Conus*	*frigidus*	Tayabas Bay
42	*Conus*	*pennaceus*	Tayabas Bay
43	*Conus*	*textile*	Tayabas Bay
44	*Conus*	*telatus*	Tayabas Bay
45	*Conus*	*figulinus*	Tayabas Bay
46	*Conus*	*quercinus*	Tayabas Bay
47	*Conus*	*striatus*	Tayabas Bay
48	*Conus*	*anemone*	Tayabas Bay
49	*Conus*	*nussatella*	Tayabas Bay
50	*Conus*	*terebra*	Tayabas Bay
51	*Conus*	*glans*	Tayabas Bay
52	*Conus*	*scabriusculus*	Tayabas Bay
53	*Conus*	*muriculatus*	Tayabas Bay
54	*Conus*	*sulcatus*	Tayabas Bay
55	*Conus*	*moluccensis*	Tayabas Bay
56	*Conus*	*insculptus*	Tayabas Bay
57	*Conus*	*mucronatus*	Tayabas Bay

59	*Conus*	*acutangulus*	Tayabas Bay
60	*Conus*	*floridulus*	Tayabas Bay
61	*Conus*	*alabaster*	Tayabas Bay
68	*Conus*	*asiaticus*	Tayabas Bay
112	*Conus*	*miliaris*	Tayabas Bay
128	*Conus*	*laterculatus*	Tayabas Bay
158	*Conus*	*pagodus*	Tayabas Bay
169	*Conus*	*tribblei*	Tayabas Bay
172	*Conus*	*recluzianus*	Tayabas Bay
174	*Conus*	*voluminalis*	Tayabas Bay
178	*Conus*	*praecellens*	Tayabas Bay
184	*Conus*	*orbignyi*	Tayabas Bay
197	*Conus*	*vexillum*	Tayabas Bay
31	*Conus*	*radiatus*	Western Luzon
45	*Conus*	*figulinus*	Western Luzon
77	*Conus*	*betulinus*	Western Luzon
85	*Conus*	*caracteristicus*	Western Luzon
135	*Conus*	*lynceus*	Western Luzon
139	*Conus*	*suratensis*	Western Luzon

Table 5.1b *Conus* species recorded from each OGU in this study.

5.3 METHODS

In this chapter I perform range analyses, areographic and ecological analyses, species-area relationship analyses, faunal provinciality analyses and ordination methods. All of these methods are described in Chapter 3. Sites in Mindanao, Philippines were not included in all the analyses due to the lack of sufficient numbers of collection sites. Additional methods are presented to further evaluate the basin isolation hypothesis. Endemism was determined from distributional information in the following references Cabrera (1984), Röckel *et al* (1995), Springsteen and Leobrera (1986) Kohn and Perron (1994) and Wilson (1993).

5.3.1 *Physical and historical measures of basin isolation*

McManus (1985) suggested that basin isolation was a result of the unique geographical configuration of the Philippines and Indonesia, in which an island arc borders marginal oceanic basins. During the Plio-Pleistocene sea level regressions, the Sibuyan Sea, Sulu Sea, Bohol Sea and Camotes Sea (Fig. 5.1) were physically isolated from the Pacific Ocean and South China Sea due to the closing or narrowing of passages when the islands bordering them increased in area. Thus it is possible to get a measure of isolation of the basins by counting the number of modern passages connecting the basins with the Philippine Sea or South China Sea. It is also possible to estimate the width of the passages during the maximum sea level regression -150 m. The level of potential isolation was estimated by the equation

$$I_{\text{Basin}} = N/W \qquad \text{Equation 5.1}$$

Where I_{Basin} is the isolation index, N is the number of passages into and out of the basin, and W is the width of all passages, summed during the last maximum sea level regression, 18,000 YBP (Heaney (1986).

5.3.2 *Estimation of species extinction (species loss) rate*

Basin isolation predicts higher rates of accumulation of species in an ocean basin relative to a larger area, such as the entire Pacific Ocean. This is due to speciation or species persistence, resulting in the high species diversity in the Southeast Asian region. In this study, species extinction rate is deduced from the Pacific Ocean species-area relationship, assuming that the Pliocene-Pleistocene species-area relationship is similar to that of today. Using the species-area parameters estimated for the habitable areas in the Philippines where the cone snails were recorded or collected, and the parameters of the Pacific Ocean species-area relationship, species loss and gain is estimated according to Rosenzweig's (1995) equation

$$E_b = (S_m - S_b)/ S_m \qquad \text{Equation 5.2}$$

Where E_b is the extinction rate over the last 18,000 years (number extinct/18,000 years), S_m is the number of species in an area of the Pacific Ocean of the same size as that of the basin in question, and S_b is the number of species observed in the geographic basin surveyed. It was assumed that the area of the Pacific Ocean has an equal distribution of species richness following that of Schoft (Schopf 1979). Note that a negative extinction rate means an accumulation of species over time.

The species-area relationship for tropical shallow water *Conus* in the Pacific Ocean was determined from my preliminary analysis as

$$S_{\text{Pacific}} = 5.4649\ A^{0.2038} \qquad \text{Equation 5.3}$$

Area represents the total area of the tropical Pacific. The Pacific Ocean represents the largest geographical unit in which the Pacific *Conus* species are found. The SPAR was plotted based on the occurrences of cone snails in six representative areas with a significant number of *Conus* records. These areas are 1) The Philippines, 2) Japan (Ryukyu Islands) 3) Great Barrier Reef Region, 4) Hawaii, 5) Guam and 6) Galapagos. The S was determined by plotting total coastal area by GIS applications from a world map [1:205,019,526] and the species number of *Conus* in the geographic areas.

Equation 5.3 is substituted for S_m of equation 5.2 to estimate extinction rate in each basin.

5.3.3 *Analysis of range size, life history and habitat in Conus*

From data on the habitat types available to *Conus* in the Philippines, published information on life history characteristics of *Conus*, and range sizes for the genus in the Philippines, a biogeographic analysis of range size was conducted.

This study aims to test the hypothesis that the dispersal potential, measured as length of observed and calculated (Kohn and Perron 1994) pre-competent planktonic stage (PS) of *Conus* is positively correlated with range size (RS) in the Philippines. This observation is known from Pacific and Indian Ocean comparisons of *Conus* distribution and range size (Kohn and Perron 1994). Another hypothesis that will be examined is whether the number of available habitats (HA) in each OGU is an important factor in determining the present range of *Conus* in the Philippines. Frequency of occurrence in a basin (O) is factored out by designating it as a covariate, since I assume that it results from local-scale processes affecting abundance. HA are the habitat types (Kohn 1967) that may be colonised by *Conus* that exist in a specific microhabitat assuming that these habitats are within the range of ecological tolerances of *Conus.* Not all *Conus* species that favour a certain habitat will be found in the geographical range of that habitat. Habitat types and their geographical distribution were collected from Cabrera (1984), Elera (1896) and from the author's field surveys.

In the intertidal and shallow water *Conus*, occurrences are determined largely by local environmental complexity and spatial heterogeneity (Kohn 1997). Since range size is positively related to increasing occurrence, *Conus* that live in habitats that are common in geographic space should have larger ranges than those that live in habitats that are uncommon. Thus it is hypothesised that habitat availability in geographical space is a significant factor in determining range size in the Philippines.

Only 27 intertidal and shallow water *Conus* species with known life history, and which were relatively common, were used in this analysis (Kohn and Perron 1994) (Table 5.2). This introduces an unavoidable sampling bias since past work on *Conus* biology has focussed on common species. The reproductive biology of other species is largely unknown due to their rarity.

Cone ID	**Genus**	**Species**	**Life history**	**Length of precompetent larval stage in days**
1	*Conus*	*marmoreus*	non-planktotrophic	3
2	*Conus*	*imperialis*	planktotrophic	20
3	*Conus*	*litteratus*	planktotrophic	22
9	*Conus*	*coronatus*	planktotrophic	27
10	*Conus*	*miliaris*	planktotrophic	25
13	*Conus*	*lividus*	planktotrophic	29
14	*Conus*	*moreleti*	planktotrophic	28
15	*Conus*	*distans*	planktotrophic	28
17	*Conus*	*arenatus*	planktotrophic	0
19	*Conus*	*varius*	planktotrophic	25
20	*Conus*	*achatinus*	non-planktotrophic	0
22	*Conus*	*striatellus*	planktotrophic	24
23	*Conus*	*vitulinus*	planktotrophic	20
24	*Conus*	*planorbis*	planktotrophic	22
25	*Conus*	*furvus*	non-planktotrophic	0
26	*Conus*	*magus*	non-planktotrophic	0
28	*Conus*	*stramineus*	non-planktotrophic	0
34	*Conus*	*capitaneus*	planktotrophic	28
35	*Conus*	*rattus*	planktotrophic	27
37	*Conus*	*miles*	planktotrophic	21
38	*Conus*	*virgo*	planktotrophic	24
42	*Conus*	*pennaceus*	non-planktotrophic	3
43	*Conus*	*textile*	planktotrophic	16
45	*Conus*	*figulinus*	planktotrophic	23
46	*Conus*	*quercinus*	planktotrophic	25
47	*Conus*	*striatus*	planktotrophic	19
51	*Conus*	*glans*	non-planktotrophic	6

Table 5.2. The 27 shallow water *Conus* species used in analysis of range size and habitat availability and analysis of range size and life history.

An ANCOVA with the following model was used to investigate effects of frequency of occurrence (O), length of pre-competent larval stage (PS), and number of available habitats (HA) on the Range size (RS) of these 27 species of *Conus*:

$$\mathbf{RS = O+PS+HA+ (PS \times HA) + Error}$$

All factors were transformed as log (x+1) before analysis to ensure homogeneity of variances and to meet the assumptions of normality.

5.3.4 *Habitat type and species richness*

The effects on the geographical distribution of species richness of the different *Conus* habitats, as defined by Kohn (1967) and modified to include other environments, are examined using stepwise multiple regression. Collection records contained field observations and habitat descriptions of the areas where *Conus* were collected. The habitat characteristics observed were counted per OGU.

In theory, all available habitats that are suited for a *Conus* species will be occupied if they experience no hindrance in colonising these habitats. In nature, the potential to occupy these habitats is constrained by barriers to dispersal, competition and decreasing ecological tolerances. Thus different *Conus* species assemblages with varying species number may occupy a single habitat type in different places in geographical space. This study evaluates what habitat type contributes most to species diversity in space. The habitat that is most variable in species diversity is hypothesised to contribute the most to geographical species diversity. There are 8 habitat classes based on substrate and geomorphologic characteristics, with some of these representing intermediate habitats (Table 5.3). Habitat type frequencies (counted as the number of recorded habitats in different collection sites in an OGU) and area of the OGU were log (x+1) transformed before analysis to assure homogeneity of variance.

Habitat code	**Habitat type**	**Shore position**	**Major substrata**
H1	Type I	Subtidal	Sand
H2	Type II	Low intertidal	Coral and algae
H3	Type III	Subtidal	Sand and coral rubble
H6	Type I-III	Low intertidal	Sand and coral rubble
H7	Type II-III	Low intertidal	Sand, coral and algae
H4	Type IV	Low intertidal	Non-coral rock
H8	Type II-IV	Low intertidal	Coral and rock
H5	Type V	Subtidal	Sand and mud

Table 5.3 Habitat characteristics of Indo-West Pacific *Conus.* Classification adopted from Kohn (1967) and Cabrera (1984).

5.4 RESULTS

Material

Seven hundred and sixty two records of shallow water *Conus* occurrences belonging to 188 species were obtained from the collections of the Philippine National Museum (PNM), the University of Santo Tomas (UST) and the University of the Philippines (UP). Secondary material consisting of 363 records was obtained from Cabrera (1984), Springsteen and Leobrera (1986) and (Kohn and Perron 1994). These records represent a collection effort from 1898-1998. Of the 188 species recorded, only 160 species were used in ordination and range analyses since these species have locality information.

5.4.1 *Endemism estimates*

The Philippine *Conus* endemics are *Conus telatus, C. zapatosensis, C. scalptus, C. thalassiarchus, C. thomae, C. kintoki, C. montillai, C. lenavati, C. neptunus* and *C. dondani* (Röckel *et al*. 1995). These species have all been recorded from the Sibuyan, Sulu and Visayas Seas (Figure 5.1). None has been recorded outside these basins. With the exception of *C. telatus, C. montillai* and *C. thalassiarchus*, all species are from deep water (> 100 m depth). There is a species that is possibly an endemic but was recorded and identified by de Elera (1896) and Cabrera (1986) as *C. anemone.* The distribution of *C. anemone* is restricted to Australia. The species status of these records that are deposited at the Pontifical University of Santo Tomas and the Philippine National Museum remain in question. The other species are most appropriately termed near endemics because they have been recorded outside the Philippines only from adjacent oceanic basins (e.g. Celebes Sea, South China Sea, Banda Sea) and the narrow distribution that McManus described. *C. asiaticus, C. aurasiaticus, C. australis, C. axelrodi, C. blandifordianus, C. broderippi, C. cernohorskyi, C. cordigera, C. darkini*, and *C. excelsus, C. fischoederi, C. hirasei, C. ichinoseana, C. ione, C. kuroharai, C. laterculatus, C. lynceus, C. polongimarumai, C. pseudokimioi, C. pseudoorbignyi, C. recluziamus, C. rolani, C. shikamai, C. stupa* and *C. subulatus* are near endemics and have mainly been recorded from the Sibuyan, Viasyas and Sulu Seas. With the sole exception of *C. lynceus*, all are recorded only from deepwater habitats.

Endemics make up 5.7 % of the total recorded Philippine *Conus* fauna of 173 shallow and deepwater species. Near endemics make up 14.4 % of this total. There are only 3 endemic shallow water species and one near endemic.

5.4.2 Ecological correlates of frequencies of occurrence

Figures 5.2a-b show the PCA plots of frequency of occurrence of *Conus* at sites in the Philippines. The Philippine assemblages of the 175 species examined are correlated primarily with cyclone frequency and coastal complexity on the PC 1 and PC 2 axes. On the PC 1 and PC 3 axes, island and latitude factors are significant (Table 5.4a). The variances accounted for by the PCA on the first and second axes are relatively low. This suggests that local ecological factors are important (e.g. the distribution of habitats) in determining diversity on a large scale. Such local factors were not measured in this study.

	PC Axis								
	1			2			3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
Number of OGU N = 14									
Philippines									
Complexity	0.285	0.081	0.077	**-0.576**	0.332	-0.143	0.344	0.118	0.231
Cyclones	-0.025	0.001	0.129	**0.674**	0.454	0.439	-0.136	0.018	-0.052
Tide	-0.355	0.126	-0.268	-0.366	0.134	-0.402	0.310	0.096	0.223
Latitude	-0.395	0.156	0.420	-0.068	0.005	0.066	**-0.501**	0.251	-0.530
Island	-0.356	0.127	-0.545	0.119	0.014	-0.061	**0.568**	0.322	0.484

Table 5.4a. Results of a PCA analysis of frequency of occurrence of 175 species of Philippine *Conus.* Table shows Pearson (r) and Kendall (tau) correlations with significant ecological factors. The numbers in bold represent factors with strongest correlations to frequency of occurrence.

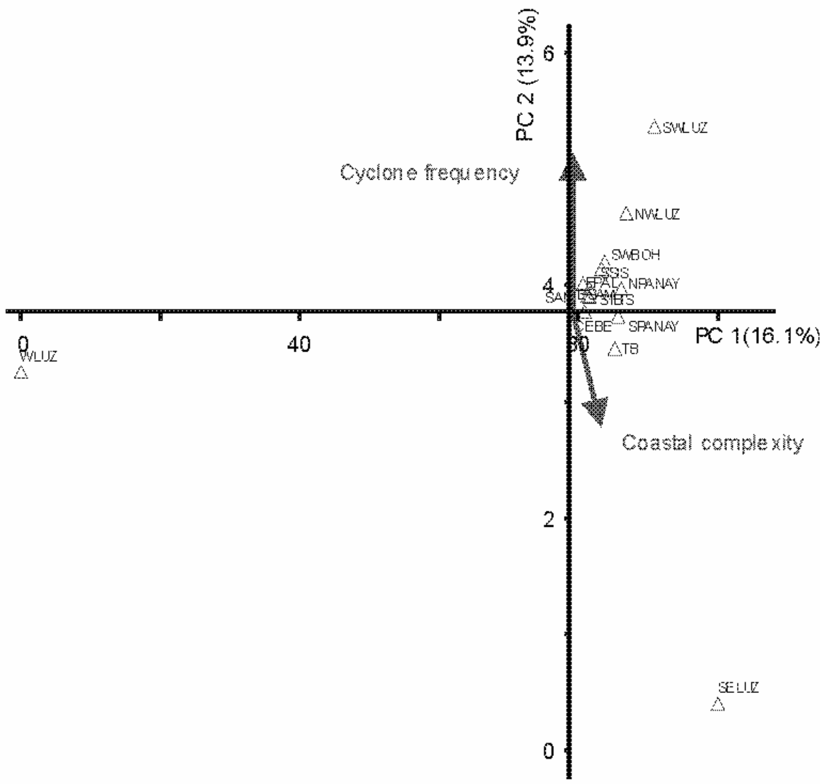


Figure 5.2a PCA bi-plot of macroecological variables of geographic regions with intertidal and shallow subtidal *Conus* assemblages in the Philippines

NWLUZ -Northwest Luzon, SWLUZ - Southwest Luzon, SELUZ - Southeast Luzon,
SIBIS - Sibuyan Sea Islands, TB - Tayabas Bay, ESAM - Eastern Samar, EPAL - Eastern Palawan
CEBE - Eastern Cebu, SWBOH - Southwest Bohol, NPANAY - Northern Panay
SPANAY - Southern Panay, and SSIS - Sulu Sea Islands

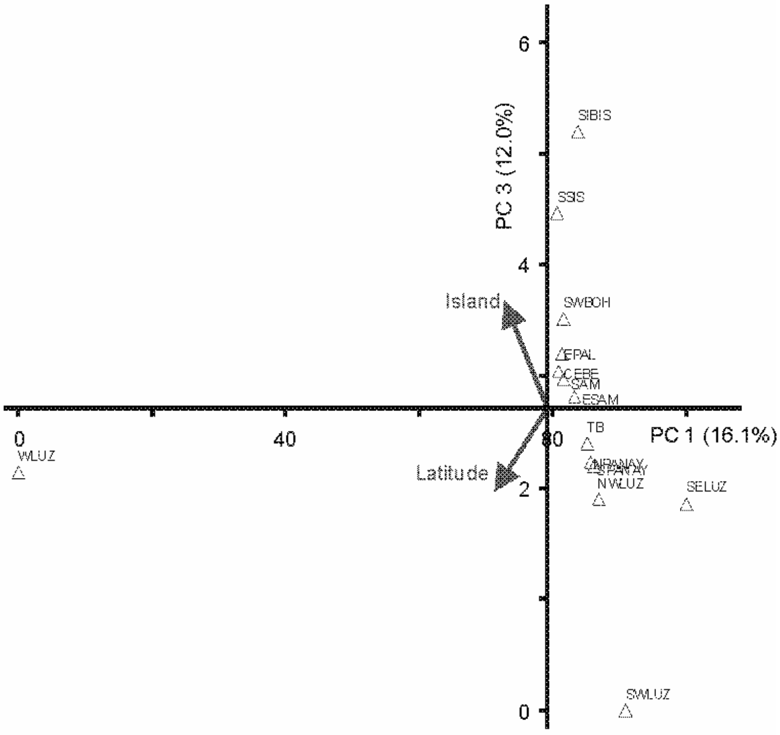


Figure 5.2b PCA bi-plot on the PC 1 and PC 3 axes of macroecological variables on geographic regions with intertidal and shallow subtidal *Conus* assemblages in the Philippines. The PC 3 axis shows the island and latitude factors in the *Conus* ecological gradient.

NWLUZ -Northwest Luzon, SWLUZ - Southwest Luzon, SELUZ - Southeast Luzon,
SIBIS - Sibuyan Sea Islands, TB - Tayabas Bay, ESAM - Eastern Samar, EPAL - Eastern Palawan
CEBE - Eastern Cebu, SWBOH - Southwest Bohol, NPANAY - Northern Panay
SPANAY - Southern Panay, and SSIS - Sulu Sea Islands

	Macroecological factor									
	Area	Cyclones	Islands	Embayment	Temperature	Rainfall	Reef	Tides	Lat	Long
Philippines N=14	0.659**	0.261	-0.049	0.359	0.115	-0.081	-0.137	-0.193	-0.049	0.021

Table 5.4b Pearson correlations of macroecological factors with *Conus* species richness in OGUs in the Philippines.

** significant at (P<0.01)

Species richness is significantly correlated with area in all bioregions in the Philippines. (Table 5.4b).

5.4.3 Species-area analysis

Figure 5.3 and Table 5.5 illustrate the species-area curve in the Philippines. The parameters of the species-area curves vary for each basin (Table 5.5). The Philippine basins of the Sibuyan Sea and Visayas Seas have the highest species richness (n= 73, 52 respectively). These regions are in the centre of the archipelago, and have the highest coastal complexity; percent of reef fringed coastline, and numbers of islands. They are also bathymetrically complex.

The Sulu Sea has a z value of 0.43. One z value from the Visayas basin shows an anomalously high z value of 1.30.

Geographic unit	Surveyed area	Survey sites	Species number	C	Z
Basin					
Philippine Sea	381.39	10	27	0.26	0.73
Visayas-Camotes	644.22	12	52	0.02	1.30
Sibuyan Sea	419.64	53	73	0.63	0.59
Sulu Sea	353.86	12	31	1.22	0.43
South China Sea	711.76	63	39	0.35	0.75
Philippines	2510.87	150	160	0.19	0.86

Table 5.5 Area (km^2), number of collection sites, *Conus* species number, and C and z estimates (see Chapter 3 for how this was calculated) of the Philippine oceanic basins.

Factor	MS	DF	F	Sig.
Philippines				
Area	1.090	1	18.79	0.004
Basin	0.089	4	0.488	0.673
Error	0.581	9	0.005	
Levene's Test	NS			

Table 5.6 ANOVA of basin and bioregion effects on the total species richness of Philippine *Conus*.

NS- not significant

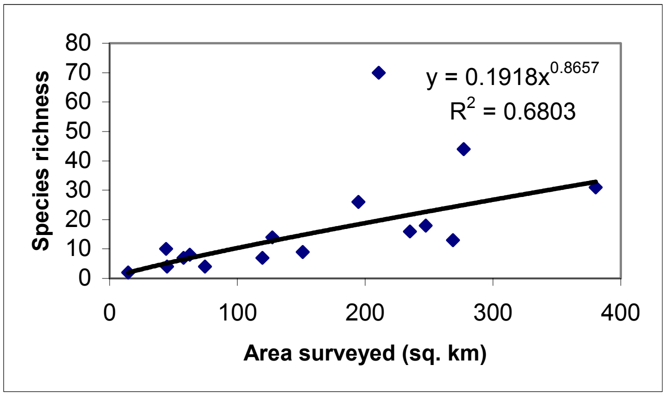


Figure 5.3. Species-area curve for Philippine *Conus*. Surveys in the Philippines were done on stretches of fringing reef coastline that form a significant physical feature of geographic regions (see Table 5.1a OGU attributes).

Area is statistically significant as a covariate of species richness ($P<0.001$), thereby implying that area effects are important in predicting basin species richness. (Table 5.6). However, the effect of Basin on species richness is not significant ($p = 0.67$).

5.4.5 ***Provinciality and Homogeneity***

5.4.5.1 Oceanic basins of the Philippines

The provinciality indices of Philippine *Conus* in the oceanic basins are shown in Figure 5.4. These indices suggest that faunal similarities between oceanic basins are low and are reflected in low percentages of homogenisation (χ^2 test, $P <0.001$)

The high provinciality indices of the Sibuyan and Visayas basins are directly related to the nature of the species-area curve in these regions. The high provinciality is a consequence of high species richness in geographic regions in these basins. The basins therefore exhibit the properties of separate biogeographical provinces, and may imply that the evolutionary history of each basin is somewhat separate from that of the others. However, a possible area independence effect, or the de-coupling of species richness with area may also contribute to this provinciality. This is a possible consequence of a large number of heterogenous habitats in a small area in a basin, differences in productivity in regions of a basin, or variability in recolonisation dynamics.

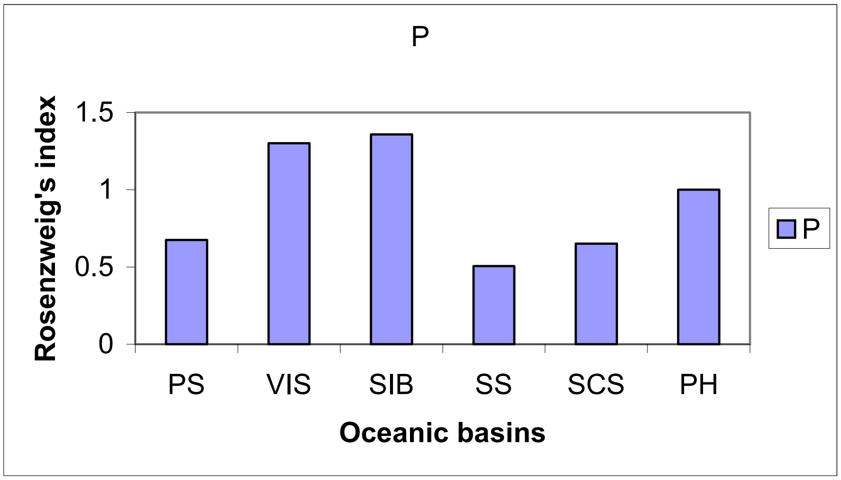


Figure 5.4. Provinciality (P) plot of Philippine *Conus* in the marginal oceanic basins.

PS – Philippine Sea, VIS – Visayas, SIB – Sibuyan Sea, SS – Sulu Sea, SCS – South China Sea, PH –whole Philippines.

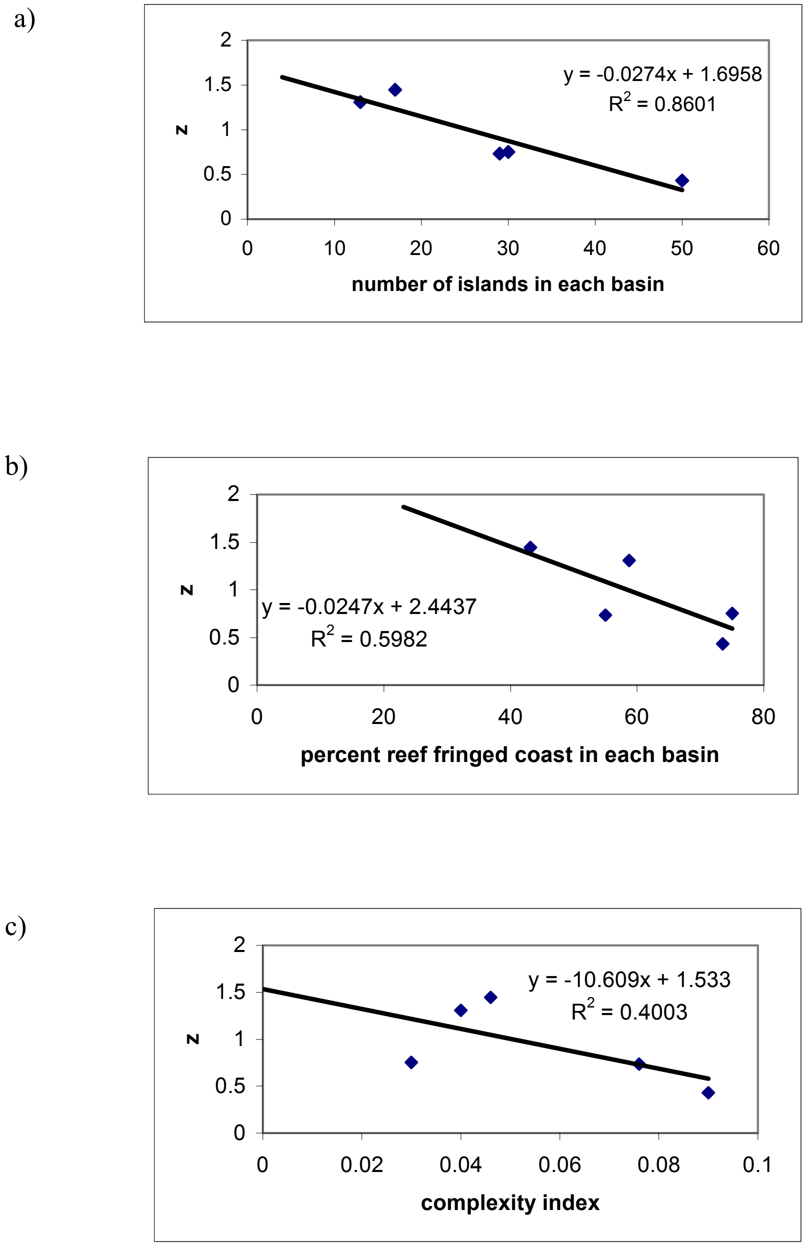
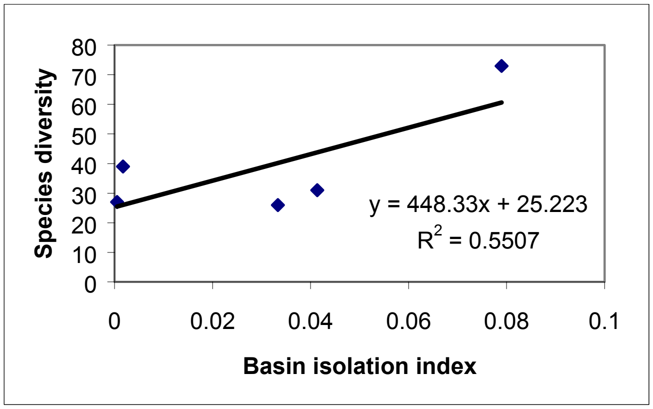


Figure 5.5a-c. Linear trends of basin z parameter with a) basin islands, b) coral reef distribution and c) coastal complexity.

a)



b)

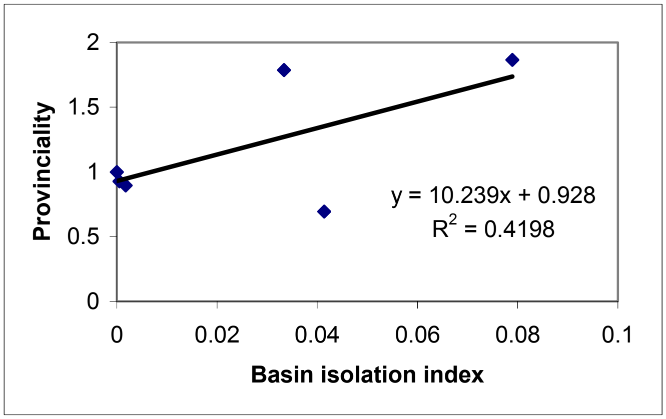


Figure 5.6a-b Positive correlation of basin isolation with a) species richness and b) provinciality.

5.4.6 Historical basin isolation, ecological factors and z estimates

In the Philippine oceanic basins, z has a negative relationship with number of islands, amount of reef fringed coast, and coastal complexity (Figure 5.5 a-c). This is related to the increase in species richness per unit area as habitats increase. It is presumed that an increasing area will have a wider suite of habitats (Rosenzweig 1995). However only the number of islands in each basin has a statistically significant negative relationship ($P<0.05$) with z. However, the sample size is low since there are only 5 basins in the Philippines.

Basin isolation measured as a physical geographic index is positively, but not significantly, correlated with species richness (Figure 5.6a) and faunal provinciality (Figure 5.6b).

5.4.7 Estimation of species loss (extinction) rate

Figure 5.8 shows the estimated species loss rates in various parts of the Indo-West Pacific and in the highly isolated regions of Hawaii and the Galapagos. This plot is based on the parameters estimated for the Pacific Ocean *Conus* species-area curve.

If isolation, whether by distance, time or physical dispersal barriers, has subdivided the fauna, these divisions would have resulted in separate evolutionary histories for the areas. These histories will be reflected in the distribution and ranges of the modern fauna. Basin isolation, and similar hypotheses, predicts higher species richness in the isolated, compared with the non-isolated, oceanic basins.

The estimates presented here suggest that the Philippine basins have a negative species loss rate (species are accumulating over the period) compared with areas of similar size in most of the rest of the Pacific. This suggests that these basins are either centres of speciation or species persistence. In contrast, the highly isolated Hawaiian and Galapagos archipelagos show a positive extinction rate, which suggest that the faunas here are losing species.

When species loss is plotted against and index of basin isolation, there is a negative, but non-significant, correlation (Figure 5.7) Increasing basin isolation may result in increased species persistence or species accumulation. Isolation patterns may have been masked by reconnection of the basins as a result of recent sea level stabilisation, thus the non-significant correlation.

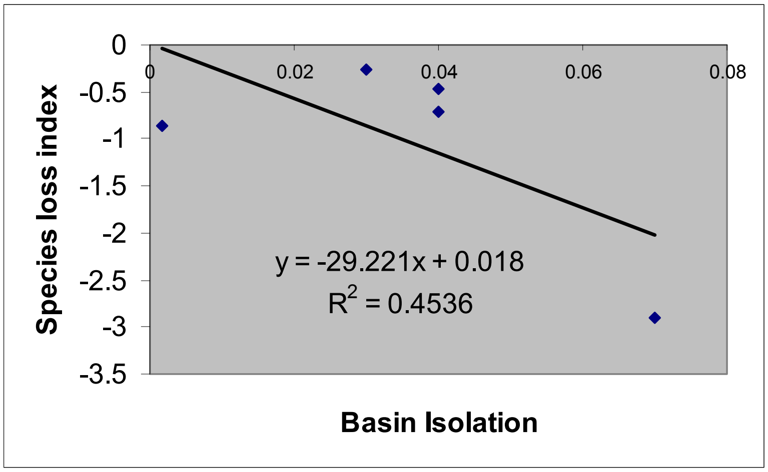


Figure 5.7 The negative relationship of an index of basin isolation and an index of species loss.

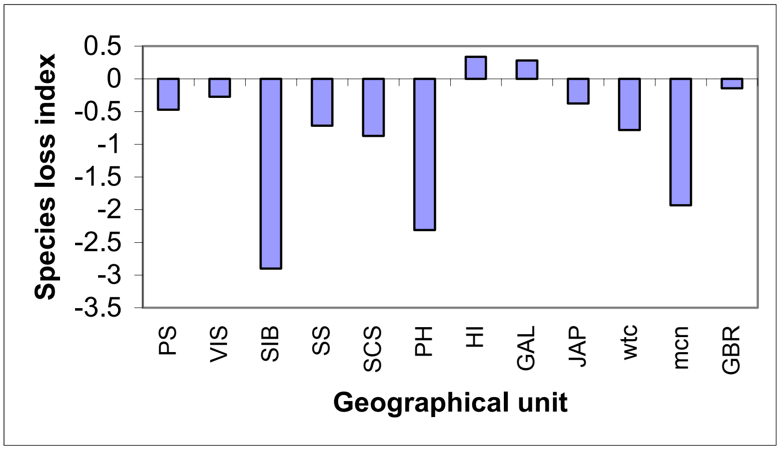


Figure 5.8 Potential *Conus* extinction rates (species loss index) in geographical regions of the Indo-West Pacific. The very isolated Galapagos and Hawaiian Archipelagos are included for contrast.

PS –Philippine Sea, VIS –Visayas, SIB- Sibuyan Sea, SS –Sulu Sea, SCS-South China Sea, PH –Philippines, HI –Hawaii, GAL –Galapagos, JAP- Ryukyu Islands, Wet Tropics Coast –Wet Tropics bioregion (GBR), Mackay Capricorn Coast – Mackay Capricorn bioregion (GBR) and GBR –Great Barrier Reef.

5.4.8 Analysis of range size, larval duration and habitat of Conus

The length of the pre-competent planktonic larval stage is not a statistically significant factor ($p = 0.064$) in determining the range size of *Conus* at the scale of the Philippine archipelago (Table 5.7). Frequency of occurrence is highly significant ($P=0.005$) as a covariate. Habitat availability, and the interaction of planktonic duration and habitat availability, affect range size significantly ($P<0.05$). These results suggest that at this geographical scale, the effect of dispersal capability in determining geographical range interacts with smaller-scale ecological determinants of species richness.

5.4.9 Habitat and species richness

In the Philippines, the frequency of shallow subtidal sandy habitats (H1) is the most significant predictor of species richness ($P<0.001$) in each geographic unit (Table 5.8) The H1 (shallow subtidal sandy habitats), H2 (intertidal coral-algae intertidal) and H8 (muddy sand) habitats are the most numerous in the Philippine archipelago. The H2 habitat accounts for 30% of the total habitats noted in this study. H2, H8 and H7 (intertidal sand-coral-algae) habitats are predominantly low intertidal environments associated with coral reefs. H2 habitats have more species than H1 habitats. H1 habitats are often present even when there are no recorded H2 habitats in an OGU. The low number of species, but variable occurrence, in H1 habitats, contributes significantly to patterns of species richness in the whole Philippines (Figure 5.9).

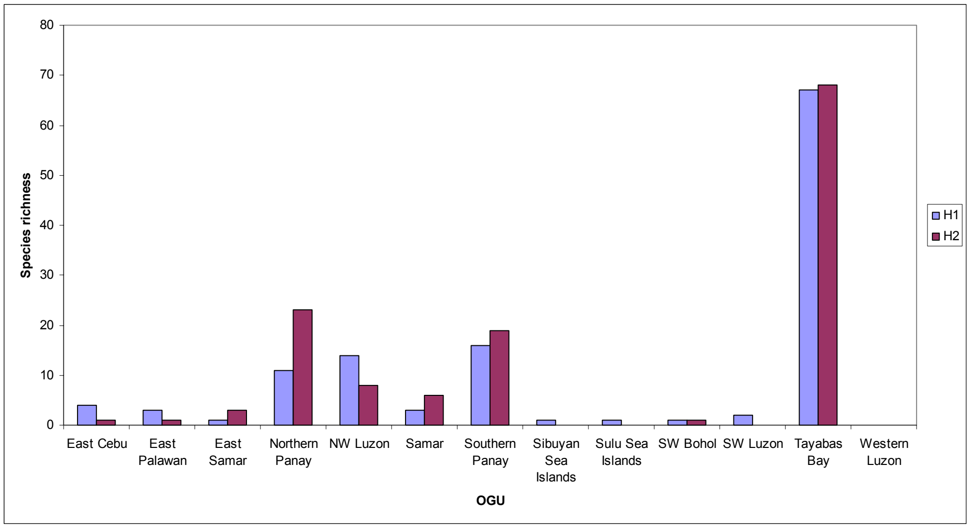


Figure 5.9 Species richness in H1 (subtidal sandy habitats) and H2 (low intertidal coral and algal bench) habitats in Philippine geographical units.

Source	df	MS	F	Sig	Power
Model	27	0.1560	8.42	0.025	0.831
Intercept	1	4.3390	234.56	0	1.000
Frequency	1	0.6060	32.74	0.005	0.985
Planktonic duration	14	0.0094	5.08	0.064	0.601
Habitat availability	7	0.1190	6.43	0.046	0.675
Plankton x Habitat	5	0.1730	9.33	0.025	0.809
Error	4	0.0180			
Total	32				
Levene's Test of Equality	NS				

Table 5.7. ANCOVA investigating factors affecting range size of *Conus* in the Philippines. On the scale of the Philippine archipelago, habitat availability predicts range size better than the length of the planktonic stage of a species. However, there is a significant interaction between planktonic larval duration and habitat availability.

Variable	Pearson correlation	Sig.	t	Sig.
Species	1.000			
Area	0.342	0.1270	0.573	0
H1 (sand subtidal)	0.847	0	5.287	0.580
H2 (coral-algae intertidal)	0.814	0	0.700	0.500
H3 (sand and coral rubble subtidal)	0.778	0.001	0.803	0.441
H4 (sand)	0.512	0.037	-1.508	0.162
H5 (sand)	0.603	0.015	-0.401	0.697
H6 (sand and coral rubble intertidal)	0.675	0.006	-0.215	0.834
H7 (sand coral and algae intertidal)	0.670	0.006	-1.263	0.235
H8 (muddy sand)	0.755	0.001	0.039	0.970

ANOVA

Model	SS	df	MS	F	Sig	r^2
Regression	0.779	1	0.7790	27.95	0.00	0.72
Residual	0.306	11	0.0027			

Table 5.8 Results of stepwise multiple regression on species richness of Philippine *Conus*. Species richness is predicted significantly by the distribution of sandy habitats (H1). Effects of all other variables were not significant.

5.4.10 Areography

In *Conus*, 60% of the Philippine ranges can be considered triangular (Figures 5.10 and 5.11). With the sole exception of *C. ebraeus*, *Conus* species have ranges less than 100,000 km^2 (Figure 5.12) When plotted against species richness, range size distributions in the Philippines show a strong skew to the right. (Figure 5.12)

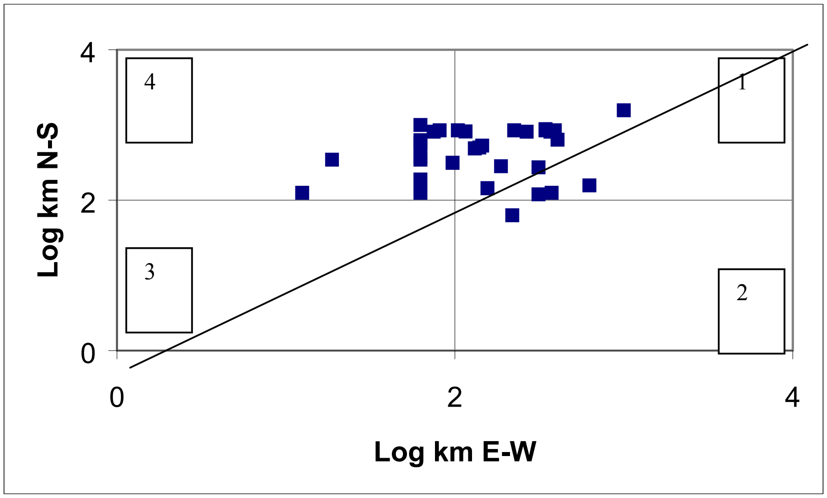
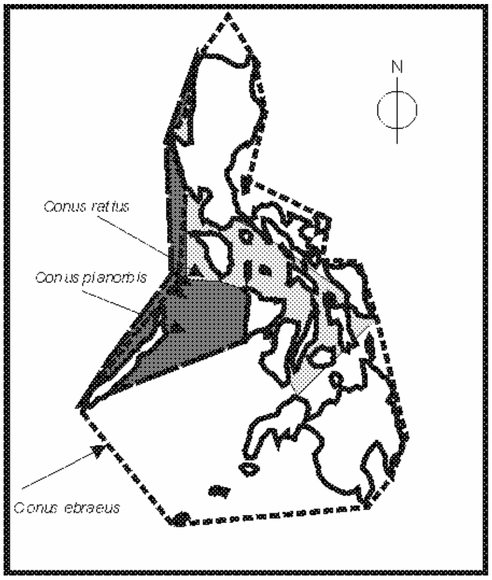


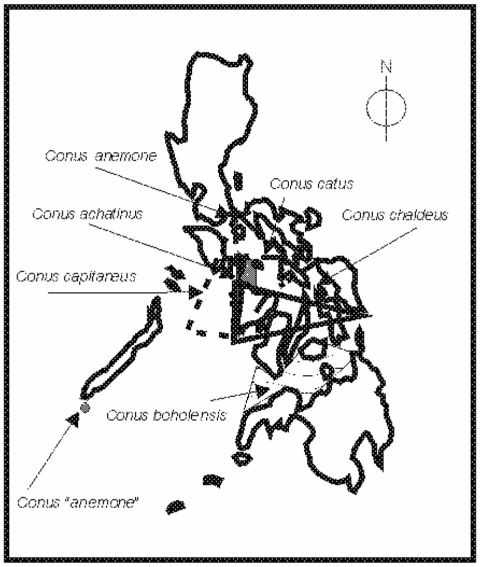
Figure 5.10 *Conus* range shapes in the Philippines

A



Conus with wide distributions in the Philippines.
C. ebraeus has polygonal distribution covering the archipelago.
C. rattus and *C. planorbis* show typical narrow ranges.

B



Conus with restricted distributions in the Philippines.
C. achatinus is restricted to eastern edge of the Sulu Sea and Sibuyan Sea. *C. chaldeus* and *C. catus* are restricted to the Visayan Sea. *C. capitaneus* is restricted to the Sulu and Sibuyan Seas. *C. boholensis* is restricted to the Bohol Sea. *C. "Anemone"* has only been recorded from Palawan and Tayabas Bay.

Figure 5.11a-b. Examples of distributions of *Conus* within the Philippines

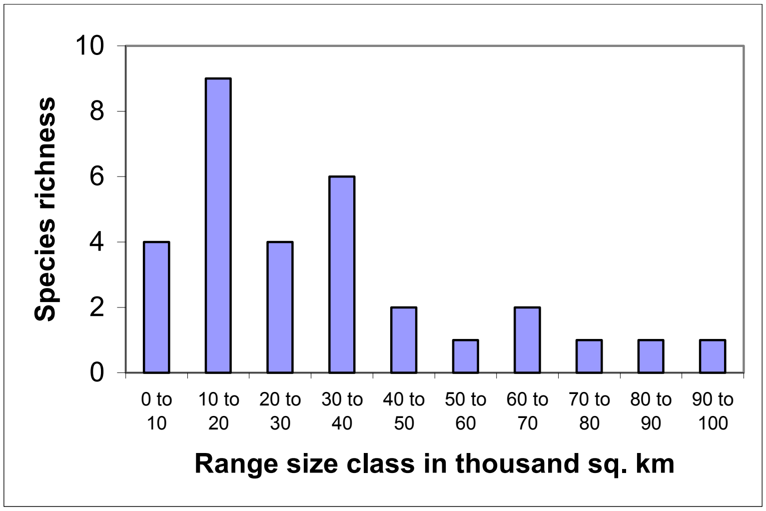


Figure 5.12. Number of species of Philippine *Conus* plotted against range size.

5.5 DISCUSSION

5.5.1 Species-area relationships and ecological correlates

The results presented are an indirect test of basin isolation as a possible mechanism to account for high marine species richness in the Philippines. McManus (1985) hypothesised that high species richness in Southeast Asia is attributable to 1) range overlap of independently evolved species 2) high rates of local speciation and 3) differentially high survival rates of species among temporally and spatially heterogeneous habitats. This chapter examined species-area curves of *Conus* in the Philippines to make inferences about Basin Isolation.

Amount of area was a significant predictor of species richness. This is consistent with observations on similar highly diverse faunal assemblages (Rosenzweig 1992; Rosenzweig 1995).

However, when one views some areas at a smaller spatial scale in these highly species-rich regions, the SPAR estimates do not predict the observed species richness well. This is a possible area-independence effect, first observed in the richness of terrestrial plant communities. This effect suggests that below a certain area size, species richness becomes independent of available habitable area (Rosenzweig 1995). Possible explanations for this include 1) the existence of a large number of heterogenous habitats in a very small area (Rosenzweig 1995) and 2) the effects of recolonization and extinction over a short time frame (Atmar and Patterson 1995). The second of these has been observed in species that have wide dispersal abilities, such as birds. Thus the area-independence effect, or the de-coupling of area with species richness, is likely dependent on the characteristics of the taxon being studied.

Since the aim of this thesis is to describe distribution, I cannot hypothesise on the possible causes of this area-independence effect based on the available data. However, one may suggest that the wide dispersal ability of many marine invertebrates supports the second explanation. However, the first explanation may also hold for *Conus*, since it is capable of existing in a wide range of habitats. Examination of SPARs of other marine taxa occupying the same regions may help in explaning current distributions.

The use of species-area relationships to estimate faunal isolation assumes that lack of past isolation results in lower z values. This has been demonstrated in similar analyses of marine fossil taxa (McKinney 1998). Isolation of faunal assemblages resulting from the Pliocene emergence of the Isthmus of Panama resulted in higher estimates of z ($0.25 < z < 0.45$) between the now isolated Panama and Caribbean provinces. Z estimates of regions within these provinces are generally much lower ($z = 0.15$).

Z values observed in the Philippine *Conus* are comparable to those observed in tropical taxa, such as corals ($z = 0.45$) (Veron 1995), tropical marine biota ($z = 0.53$) (Briggs 1986), Caribbean echinoderms ($z = 0.30$), and Strombidae from the Panama region ($z = 0.46$) (McKinney 1998).

However, there is one fundamental difference between the past situation in the Philippines and the closure of the Panama Isthmus. The oceanic basins of the Philippines were physically isolated in the past, but are now partly connected. Any isolation event in the Plio-Pleistocene may have resulted in possible species endemism, and higher z values. The positive (but not significant) correlation of z with the index of basin isolation supports the hypothesis that geographical isolation in the past has contributed to increased z estimates and provinciality. These patterns may be further confirmed by looking at endemism patterns within the basins. Basin endemics in *Conus* are found only in the central basins of the Philippines.

A high z estimate for the Visayas Basin suggests that this area was possibly isolated by low sea level for longer periods than other basins. The results of this study support this hypothesis. It is possible that rapid species divergence occurred here, and with the higher habitat heterogeneity provided by numerous islands, rapid speciation was favoured. It is also possible that relict fauna more related to fossil assemblages may co-exist with more modern fauna (Petuch 1987). The estimates of extinction rates suggest that these areas are accumulating species. The endemism estimate of *Conus* in the Philippines is around 7% of the total fauna. This is more than that estimated for other Philippine molluscan taxa (including bivalves) at 4-5% (Springsteen and Leobrera 1986).

This high estimate of z for the Visayas Basin should usually occur only in highly diverse tropical systems. In addition high z values also imply that geographical regions within the basins have high species diversity. The regions within the basins therefore, show the properties of provinces, where z values approach unity. However, the SPAR estimates in the Visayas and Sibuyan Sea basin do not predict species richness well. This is due to the fact that species richness on a locality level in these regions is very variable. Some sites have high species richness and some low. This results in possible area independence or a small island effect (Macarthur and Wilson 1967) that may be a consequence of a large environmental variability in a small area (Rosenzweig 1995).

The basins with the most number of islands are the largest basins of Sulu Sea, South China Sea and the Philippine Sea. Islands along these coastlines are on the edges of the ocean basins. Z variability here is lower likely due to "tighter" SPARs. This is likely due to the greater area and nearness of the main coastal islands. This is unlike the central Philippines, where islands may be found in the centre of the basins (e.g. Marinduque, Masbate, Camotes, Romblon, Cuyo). While the central basins may have coral islands and cays, these islands are likely to support variable numbers of *Conus*. Some islands will have very low species richness. Because of this widespread variability between islands, which is reflected in the SPAR estimates, a high provinciality is observed in these basins. The consequence of this high variability is a less "tight" SPAR.

The high z estimates for the Philippine basins are consistent with what is known about high diversity tropical systems such as rainforests (Rosenzweig 1995). In these high diversity systems, the species-area curves of various biotas are linear, with a z value approaching unity. Inter-provincial curves have typically higher slopes than those of intra-provincial curves. This is due to the relative isolation of biotic provinces that reduces exchange of species with extensive dispersal abilities, and thus encourages species diversification. Low z estimates are indicative of the presence of sink species or species that are constantly under threat of local extinction. On small islands, where habitat-richness is theoretically less than on mainland and larger islands, sink species on average do not persist, but are replaced either by immigration or local speciation. If the central Philippines basins had experienced long periods of isolation, the molluscan fauna in these basins should have higher species richness than the coasts bordering the South China Sea and Philippine Sea basins.

The Rosenzweig (1995) and McKinney (1998) hypotheses say that increasing geographical isolation results in higher z values and hence provinciality. The patterns observed here partially support the two hypotheses. The isolation observed here is a consequence of islands with varying SPAR parameters separating the basins. However this isolation is not due to distance isolation or isolation presupposed by the fragmentation of habitat.

This study suggests that coastal features such as reefs, islands and features such as cyclones, are major factors affecting the modern distribution of *Conus*. Cyclones have been known to reduce *Conus* densities and diversities on shallow reef flats (Kohn 1980). Furthermore, cyclones are believed to be major factors maintaining diversity of coral reefs (Connell 1978)**.** An examination of the distribution of cyclones with respect to patterns of diversity of marine organisms observed in the Indo-Pacific could be a fruitful area of future research.

5.5.2 Areography of range size of Conus

Properties of range sizes may give insights into the nature of speciation and the maintenance of biological diversity (Brown 1996). In Philippine *Conus*, the frequency distribution of range sizes is similar to that observed for diverse terrestrial taxa (Kolasa 1996).

Narrow and small species ranges may be limited by habitat availability and dispersal capabilities (Gaston 1996). In addition, ecological tolerances and history affect species range size (Brown 1996). However how history, which includes speciation, affects range size is unclear. Firstly, species with large ranges may be prone to give rise to new species with restricted ranges through range fragmentation by vicariance. This is often sugested to explain nested and overlapping distributions in high diversity regions (Kolasa 1996). Secondly, species with small ranges may speciate more through sympatry. Distinguishing between these two hypotheses will require studies of temporal dynamics of species ranges, detailed molecular studies and a geographic approach to community structure (Kolasa 1996; Maurer 1999).

Ecological and historical factors probably can explain the frequency distribution of *Conus* ranges in the Philippines. The Philippines, with its potential historical isolation, is an ideal place to investigate the occurrence of narrow species ranges. The Philippines is likely to contain co-evolved species with narrower ecological tolerances, due to its isolation and the peculiarity of geography and climate.

5.5.3 Analysis of range size of Conus: effects of larval duration and habitat availability

Marine provinces do not fit the strict definition proposed by Rosenzweig (1995). He states that provinces derive their species largely by speciation. By this definition the Indo-Pacific would be the only province in the region. Recognised marine provinces, however, are more inter-connected, due to the planktonic larvae of most marine animals. Marine provinces are therefore inherently "leaky" (Rosenzweig 1995). While distributions of marine organisms tend to be large, factors such as life history and habitat selectivity may determine the realized extent of these distributions.

As the most species-rich of intertidal gastropod taxa, *Conus* has been the focus of many studies of the factors that may determine species richness and distribution (Kohn 1997). At inter-oceanic scales, life history strategies such as a long pre-competent planktonic larval stage correlate significantly with range size (Kohn and Perron 1994). Like the fauna of most Indo-Pacific archipelagos, shallow water *Conus* of the Philippines have almost exclusively planktonic larval stages and wide geographical ranges (Kohn and Perron 1994). Thus sixty-three of the 100 relatively common shallow water species in the Philippines have representatives in the central Pacific. A major aspect of range size in Indo-Pacific *Conus* is thus probably determined by life history strategies that include long planktonic stages, and egg sizes and egg capsules susceptible to rafting.

Since 22 of the 27 shallow water Philippine *Conus* in this study have excellent larval dispersal potential, it can be assumed that if suitable ecological conditions are available, the various species will be able to colonise the whole archipelago. The distributions of *Conus* in the country, with the exception of the ubiquitous *C. ebraeus*, are normally narrow and triangular.

In a high diversity system, co-evolution can produce species with narrow habitat ranges (Rosenzweig 1995). This is less likely to occur in less diverse systems. Thus, a given species may occupy more habitat types in a low than a high diversity system. For example, in Easter Island there is only one species of *Conus*, *C. miliaris* that expanded its diet considerably in the absence of competitors (Kohn, 1979). However the lack of suitable habitats prevents it from expanding its range (Kohn, 1979).

5.5.4 Habitat type and species richness

The distribution of sandy habitats (H1) contributed significantly to patterns of species richness of *Conus* in the Philippines. H1 habitats have the least species richness of *Conus* on a local scale, but species richness in these habitats is extremely variable geographically (Kohn 1997). The distribution of H1 habitats with variable species richness contributes significantly to the overall species richness in the Philippines. This is perhaps due to the fact that H2 habitats (that have high species richness) are not recorded in some areas where H1 habitats are observed. Even if these H1 habitats have low species richness, they still contribute overall to the total species richness of Philippine *Conus*.

H1 habitats are typical of coral reef lagoon environments. The extreme variability in species richness in these habitats suggests that species with wide habitat requirements may tend to use unoccupied H1 habitats, if conditions are favourable. As other habitats have similar and less variable species composition per unit area, variability in species richness in H1 habitats will contribute significantly to species richness at geographic scales.

Other habitat types consisting of mixed sand and coral rubble (H2 and H3), have the highest species richness per unit area of intertidal *Conus*, with an average of 8 co-occurring species (Kohn 1997). However, species composition in these assemblages is less variable than in H1 habitats, or in the more species rich subtidal reef platform habitats H6 and H8.

These results support Kohn's (1997) hypothesis proposed to account for the high species richness of *Conus.*

5.5.5 Extinction, persistence and endemism of Philippine Conus

It is hypothesised that the high z estimates for the central Philippines basins are related to the presence of island complexes and their associated habitat heterogeneity. These central Philippine basins are smaller than the Philippine Sea and South China Sea basins. Large island coastlines bordering these central basins have a higher diversity of habitats, and have more species. In smaller islands mainly found near the centre of the basins, there are fewer species. In the isolated Hawaiian archipelago, faunal instability can be inferred from the fossil record. In Hawaii, modern assemblages have replaced suites of Pleistocene gastropod assemblages (Kay and Palumbi 1987). This includes the extinct *Conus kahiko*, now replaced by the widely distributed *C. chaldaeus*. This suggests that island habitats do not favour the dominance and persistence of a single, or a few, species, possibly as a result of faunal instability.

Extinction rate estimates calculated from species-area parameters suggest that the Philippine oceanic basins are regions of species accumulation and speciation. This is supported by ecological and evolutionary studies (Vermeij 1987), for example the range contraction of many marine molluscs during the Pliocene and Pleistocene. The level of endemism in the *Conus* of the Philippines (7%), which is less than the level of endemism in isolated archipelagos like Hawaii (10%) (Kay and Palumbi 1987), does not give any inference about the mechanisms that may have led to this endemism. However, it may give insights into the evolutionary constraints on *Conus* endemism.

Assuming that endemism suggests rapid speciation, the endemism estimates of Philippine molluscs (5%) suggests that the Philippines is not a centre of rapid speciation at present, but of species accumulation. In contrast, the isolated Hawaiian and Galapagos archipelagos have positive extinction rates. Hawaii and the Galapagos are not accumulating species. Intermittent gene flow to these isolated islands has allowed the evolution of new species, thus accounting for high levels of endemism.

On the other hand, endemism may not suggest rapid speciation in the marine environment. Wallace (1997) has determined that in Indonesian *Acropora* corals, endemics have pleisomorphic characters, thus making them likely Tethys Sea relicts. The presumably younger species with apomorphic characters have typically wide IWP distributions. Thus evolution has allowed for new species to rapidly disperse throughout the region. A similar process may have affected modern *Conus*. The last major radiation of *Conus* in the IWP occurred in the Pliocene to Pleistocene (Kohn 1990). This radiation has contributed substantially to the wide-ranging modern fauna. Thus the Philippines shares a large percentage of the Pacific Ocean fauna that were derived from the pan-Pacific Tethyan biota (Poore 2000).

Vermeij (1987) tested the species accumulation model for central and eastern Pacific molluscs. In *Conus*, and sand dwelling taxa such as *Oliva* (Tursch and Greifeneder 2001), seperation by large distances selects against sand dwelling species, because it is possible that sand dwelling caenogastropods have shorter larval stages. It is also possible that the decline in space of species diversity in these gastropods is associated with the decline in numbers of suitable habitats or by declining primary productivity (Vermeij 1987; Vermeij 1990). These species have narrow ranges and consequently a higher extinction probability. Such species do not form a large part of the Central Pacific *Conus* assemblages, and probably became extinct on oceanic atolls due to sea level regressions. Fifty-four percent of Indo-Pacific Type I (sand dwelling) *Conus* species (Röckel, Korn et al. 1995) occur in the IWP island arc.

Rosenzweig (1995) also predicts the fate of global marine species diversity, using species-area analysis. Since global marine provinces have an inter-provincial z value of 0.3, biotic isolation is predicted to result in a 62% increase in species diversity. Using this model with the Philippine estimate of z (0.86), the predicted accumulation of *Conus* diversity in the Philippines due to basin isolation is 25%, a value similar to the effects of biotic isolation (33.5%) on terrestrial high diversity systems in the tropics (Rosenzweig 1995). McKinney (1998), used the provinciality model to evaluate the effects of the closure of the Panama Isthmus on species diversity of the Caribbean and Pacific faunas. He predicted a 45-60% increase in diversity due to the closure.

5.5.6 Marine biogeographic characterisation of the Philippines

Earlier marine biogeographic characterisation of the Philippines has suggested that the country could be divided into two marine provinces (DENR and UNEP 1997). The main oceanic basins bordering the country, the Philippine Sea and the South China Sea, define these provinces. Based on studies on scleractinian coral diversity, Aliño *et al* (1993) further subdivided these provinces into bioregions coincident with the marginal oceanic basins.

The results of this study support the hypothesis that the marginal oceanic basins of the Philippines are distinct biogeographical units that may have had separate evolutionary histories. This is supported by the differing SPAR and provinciality properties of the basins.

5.5.7 Further tests of the Basin Isolation Hypothesis

McManus' proposed basin isolation hypothesis has been examined here using the species-area-time relationship first proposed by Rosenzweig (1995). The results of this study tend to support the role of diverse habitats in accounting for the high species diversity observed. This habitat heterogeneity is likely an eco-geographical property of the oceanic basins of the Philippines.

Isolating factors that have operated in the past may be tested by phylogenetic analysis of representative taxa with wide-ranging and localised distributions (Duda and Palumbi 1999; Duda et al. 2001). This will provide insight into the possibility of endemic and plesiomorphic relicts coexisting with the modern and younger fauna (Duda and Palumbi 1999). An important area of interest here is the occurrence of sibling species with east-west distributions (Duda et al. 2001). It is important to determine the sympatric or allopatric character of such distributions. Also an evaluation of genetic connectivity of species assemblages between and within basins may test modern basin isolation (Barber et al. 2000). Such studies will test the speciation aspect of the hypothesis.

The confirmatory test of basin isolation is to examine the paleontological record, where *Conus* has been recorded from fossil sequences in Panay (Dickerson 1927), and thus directly measure speciation and extinction rates. The genus *Conus* is an excellent taxon to test this. The basic conical form of the shell has been constant throughout most of its evolutionary history, and thus is easily recognised. Rapid evolutionary divergence in the genus is coincident with the rapid development of coral reefs in the Cainozoic (Kohn and Perron 1994). Uplifted coral islands, such as eastern Cebu and Bohol, may provide interpretable paleontological sequences to test the hypothesis. The Miocene and the latest Pleistocene radiation of the genus may be examined within the Philippines from fossil records.

The narrow distributions of *Conus* in the Philippines imply a local-scale, environmentally determined distribution, likely due to the distribution of suitable microhabitat (Kohn 1997) and the distribution of potential prey items (Kohn 1969). Co-occurring *Conus* species are known to use different foods, microhabitats or both (Kohn and Nybakken 1975). Dispersal, while an important determinant on inter-oceanic scales, does not appear to be a highly significant determinant of range size and shape at the scale of the Philippines.

5.6 CONCLUSIONS

1. The high species richness of the Indo-West Pacific was examined using the caenogastropod *Conus.* The Philippines has a high level of species richness.

2. In the Philippines, 10 endemic species are recorded only from the central Philippine basins. Seven of these species are recorded from deepwater habitats. Near endemics are recorded only from adjacent oceanic basins.

3. Cyclone frequency, coastal complexity, presence of islands and latitude correlate with distribution patterns of Philippine *Conus*.

4. The nature of the species-area relationship in *Conus* provides some evidence for basin isolation. The z parameter for each ocean basin is positively correlated with a basin isolation index. The provinciality index of oceanic basins correlates positively with the basin isolation index. However a possible explanation of high provinciality is related to the varying diversities of OGU and sites. This may suggest a de-coupling of species diversity with area. This is an area-independence effect, possibly arising from the large number of heterogenous habitats in a single area.

5. Triangular, overlapping and nested distributions within the Philippines, as predicted by McManus, are observed in *Conus*. These distributions are correlated with the presence of factors like islands, reefs, and embayments.

6. The frequency distribution of range size of *Conus* versus species richness of *Conus* for Philippine basins is right (positive) skewed.

7. Larval duration does not affect range size of *Conus* significantly in the Philippines. The interaction of this life history characteristic with habitat does, however, affect range size significantly.

8. Predominantly sandy habitats (H1) contribute significantly to patterns of species richness of *Conus* in the Philippines. This habitat is extremely variable in species richness at a local scale. The predominantly low intertidal coral reef associated habitats (H2, H7 and H8) are numerous in the areas sampled, but they are not significant contributors to species richness.

9. Extinction rates estimated from the species-area properties of tropical Pacific *Conus* suggest that the Philippines and the IWP are centres of species accumulation or speciation**.** The isolated Hawaiian and Galapagos archipelagos have positive extinction rates. These observations need to be tested by paleontological, phylogenetic and genetic studies of comparable marine taxa.

CHAPTER 6

The biogeography of a sand dwelling coral reef gastropod, *Oliva*, in the Philippines

There is so much to do: unanswered questions lurk in every page
Bernard Tursch (2001) in "Oliva Shells "

This chapter examines distributions and morphological diversity in the gastropod genus *Oliva* in the Philippines. Some representatives of the genus in the Philippines have distributions which are localised in ocean basins. Some species are found only in certain basins, even though they have a wider IWP distribution. The morphological diversity of polytopic (species that live in a many kinds of substrates) and monotopic (species that live in a single kind of substrate) species are examined. I investigate

1. If *Oliva* have similar distributions to *Conus*
2. If morphological diversity in *Oliva* varies with oceanic basin
3. The possible origins of IWP species in the genus.

6.1 INTRODUCTION

The genus *Oliva* has 74 species. These are found only in tropical regions of the Atlantic, Indian and Pacific oceans (Tursch and Greifeneder 2001). The genus is exclusively found on soft substrates, mainly sand, from the intertidal to 100 m depth, with a majority of species found between 0-30 m. The genus is considered a shallow water (0-60 m) genus (see Chapter 4). The highest species diversity in the IWP representatives of the genus is found at approximately 5 m depth (Tursch and Greifeneder 2001).

There are 59 species in the IWP. Thirty-five species occur in the Philippines (Tursch and Greifeneder 2001). The Philippines has one endemic species*, O. vicdani*. *O. vicdani* has been recorded from the Sulu Archipelago only, and its ecology is unknown. It was trawled from deepwater. In terms of shell morhology it resembles *O. multiplicata*, a species found only within the IWP intertidal.

The Philippines is the centre of species richness of the genus. Most species are found in the central Philippine oceanic basin of the Sulu Sea (Springsteen and Leobrera 1986). The genus has the highest richness in the IWP island arc. This decreases eastwards or westwards from the central IWP. The region near Panama contains representatives that are derived from the Atlantic.

Oliva has variable feeding habits, anatomy,and shell characteristics (colour, pattern and shapes) (Tursch 1994; Tursch 1998; Tursch and Greifeneder 2001). This variability has contributed to difficulties in species identification in the genus. The almost total absence of meristic characters of the shell has contributed to this uncertainty. Tursch and co-researchers have separated species by shape (Tursch 1994; Tursch 1998; Tursch and Greifeneder 2001) and defined morphospecies. This approach reduced the number of species from 176 (Petuch and Sargent 1986) to 74 (Tursch 1994; Tursch 1998; Tursch and Greifeneder 2001).

Little is known about the ecology of *Oliva* species. *Oliva* species assemblages correlate with depth and sediment characteristics (Van Osselaer and Tursch 1993). The genus may cause significant bioturbation of sandy habitats. *O. tigridella* prefers sandy substrata, but has no specific food preferences (Malijan 2003). In *O. reticulata,* there is no correlation between shell patterning and substrate characteristics (Tan 2003). *Oliva* are probably opportunistic predators and scavengers, feeding on crustaceans and other gastropods (Tursch and Greifeneder 2001).

(Tursch and Greifeneder 2001) summarised habitat characteristics of IWP *Oliva.* (Table 6.1) Several species are monotopic, living only in a single type of substrate. Others are polytopic, living in several substrate types. The colour of the shell is often used for camouflage, and thus is related to the colour of the substrate. Tursch and Greifeneder (2001) hypothesised that predation pressure on *Oliva* may be the factor affecting shell colour. Co-occurrences of different species, but not different colour forms of the same species, of *Oliva* are observed (Tursch 1994; Tursch and Greifeneder 2001).

Habitat code	Description
1	sand
2	coarse sand
3	coral sand
4	coral-volcanic sand
5	fine sand
6	muddy sand
7	mud
8	gravelly sand
9	multisubstrate
10	sand and rubble
11	Volcanic sand

Table 6.1 Habitat codes of Indo-west Pacific *Oliva* used in the text.

The life history characteristics of *Oliva* are not well known. Aquarium observations by Ziegler (1969) of *O. sayana* from Florida suggest a short larval duration (1 week) and that larvae may be benthopelagic. It is possible that chemical cues from the substrate initiate settlement. Settlement may be restricted by the availability of suitable sand habitats (Tursch 1994). The population genetics of *Oliva* has not been studied in detail in the IWP. Some structure has been observed in the population genetics of *O. amethystina* and *O. reticulata* in the Visayas region of the Philippines (Chua and Panlilio 2002). Aldana and Dizon (2003) reported genetic structure in populations of *O. reticulata* in a 2 sq km bay in Batangas, Philippines (Aldana and Dizon 2003).

The evolutionary history of *Oliva* has been reviewed (Petuch and Sargent 1986, Tursch and Greifeneder 2001). *Oliva* probably originated in the Miocene, 30 MYBP, from Cretaceous volutes. The earliest *Oliva* has been recorded from the Eocene. Two radiations are hypothesised to have occurred in the Miocene. One was in the future IWP island arc, and the other in what became the Southern USA. However no phylogeny of the genus has been published.

Oliva provides a potentially informative comparison with *Conus* (Chapter 5). Both genera are carnivorous, but each occupies a completely different habitat. Habitats of *Conus* are three dimensional (intertidal benches, sand patches etc). Habitats of *Oliva* are less structurally complex, and differentiated by the characteristics of the sandy substrate. Spatial patterns of species diversity of *Conus* are predicted mainly by the presence of sandy habitats (Chapter 5). This chapter examines the distribution and biogeography of a sand dwelling coral reef gastropod *Oliva*.

6.2 MATERIAL

This study used material deposited at the Delaware Museum of Natural History (DMNH). The DMNH has one of the most extensive collections of Philippine molluscs in the world. These were collected during the period of American sovereignty (1898- 1946) in the Philippines and in the two decades after independence (1950-1970). Ten percent of the mollusc collection is Philippine material.

6.3 METHODS

From the DMNH collection, I initially consulted the museum's database for taxonomic, distribution and ecological information on *Oliva*. There were 3065 museum records for *Oliva*. Six hundred and fifty records pertain to the Philippines. Only records with province, locality, and municipality collection information were used in the study. Taxonomic identifications and ecological data were verified and revised when needed using Tursch and Greifeneder (2001) Five hundred and ninety six (596) specimens of *Oliva* in 29 species, were examined. The geographical locations of collection sites of the specimens were plotted on a map

Methods of data analysis used in this chapter (range analysis, areographic analysis, species-area analysis, faunal provinciality analyses and ordination methods) were described in Chapter 3. Sites in southern Mindanao, Philippines, were not included in analyses due to the lack of data. Ecological information was not available from many of the sites where *Oliva* were recorded. Thus correlations of ecological data with results from the PCA were not possible. Methods of analysis of spatial patterns of species richness are the same as those performed on *Conus* in Chapter 5.

6.3.1 Species Identification and Endemism estimates

In the DMNH collection, taxonomic identification followed that of earlier authors. I revised these identifications, using the revision by Tursch and Greifeneder (2001). Endemism was assessed from distributions reported by Tursch and Greifeneder (2001). This is the most reliable distribution information available to date.

6.3.2 Morphometric analysis

Oliva reticulata and *O. amethystina* were used to test if certain morphological attributes (shell length, shell width, flare length) can be grouped to the Sulu Sea, South China Sea, Philippine Sea, Sibuyan Sea and Davao Gulf, and if such patterns were related to the general ecology of each species. *O. reticulata* is a polytopic species found in various substrates in seagrass beds and on reef flats. *O. amethystina* is a monotopic species preferring coral sand, often near *Acropora* colonies. Both species are widely distributed in the central Philippines.

The following metrics (Figure 6.1) following that of Tursch (1998) were used: Shell Height from spire to base (H), Shell length from shoulder to base (L), Shell Width or Diameter (D), and Flare or Lip length (LW). These were measured using a vernier calliper (mm to 0.01). Fifty-three (53) shells of *O. amethystina* and 92 shells of *O. reticulata* were measured. Morphometric differences within species in geographical regions were investigated using multiple discriminant analysis (SPSS 10.0 for Windows). The predictive power of this analysis was assessed by an *a posteriori* test, in which individuals were classified into the prior group based solely on the shell morphometry,

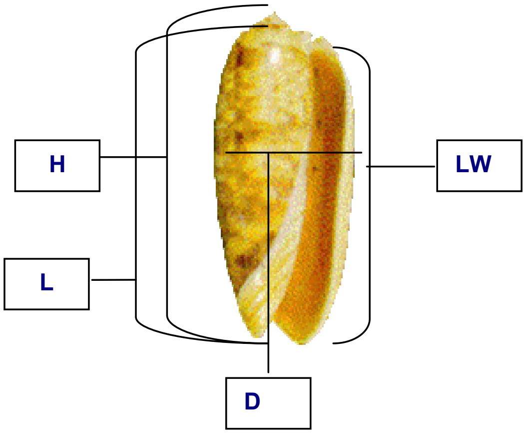


Figure 6.1 Metrics used in morphometrics analysis of shell shape in *Oliva*. See text for details

6.4 RESULTS

6.4.1 Endemism and species number in basins

The number of species of *Oliva* from each of the oceanic basins of the Philippines is given number in Table 6.2. Tursch and Greifeneder (2001) reported 35 species in the Philippines. However, the DMNH material had only 29 species. I used 29 species as the Philippine total, based on the DMNH material. Twenty-seven of the 29 species occurred in shallow water. *O. lacanientai* and *O. pacifica* were trawled off Panglao, Bohol at 300 m depth.

Basin	Species richness
Celebes Sea	11
Philippine Sea	13
South China Sea	25
Sibuyan Sea	22
Sulu Sea	15
Visayas-Camotes Sea	19

Table 6.2 Number of species of *Oliva* in the Philippine Oceanic Basins (see Figure. 2.1 for locations of basins).

Tursch and Greifeneder (2001) reported one endemic species *O. vicdani*. This is not in the DMNH collection.

Earlier assessments of species richness suggest that the Sulu Sea basin is the centre of *Oliva* diversity in the Philippines (Cabrera 1986; Springsteen and Leobrera 1986; Cabrera 1999; Vallejo 2001). This is revised by findings in this study.

6.4.2 Ranges

Figure 6.2 shows 4 general distributions of *Oliva* in the Philippines/. These are 1) central Philippine basins, 2) the edges of basins 3) Central basins with a northward extension, 4) the Eastern Philippines (Figure. 6.2). Some species have been recorded only from one locality (e.g. *O. lacanientai*). A range cannot be defined in these cases. Full range information on the species investigated is given in Appendix 7. The distributions were determined by plotting the occurrences of the 29 reported species on an equal-area map.

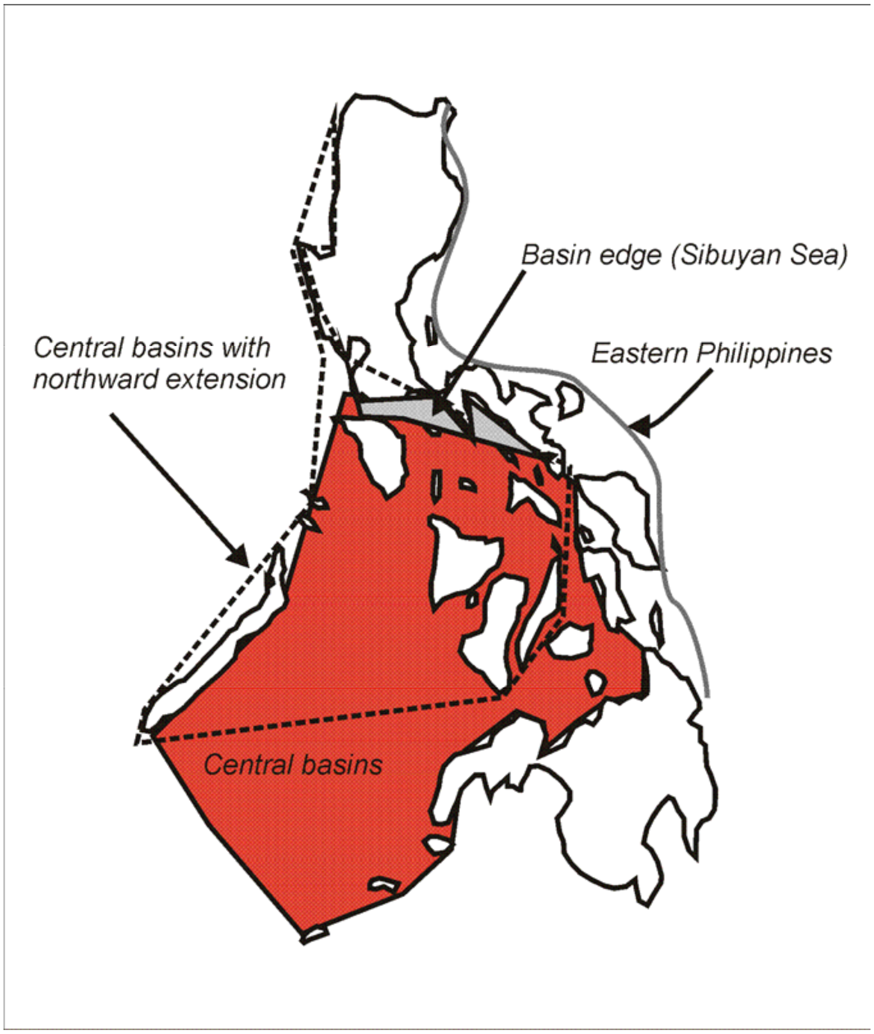


Figure 6.2. Four general distributions of *Oliva* in the Philippines. 1) Central basins, 2) Central basins with northward extension, 3) Sibuyan Sea basin edge, 4) Eastern Philippines

6.4.3 Species-area patterns and provinciality

The Species-area (SPAR) curve for Philippine *Oliva* is shown in Figure 6.3. Table 6.3 show SPAR parameters for the oceanic basins. The relationship is statistically significant (P<0.001) (Table 6.4). The Philippines z value is 0.38. The basin with the steepest slope is the Sibuyan Sea with a z value of 0.63. This z value is not near the 0.8 observed for *Conus* (Chapter 5), and that characterises extremely species-rich biogeographical regions. This is probably due to the fact that the species pool in *Oliva* is less than that of *Conus*.

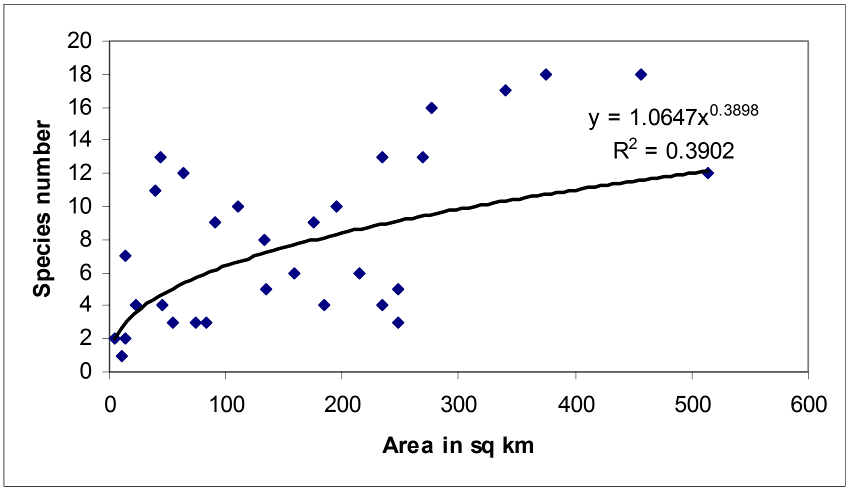


Figure 6.3. SPAR plot for Philippine *Oliva*

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Basin	C	Area	Z	Species number
Philippine Sea	1.37	1119.25	0.27	13
South China Sea	4.97	894.8	0.21	25
Sibuyan Sea	0.34	1461.66	0.63	22
Sulu Sea	1.23	821.11	0.26	15
Visayas-Camotes	2.13	765.89	0.31	19
Philippines	1.06	5102.71	0.38	29

Table 6.3 SPAR estimates of *Oliva* species richness in the oceanic basins

Regression Statistics					
Multiple R	0.622588				
R Square	0.387616				
Adjusted R Square	0.3665				
Standard Error	4.065492				
Observations	31				
ANOVA					
	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	303.3911	303.3911	18.35594	0.000184
Residual	29	479.3186	16.52823		
Total	30	782.7097			

Table 6.4 Species-area regression statistics. There are 31 observations representing the geographical regions used in this study (see Table 6.2).

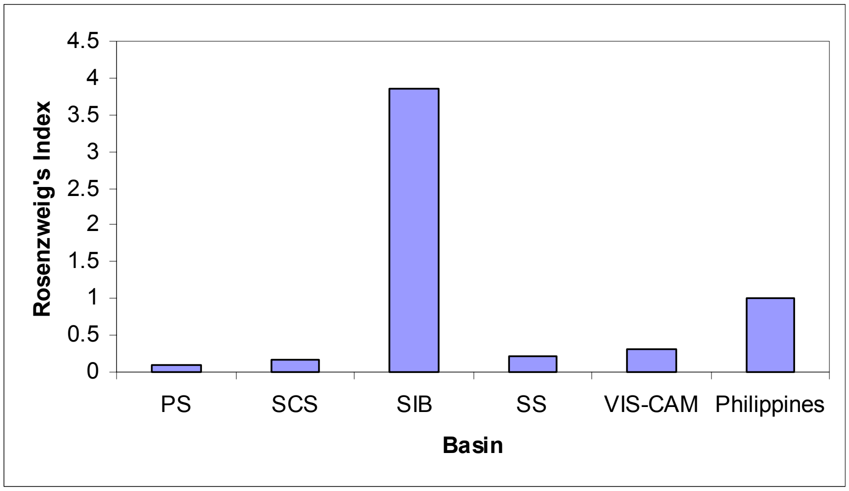


Figure 6.4 Provinciality estimates for *Oliva* in the Philippine oceanic basins PS-Philippine Sea, SCS-South China Sea, SIB –Sibuyan Sea, SS- Sulu Sea, VIS-CAM- Visayas- Camotes Seas

The provinciality index for each basin is shown in Figure 6.4. The most provincial basin is the Sibuyan Sea. The z estimate for the Sibuyan Sea is well within the predicted z values (0.3-0.8) of marine inter-provincial SPAR curves.

GEOGRAPHICAL UNIT	Species number	Frequency of Occurrence
BOHOL	2	3
CALAMIAN	3	11
CEBU EAST (MACTAN)	16	42
CUYO	4	7
DAVAO	11	30
EAST LUZON	2	2
EAST PANAY	4	5
EAST SAMAR	5	5
LEYTE	13	18
MARINDUQUE	10	14
MASBATE	9	14
MINDORO ORIENTAL	18	64
MINDORO OCCIDENTAL	12	19
NEGROS ORIENTAL	7	13
NORTH LUZON	5	5
NORTH PANAY	3	3
PALAWAN	4	9
WEST QUEZON (BONDOC)	17	41
SAMAR	10	23
SOUTHEAST LUZON (BICOL)	8	14
SORSOGON	6	10
SOUTHERN PALAWAN (BALABAC)	3	6
SOUTH PANAY	3	6
SULU	13	48
SURIGAO DEL NORTE	6	12
SURIGAO DEL SUR	4	7
SOUTHWEST LUZON	13	28
WESTERN LUZON (ILOCOS)	18	61
ZAMBALES	12	19
ZAMBOANGA AND BASILAN	9	19
ZAMBOANGA DEL NORTE	1	1

Table 6.5 Species number and frequency of occurrence from DMNH records of *Oliva* in the geographical regions studied. The numbers suggest that larger geographical regions have more recorded species and more frequencies of occurrences.

6.4.4 Geometry of Species Ranges: Areography

The frequency distribution of range sizes of *Oliva* in the Philippines is shown in Figure 6.5. The distribution is skewed to the right. This is typical of species-rich biogeographic regions.

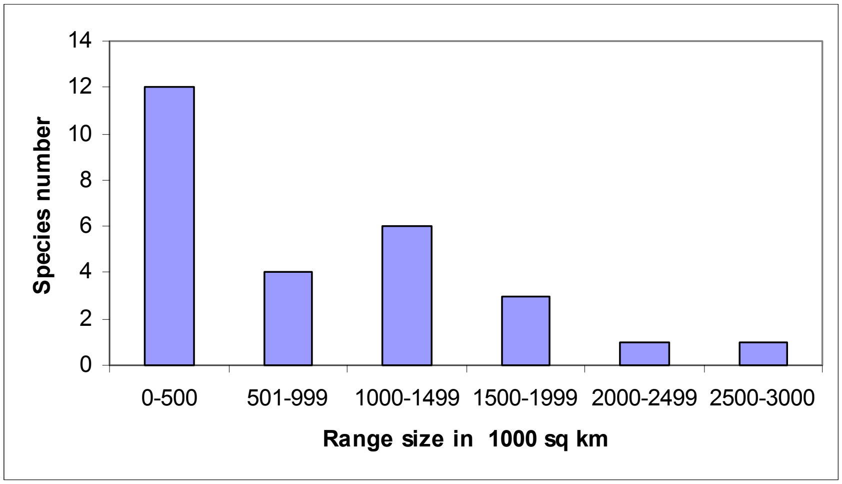


Figure 6.5 Range size frequency distribution in Philippine *Oliva*.

The frequency distribution of range sizes of *Oliva* is partially bi-modal. A majority of species have a range size less than 500,000 sq km. These species have narrow ranges almost all confined to the central Philippines oceanic basins. A second mode occurs at a range size of 1-1.5 million sq km.

6.4.5 Range shape

The majority of geographic ranges of species of *Oliva* are polygonal (Figure 6.6). Since they mostly lie below the diagonal of Figure 6.6, these ranges are not orientated north to south. These distributions cover the central oceanic basins (Quadrant 1 in Figure. 6.6). A few ranges are narrow and orientated east to west (Quadrant 2). These ranges are limited to the edges of oceanic basins. The results show that Philippine *Oliva* species are mainly found in the central Philippines.

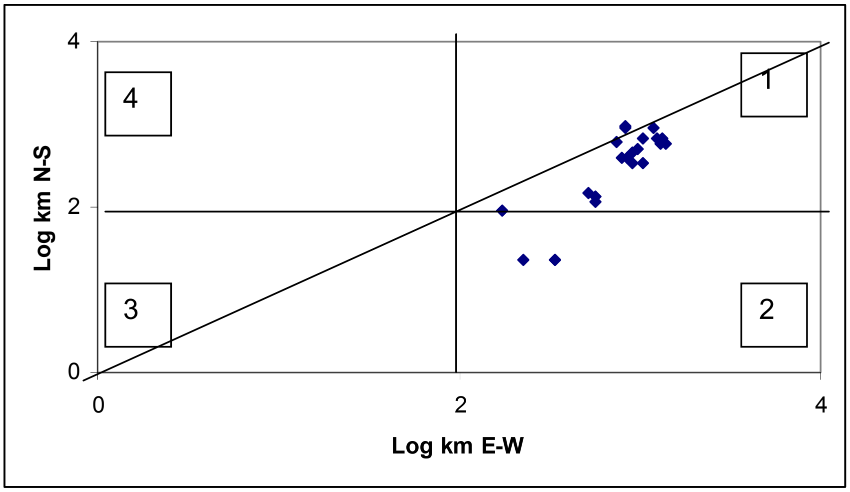


Figure 6.6. Range shape in Philippine *Oliva* species (see Figure 3.3 for diagrams of the 4 range shapes).

6.4.6 Principal Components Analysis of species richness and occurrence

The plot of the PCA ordination is shown in Figure 6.7. Table 6.6 shows the OGU loadings on the PC axes. The first PC axis (43.52 % of variation) is associated with high frequency of occurrences in the geographical regions studied. As discussed in Chapter 4, frequency of occurrence is the number of times a species has been recorded from an OGU. It is not a direct measure of abundance but may reflect general trends in abundance. The regions that are negatively associated with PC 1 are highly diverse with numerous frequencies of occurrences of species recorded in these regions. PC 2 accounts for 14.77 % of the variation and is associated with variable species richness and lower frequencies of occurrence on island coastlines. The PC1 axis separates high species-rich regions (found on the coastlines of the larger Philippine islands) from less species-rich regions found on smaller islands. Consequently, these smaller islands have less frequencies of occurrence of species recorded. The relationship of species number and frequency of occurrence is shown in Figure 6.8. As species number increases in a geographical region, the frequency of occurrence increases. The PCA suggests that *Oliva* species richness is affected by island area.

		Axis Component		
GEOGRAPHICAL REGION	CODE	1	2	3
BOHOL	BOHOL	2.2246	0.3924	-0.6776
CALAMIAN	CAL	3.4159	1.1903	-0.8021
CEBU EAST (MACTAN)	CEBE	-6.1805	0.3973	3.0731
CUYO	CUYO	2.5644	-1.134	0.9658
DAVAO	DAV	-5.4675	5.4057	0.4826
EAST LUZON	ELUZ	3.3187	1.0209	-0.1765
EAST PANAY	EPANAY	2.8889	0.345	-0.5696
EAST SAMAR	ESAM	1.9393	0.2101	-0.2472
LEYTE	LEYTE	-0.4978	1.6105	-0.5592
MARINDUQUE	MARIN	0.1817	1.44	-0.1457
MASBATE	MASBATE	1.6557	0.6343	-2.1049
MINDORO ORIENTAL	MINW	-9.9638	-5.334	-7.2325
MINDORO OCCIDENTAL	MINE	2.0386	-0.6408	-0.0461
NEGROS ORIENTAL	NEGOR	2.554	-1.6249	1.6232
NORTH LUZON	NLUZ	3.1011	0.313	0.0373
NORTH PANAY	NAPANAY	3.215	0.8128	-0.0605
PALAWAN	PAL	2.4351	-0.8703	1.6499
WEST QUEZON (RAGAY)	QUEZONW	-4.8981	-2.1837	0.9824
SAMAR	SAM	1.0772	-3.3549	4.423
SOUTHEAST LUZON (BICOL)	SELUZ	2.9115	-0.405	1.1418
SORSOGON	SORS	2.8597	-0.2361	1.4141
SOUTHERN PALAWAN (BALABAC)	SPAL	2.1413	0.2256	-1.085
SOUTH PANAY	SPANAY	3.3078	0.4333	-0.3324
SULU	SULU	-10.2832	8.5105	1.2018
SURIGAO DEL NORTE	SURIN	1.6765	0.553	-2.3027
SURIGAO DEL SUR	SURIS	2.4528	0.8113	-0.9534
SOUTHWEST LUZON	SWLUZ	-4.2882	1.2927	-2.6911
WESTERN LUZON (ILOCOS)	WLUZ	-12.105	-5.2612	3.8768
ZAMBALES	ZAMBA	1.3826	-3.1268	1.2742
ZAMBOANGA AND BASILAN	ZAMBO	1.2737	-1.9694	-2.342
ZAMBOANGA DEL NORTE	ZAMBON	3.068	0.5426	0.1828

Table 6.6 PC loading of geographical units on the first three PC axes.

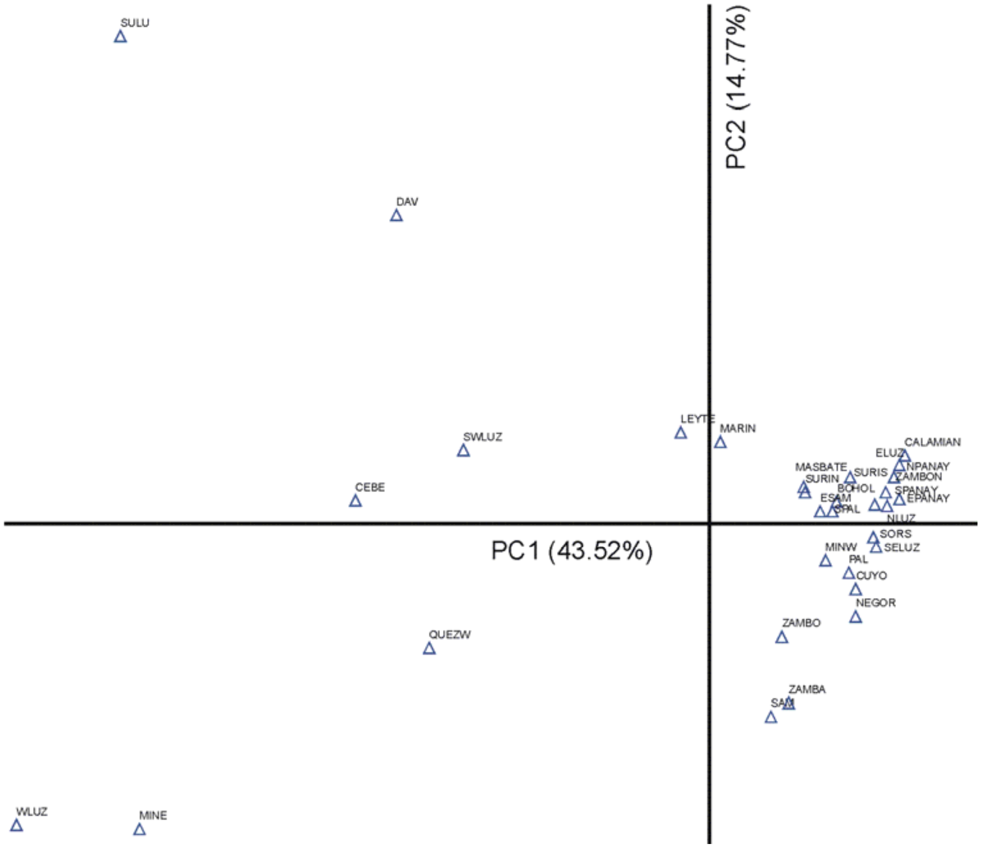


Figure 6.7. PCA ordination of species richness and occurrences of *Oliva* in the Philippines. See Table 6.6 for geographical region codes.

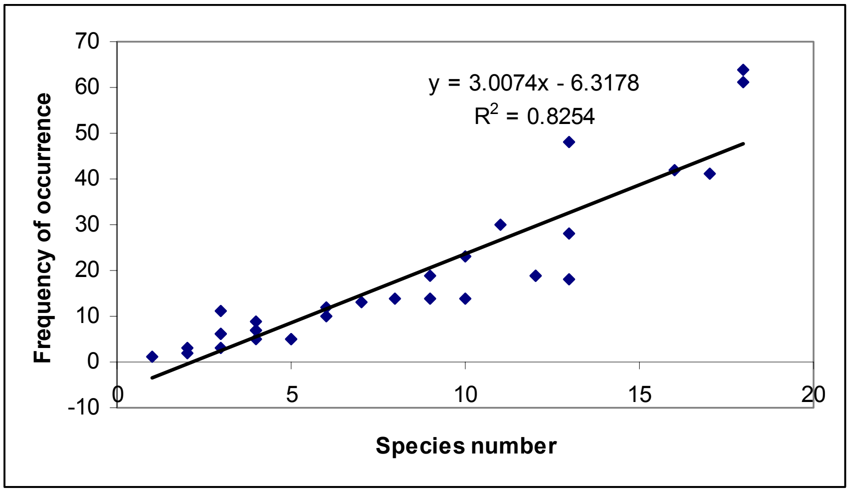


Figure 6.8. Species number increases with frequency of occurrence.

6.4.7 Geographical distribution of species richness: What habitat type predicts geographical species richness?

All types of sandy habitats (see Table 6.1) were significant predictors of geographical species richness of *Oliva*. Regression statistics are shown in Table 6.7. Since all predictors are significant, all have been retained in the regression.

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	.903(a)	.816	.810	6.490
2	.943(b)	.889	.881	5.137
3	.965(c)	.931	.924	4.113
4	.981(d)	.962	.956	3.126
5	.992(e)	.984	.981	2.062
6	1.000(f)	1.000	1.000	.000

a Predictors: (Constant), CORAL
b Predictors: (Constant), CORAL, MUD
c Predictors: (Constant), CORAL, MUD, SAND
d Predictors: (Constant), CORAL, MUD, SAND, MUDDY
e Predictors: (Constant), CORAL, MUD, SAND, MUDDY, MULTISUB
f Predictors: (Constant), CORAL, MUD, SAND, MUDDY, MULTISUB, COARSE

Table 6.7: Summary of stepwise regression statistics of habitat and species richness.

6.4.8 Morphometric analysis

Discriminant analysis suggests that the monotopic *O. amythesitina* species has shell morphologies that are distinct between at least 2 major groups of ocean basins (Figure 6.9). This is not observed in the polytopic species *O. reticulata*. Classification statistics are given in Tables 6.8.

Both *O. amethystina* and *O. reticulata* occur in the central Philippines basins of Sibuyan, Sulu and Visayas-Camotes. However *O. amethystina* can be classified to the correct basin 66% of the time. *O. amethystina* can be correctly classified to the Sulu Sea and Sibuyan Sea basins 80-88.9 % of the time. *O. reticulata* can be classified only to the correct basin 44% of the time. *O. reticulata* in the Sibuyan Sea have high rates of correct classification (78%).

Classification Results *O. amethystina*

	CODE		Basins						Total
			PS	SS	SIB	VIS-CAM	SCS	DAV	
Count of individual classified	PS	Philippine Sea	5	4	0	0	0	3	12
	SS	Sulu Sea	1	8	0	0	0	1	10
?	SIB	Sibuyan Sea	0	0	8	0	0	1	9
	VIS-CAM	Visayan-Camotes	0	1	2	1	1	1	6
	SCS	South China Sea	0	0	1	0	10	1	12
	DAV	Davao (Celebes Sea)	0	1	0	0	0	3	4
% classified	PS	Philippine Sea	41.7	33.3	.0	.0	.0	25.0	100.0
	SS	Sulu Sea	10.0	80.0	.0	.0	.0	10.0	100.0
?	SIB	Sibuyan Sea	.0	.0	88.9	.0	.0	11.1	100.0
	VIS-CAM	Visayan-Camotes Sea	.0	16.7	33.3	16.7	16.7	16.7	100.0
	SCS	South China Sea	.0	.0	8.3	.0	83.3	8.3	100.0
	DAV	Davao (Celebes Sea)	.0	25.0	.0	.0	.0	75.0	100.0

a 66.0% of original grouped cases correctly classified.

Classification Results(*O. reticulata*)

	CODE		Basins						Total
			PS	SS	SIB	VIS-CAM	SCS	DAV	
Count of individual classified	PS	Philippine Sea	8	4	11	5	3	2	33
	SS	Sulu Sea	0	2	0	0	0	0	2
	SIB	Sibuyan Sea	1	0	11	0	1	1	14
	VIS-CAM	Visayan-Camotes	3	1	5	7	4	1	21
	SCS	South China Sea	0	3	1	2	10	0	16
	DAV	Davao (Celebes Sea)	1	0	0	1	1	3	6
% classified	PS	Philippine Sea	24.2	12.1	33.3	15.2	9.1	6.1	100.0
	SS	Sulu Sea	.0	100.0	.0	.0	.0	.0	100.0
	SIB	Sibuyan Sea	7.1	.0	78.6	.0	7.1	7.1	100.0
	VIS-CAM	Visayan-Camotes Sea	14.3	4.8	23.8	33.3	19.0	4.8	100.0
	SCS	South China Sea	.0	18.8	6.3	12.5	62.5	.0	100.0
	DAV	Davao (Celebes Sea)	16.7	.0	.0	16.7	16.7	50.0	100.0

a 44.6% of original grouped cases correctly classified.

Table 6.8 Summary of discriminant analysis classification results for O. *amethystina* and O. *reticulata*

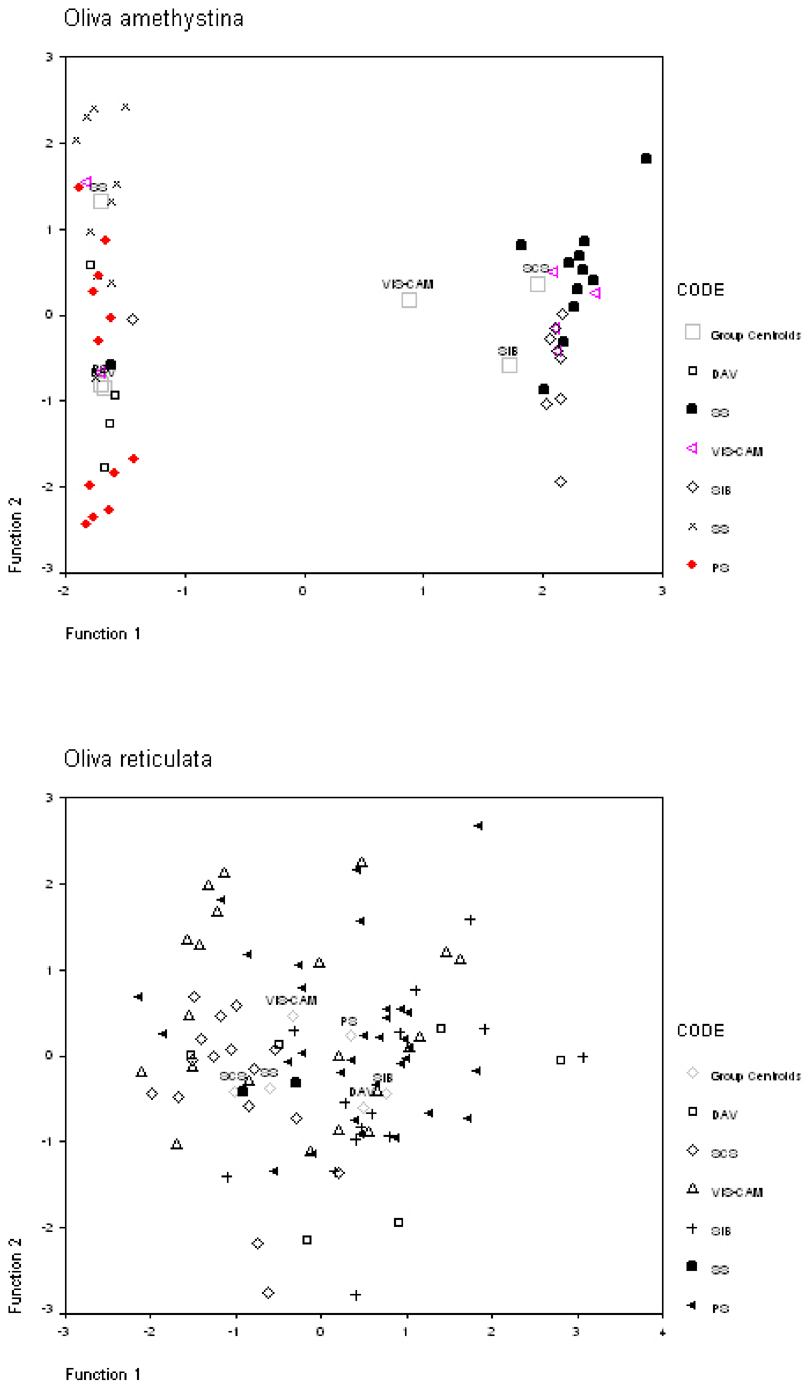


Figure 6.9 Discriminant plots of *O. amethystina* and *O. reticulata* morphometric measures from samples collected from the different oceanic basins. PS-Philippine Sea, SS-Sulu Sea, SIB-Sibuyan Sea, VIS-CAM-Visayas Camotes Seas, SCS-South China Sea and DAV –Celebes Sea (DAVAO COAST)

6.5 DISCUSSION

The distributions of Philippine *Oliva* are similar to those of *Conus* described in Chapter 5. The Sibuyan Sea has the highest species richness for *Oliva* in the Philippines. This basin has the highest provinciality for much of the Philippine fauna (Vallejo 2001). There is only one endemic *Oliva*, based on species identifications of Tursch and Greifeneder (2001). Springsteen and Leobrera (1986) estimate four percent (4%) endemic species for the total marine mollusc fauna in the Philippines. However, these estimates include only macrogastropods.

Range size characteristics in Philippine *Oliva* are largely similar to those of *Conus*. Most *Oliva* species are found in the central Philippine oceanic basins. Thus most distributions are polygonal, and cover these basins. In *Conus*, there are more narrow ranges that straddle just two basins. In contrast, most *Oliva* distributions that are narrow are found on the edges of single oceanic basins.

The frequency distribution of observed range sizes in the Philippines is skewed to the right, and similar to that observed in *Conus*. However the *Oliva* distribution of range sizes is bimodal. This may be related to the distribution of sandy habitats in the oceanic basins, or to the fact that *Oliva* species richness is much less that that of *Conus*. Geographical species richness is correlated with habitat. There is a significant correlation of all habitat classes with species richness in all the geographical regions. This suggests that *Oliva* species richness is not as variable in space as that hypothesised for *Conus* in Chapter 5. The ecology of *Oliva* has not been studied as much as that of *Conus* (Tursch and Greifeneder 2001). Substrate suitability may be the most important factor affecting their distribution. There is very little information on *Oliva* feeding. The few studies available suggest that *Oliva* are not trophically specialised (Ziegler 1969; Tursch and Greifeneder 2001; Malijan 2003). *Oliva* species that overlap in distribution may be more likely to utilise different substrates than different food resources. This contrasts with results for sympatric *Conus* species, that often partition food resources (Kohn 1997). Given that sandy habitats may be more widely distributed in space than the specialised intertidal and subtidal habitats of *Conus*, numbers of species of *Oliva* may not be variable in space, although the species that compose these assemblages may differ.

Principal components analysis suggests that species richness of *Oliva* differs on large island coastlines and smaller islands. The large islands have more species than smaller islands. This agrees with the results of species-area analysis. Since *Oliva* does not have the same level of species richness in the Philippines as *Conus*, I cannot propose area independence. Since most *Oliva* occur in shallow water, the extent of their habitats is a function of the area of the islands themselves. Area is therefore a good predictor in *Oliva* species richness (Tursch and Greifeneder 2001).

The frequency of occurrence increases linearly with species richness because of a data collection artefact. In museum collections, even if these are representative enough, the standard protocol is to collect at least three specimen lots as a record for a region. If a region is larger, more lots will be collected as more species are recorded. However, this data artefact does not affect the general trends in species richness and area.

Analysis of two species of *Oliva* suggests that habitat specificity may influence spatial variation in shell morphology. Divergence in isolated monotopic Papua New Guinea *O. amethystina* has been observed to be rapid (Tursch and Greifeneder 2001). Monotopic *O. amethystina* have shell morphologies that are specific to some ocean basins. However these groupings cannot be generalised to represent east-west discontinuities. *O. amethystina* from the Philippine Sea and the Sulu Sea are grouped together. In addition, Sibuyan Sea, South China Sea and the Visayas-Camotes Sea group together. The Sulu Sea is located within the Philippine archipelago. If an east-west morphological separation occurred, then the South China Sea should group with the Sulu Sea and the other central basins should group with the Philippine Sea. Perhaps the Sulu Sea and the coasts of the Philippine Sea group together because they have similar exposure to the monsoons.

Polytopic *O. reticulata* had no spatial variation in shell morphology. This suggests a morphological continuum in populations. Morphological characteristics intergrade in space. A polytopic species is able to utilise a greater suite of environments. Each response to a particular environment will be reflected as a particular morphological adaptation. Since the environments intergrade in geographical space, a morphological continuum may be observed (Tursch 1994; Tursch 1998; Tursch and Greifeneder

2001). Partial genetic isolation along the morphological continuum may occur, although this has not been verified (Tursch and Greifeneder 2001).

The results of the *Oliva* investigations support the suggestion that the basins are somewhat unique biogeographical units. The high provinciality of the Sibuyan Sea may be related to the numerous habitats and islands in this basin. This has an historical basis, for the basin is tectonically complex, and was associated with significant volcanism in the Miocene. The tectonic reconstruction of the IWP island arc by Hall (1998) shows that the Sibuyan Sea was once a passageway between the Indian and Pacific Oceans. Closure occurred with the rotation of Luzon to its modern orientation, beginning in the early Miocene. Subsequent northward movement of the Visayan islands as a result of Australia's northward movement, narrowed the connection of the Sibuyan Sea from Pacific and Indian Oceans in the late Miocene. Other seas that had similar histories are the Moluccas and Banda Seas. However these seas were not as landlocked as the Sibuyan. In the Pleistocene, the Sibuyan basin was almost completely isolated from the Indian and Pacific Oceans (Heaney 1986). An alternative explanation for the high provinciality of the Sibuyan Sea is its current small size. Basins of small size, but with large numbers of habitats and thus species, will invariably give high provinciality estimates (see Equations 3.5 and 3.6). However, this would suggest that the Visayan basin should also show high provinciality, but it does not.

The timing of speciation events in *Oliva* is an important future focus of research. Tursch and Greifeneder (2001) hypothesise that much of the *Oliva* speciation occurred after the closure of the Tethyan Seaway and the modern species ranges conserve much of the information of this historical event. The evolutionary history of the genus has been reviewed by Petuch and Sargent (1986). The mid to late Miocene saw two major species radiations in the genus. One radiation occurred in what became the IWP island arc and another in what became the south-eastern United States. With Hall's tectonic reconstructions, the radiation of *Oliva* in the IWP may have been associated with numerous closures of seaways in the Miocene. One of those seaways was the Sibuyan Sea.

In the Pleistocene, a second IWP radiation occurred (Petuch and Sargent 1986). This is hypothesised to be related to sea level changes as a result of glaciation. That many IWP species are wholly contained within the IWP island arc supports this hypothesis (Tursch and Greifeneder 2001).

It is possible that *Oliva* was prone to basin isolation, and that this promoted speciation in the IWP. If their hypothesised short larval life is confirmed, and if this has been conserved in its evolutionary history, then the hypothesis of origin within the IWP island arc may be testable. This requires a molecular phylogeny

In the next chapter, I examine the nature of speciation within the IWP island arc of *Conus*.

6.6 CONCLUSIONS

1. The distributions of most Philippine *Oliva* are within the central Philippines. Thirty-five species were reviewed in Tursch and Greifeneder (2001). Twenty nine (29) species were used in this study.
2. Ranges of *Oliva* occur in 4 general distributions. The frequency distribution of range sizes in the Philippines is bi-modal but right skewed.
3. Species richness increases with area sampled. The Sibuyan Sea has a high degree of provinciality. This agrees with earlier observations on other taxa.
4. All habitat classes correlate positively with species richness of *Oliva* in all geographical regions. This suggests that *Oliva* species richness is not variable between regions.
5. PC analysis suggests that larger islands have more species than smaller islands. This agrees with the SPAR analysis.
6. The monotopic *O. amethystina* fall into two distinct geographic groups based on shell morphology. This is not clearly observed in the polytopic species *O. reticulata*.
7. *Oliva* may be a useful taxon to test the IWP centre of origin hypothesis. This will require a detailed phylogeny based on molecular marker techniques.

CHAPTER 7.

Inferring the mode of speciation in Indo-West Pacific (IWP) *Conus*

"Obviously, even if all these assumptions should turn out to be invalid, this would not necessarily prove that the basic hypothesis is wrong. In any case, a critical evaluation of the various assumptions will lead to a clearer understanding of the problem."
Ernst Mayr (1947)

7.1 INTRODUCTION

Several hypotheses have been proposed to account for the origin of high marine species diversity in the IWP island arc (Rosen 1988; Rosen 1988). They can be grouped into 1) centre of origin (McManus 1985; Briggs 1987; Briggs 1992; Briggs 1996; Briggs 2000) and 2) center of accumulation hypotheses (Jokiel and Martinelli, 1982). The former is based on the age and area hypothesis of Stehli and Wells (1968). It assumes that older taxa have wider ranges and are found near the centre of origin of the lineage. The latter is based on the geometry of modem species distributions and the occurrence of endemics in the Indian and Pacific Oceans.

The two hypotheses are framed in the context of a complex geology, oceanography and geography of the IWP island arc (Hall 1998). The isolation of marginal ocean basins during reduced sea level periods in the Pleistocene may have contributed to possible speciation within the IWP island arc (McManus 1985; Potts 1985). Recent studies have focused on the biotic history of the island arc (Pandolfi 1992; Wilson and Rosen 1998) in order to test either hypothesis.. The molecular biogeography of widely distributed marine invertebrates in the IWP suggests that there is population genetic structuring (Palumbi 1997) despite the presence of ocean currents that allows for genetic connectivity. There is also evidence of a biogeographic break in *Linckia* seastar colour morphs between the Indian and Pacific Oceans (Williams and Benzie 1998). The population genetic structuring in *Tridacna* populations in the IWP are not coincident with modem ocean current systems (Benzie 1998). This may be a result of previous dispersal by paleo-currents. The molecular biogeographic evidence supports either hypothesis, depending on the taxon investigated. The contrasting molecular evidence may support a third general hypothesis, that successive isolation at any place in the IWP may have resulted in speciation rather than speciation just from the IWP arc itself (Pandolfi 1992).

In *Conus*, range extents in the IWP suggest that dispersal is an important determinant of range size in many of the shallow-water coral reef dwelling species (Kohn and Perron 1994). Many reef species have a distribution encompassing the Indian and Pacific Ocean (Röckel et al. 1995). The length of the pre-competent planktonic stage in a species is related to the size of the range (Kohn and Perron 1994).

Distributional ranges can be indicative of niche breadth (Brown 1996; Gaston 1996) and history of speciation (Berlocher 1998; Maurer and Nott 1998). Ranges can thus be used to infer the nature of speciation (Berlocher 1998) if there is phylogenetic information available. The range extents of *Conus* with widely distributed species are usually sympatric or overlapping. Some endemic species can occur on the edge of the known ranges of the most widely distributed members of the genus.

Allopatric speciation is the most common mechanism assumed to account for marine species diversity. In this mode of speciation, the fragmentation of geographical ranges has resulted in reproductive isolation, leading to speciation (Mayr 1976). The other mode of speciation is sympatric , with species arising within the parent geographic range (Maynard-Smith 1966).

A geographical range may have thus resulted from either allopatric or sympatric speciation. It is extremely difficult to infer mode of speciation from range size and geometry alone. It is necessary to determine from historical inference what the likely origin was. Gaston (1996) suggested that species with larger range sizes are more likely to speciate than those with smaller ranges. and thus spawn smaller ranges. Species with large range sizes tend to persist longer in evolutionary time, and thus have a higher probability of allopatric speciation. Gaston considers two allopatric speciation modes, the allopatric vicariant mode (geographical fragmentation within the range) and the peripheral vicariant mode (fragmentation of ranges at the edge of the parent distribution). Gaston's hypotheses on allopatric speciation can only be investigated by relating range sizes with phylogenetic information.

According to Barraclough et al (1999), there are four events that could lead to present day patterns of species diversity (Figure 7.1). In sympatric speciation, two events are possible. Range sympatry will tend to decrease as node height increases. The other situation is no change in range sympatry at all. In allopatric speciation, range sympatry increases with node height as new species arise but since geographical space is limited, there will be a level of maximum sympatry. The other situation is a no range change after speciation. In these models new species are formed by allopatric and sympatric speciation. New ranges are then formed that may either expand or contract. As ranges expand or contract, natural selection will cause changes in genotypes and phenotypes. Lastly, range contraction may lead to extinction. The main premise for the models is that range sympatry is a product of purely range expansion after speciation.

Range expansion and contraction operates in ecological time. Environmental and geographical factors affect range extents and the subsequent genotypic and phenotypic changes. Phylogenetic information at the species level may provide information on how these factors contributed to this process. However information on conditions in the past may not be accurately preserved in modern species and their ranges. In order to get the most information, it is necessary to compare present day range extents and the hypothesized phylogeny with a null model (Barraclough et al. 1999).

The approach of Barraclough et al (1999) is to plot the degree of sympatry (range overlap) with node height as a measure of evolutionary divergence The degree of range overlap is measured as sympatry, while node height is a relative distance from the node to the tips of the phylogeny. Node height is used as a measure of divergence in the DNA sequences. A low node height for a species suggests that the species had diverged recently. Under a null model, the size of a geographic range is independent of phylogeny. As node height increases in the null model, the degree of sympatry increases (Figure 7.1). Sympatry increases as more species are produced. If speciation had been sympatric, an intercept of greater than 0.5 is expected, since one of the species' range should be contained within the parent species range. If allopatric speciation has occurred, the intercept is at 0 since, at the start, the parent and daughter ranges were separated.

In allopatric speciation, the range of the daughter species should expand. This would result in increasing sympatry as geographic space is occupied by an increasing number of species. In sympatric speciation, assuming that ranges expand, there is a decrease in sympatry with species diversification. Zero sympatry would suggest a vicariance event. The approach of Barraclough et al (1999) has been used to distinguish broad geographical speciation patterns in tiger beetles *Cicindela,* Madagascar lemurs, auks, warblers, cranes, *Xiphophorus* platies and swordtails, fruitflies and leaf hoppers (Barraclough and Vogler 2000)

Berlocher (1998) explores Barracloughs' models by predicting sympatric speciation with host shift (in parasitic species), habitat shift (in non-parasitic species) and polyploidy or hybrid speciation. Since *Conus* is not a parasitic species but a species with defined habitat preferences (Kohn 1967; Kohn 1969), it is possible to infer the mode of speciation if this was accompanied by habitat shifts. Sympatric speciation can only occur with habitat shift in two sister species.

According to the habitat-shift hypothesis, species will be monophyletic if speciation had been sympatric. This also implies that sympatric species are always sister species. The assumption is that there are no obvious barriers in the geographic unit in which the hypothesized speciation occurred. The habitat-shift hypothesis can thus be investigated with phylogenetic evidence.

In this study, I explore the possible mode of speciation in IWP *Conus* by relating its calibrated molecular phylogeny with modern range extents, and habitat information..

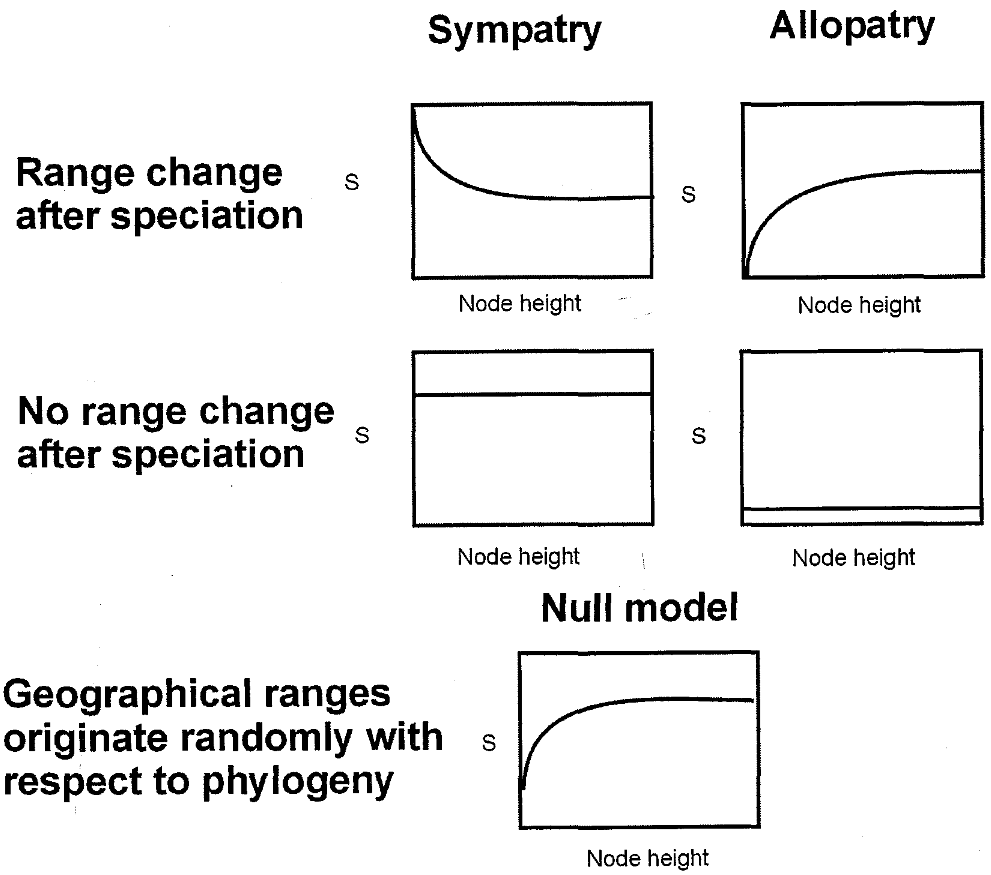


Figure 7.1. Degree of sympatry (S) (= PROPORTION OF RANGE OVERLAP) and node height as a measure of evolutionary divergence in sympatric and allopatric modes of speciation. The bottom figure is a null model where speciation occurs randomly over geographic space with respect to phylogeny (Figure adapted from Barraclough et al 1999)

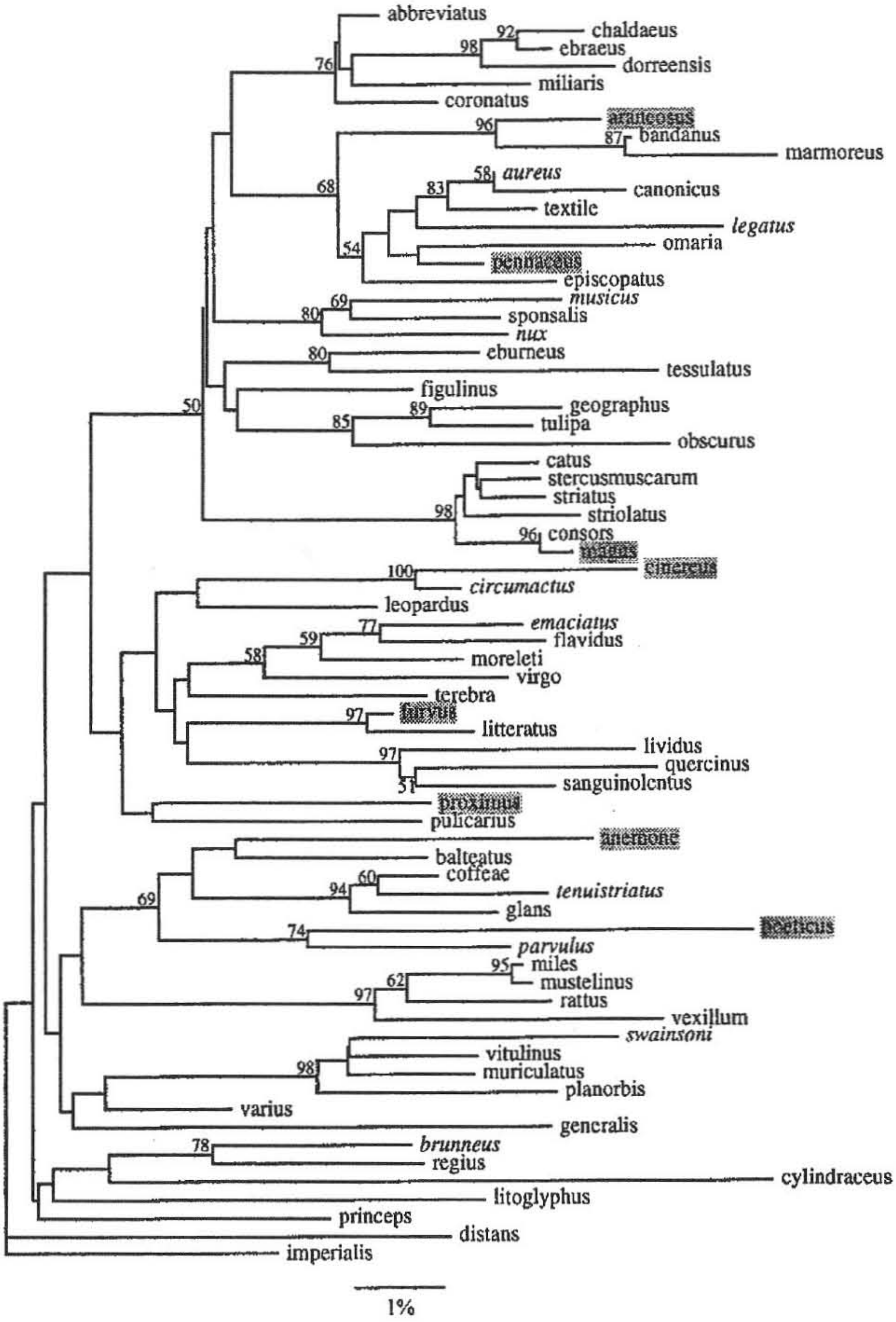
7.2 MATERIALS AND METHODS

7.2.1 Species and Phylogenies

Molecular phylogenetic information on 70 shallow-water species of *Conus* is based on Duda and Palumbi (1999). This phylogeny used calmodulin sequences, and clades were reconstructed from mtDNA analyses (Figure 7.2): Duda and Palumbi calibrated the rate of sequence evolution using fossil sequences. I used only species that formed monophyletic clades with a bootstrap support of > 95%. Bootstrapped clades have been earlier determined by Duda and Palumbi. Bootstrap values > 95% suggests high precision in reconstructing the most common splits in a tree (Page and Holmes 1998). Since the *Conus* phylogenetic tree is a consensus of numerous trees, clades with high bootstrap values are likely to be robust (Duda and Palumbi 1999). Thirty nine species from 11 clades of shallow water *Conus* were used for my analyses (Table 1). I then measured the length from the base of the node to the tips of the branches (Gaston 1996) from the published phylogeny. The node length is an estimate of evolutionary divergence. Node height is expressed as a ratio of the length of the 1% scale bar with the length of the node (Figure 7.2)).

Genus	Species	Diet	Habitat	Habitat Code	Clade	Range size in million sq. km
Conus	*abbreviatus*	polychaetes	Intertidal bench	2	0	5
Conus	*chaldeaus*	polychaetes	Intertidal bench	2	1	189
Conus	*ebraeus*	polychaetes	Intertidal bench	2	1	195
Conus	*doreensis*	polychaetes	Intertidal bench	2	1	3
Conus	*miliaris*	polychaetes	Intertidal bench	2	1	83
Conus	*coronatus*	polychaetes	Intertidal bench	2	1	12
Conus	*areonosus*	molluscs	sand	3	2	34
Conus	*bandanus*	molluscs	sand	7	2	43
Conus	*marmoreus*	molluscs	sand	7	2	87
Conus	*eburneus*	Worms/fish	sand	2	3	99
Conus	*tessulatus*	Worms	sand	1	3	113
Conus	*figulinus*	Worms	sand	5	4	9
Conus	*geographus*	Fish	sand	6	4	83
Conus	*tulipa*	fish/molluscs	sand	7	4	93
Conus	*obscurus*	Fish	sand	7	4	106
Conus	*catus*	Fish	Intertidal bench	2	5	106
Conus	*stercumuscarum*	Fish	sand	7	5	26
Conus	*striatus*	fish/molluscs	sand	1	5	111
Conus	*striolatus*	worm/fish	sand	5	5	25
Conus	*consors*	worm/fish	sand	1	5	65
Conus	*magus*	Fish	sand	1	5	38
Conus	*miles*	worm/fish	sand	2	6	120
Conus	*mustelinus*	Worms/nereids	sand	8	6	35
Conus	*rattus*	Worms/nereids	sand	8	6	97
Conus	*vexillum*	Worms/eunicids	sand	7	7	109
Conus	*swainsonii*	Worms	sand	1	7	1
Conus	*muriculatus*	Worms	sand	8	7	53
Conus	*planorbis*	polychaetes	sand	8	7	90
Conus	*lividus*	terebellid/worms	reef/subtidal	8	8	91
Conus	*quercinus*	polychaetes	sand	1	8	92
Conus	*sanguinolentus*	polychaetes	Intertidal /sand	2	8	61
Conus	*tenuistriatus*	polychaetes	reef/subtidal	3	9	29
Conus	*coffeae*	Worms/eunicids	sand/coral	3	9	56
Conus	*glans*	Worms/eunicids	reef/subtidal	2	9	100
Conus	*circumactus*		sand	1	10	31
Conus	*cineraeus*	Fish		3	10	37
Conus	*furvus*	Molluscs	sand	1	11	15
Conus	*litteratus*	polychaetes	sand	7	11	97

Table 7. 1. *Conus* species used in this study. Underlined species are those with a non-planktonic life history



Node height = node length/ length of 1% scale bar

Figure7.2. Neighbour-joining tree phylogeny constructed from calmodulin intron sequences of IWP *Conus*. Bootstrap values are indicated at the nodes. Names in italics are species where life history characteristics are unknown. Shaded names are species with non-planktonic life histories. (From Duda and Palumbi, 1999).

7.2.2 Determination of range extents

The range extents of the 39 species were determined from Rockel et al (1995). Each published map was appropriately scaled and I estimated range size by counting the number of scaled grids and multiplying this with a scaling factor.

7.2.3 Sympatry and evolutionary divergence

I plotted the extent of sympatry, or the degree of range overlap and node height, in the 39 *Conus* species. The resulting relationship was plotted as a linear regression.

7.2.4 Sympatry and length of pelagic stage

I also plotted extent of sympatry against the length of the precompetent pelagic stage reported in Kohn and Perron (1994)

7.2.5 Sympatry and habitat characteristics

I classified *Conus* species as "non-specific" if they occupied more than two kinds of habitat (generalists). *Conus* species that occupy a single kind of habitat were defined as "habitat-specific" (specialists). I explore the trends in sympatry and evolutionary divergence in *Conus* among habitat-specific and non-specific *Conus* species, by plotting sympatry and node height. The resulting relationship was plotted as a linear regression.

7.3 RESULTS

7.3.1 Sympatry and node height

The relationship between extent of sympatry and node height is shown in Figure 7.3.

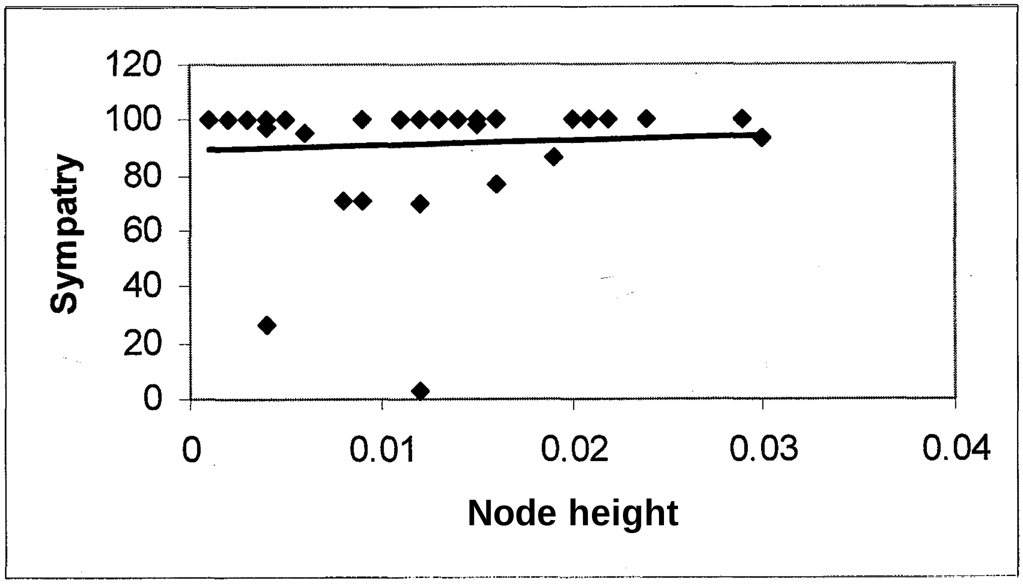


Figure 7.3. The relationship between syrnpatry and node height in the *Conus* phylogeny.

The relationship between node height and extent of sympatry is not informative. Even for species that had diverged recently (low node height), sympatry with other *Conus* was near 100%. The regression is not significant (p = 0.77). This pattern suggests a high degree of sympatric speciation under the Barraclough et al (1999) model.. However, their model also predicts that sympatry will decrease as node height increases. This is not the case here. The pattern suggests that ranges have retained little if any information on the location of speciation. The ranges have changed regardless of the time of speciation. However in a few species with parapatric distributions, there is an increase in sympatry with node height since these species have distributions that are smaller and have less sympatry with the wide ranging species. The fact that many of these species have a node height of less than 0.02 suggests a recent divergence. A species with 3.37% sympatry is C. *doreensis* that belongs to the *ebreaus* clade. This species has a distribution confined to the coastline of Western Australia. Its low node height suggests a recent divergence due to a vicariant event. *C. abbreviatus,* as an outgroup of that clade, has a sympatry of 27%

and is confined to the Indian Ocean. This also suggests speciation due to vicariance. The phylogenetic and historical range information have been conserved in these species.

If sympatric speciation occurs, species with an unusually large sympatry with a low node height will occur. This is observed in the *Conus* data. Species with low node height and 100% sympatry with members of their clade include *C. bandanus, C. consors* and *C. miles.* However in these species, their ranges are large. For example, *C.miles* is largely sympatric with *C. rattus.* If sympatric speciation did occur, the historical information on where and how this happened has been obscured.

Most members of Clade 1 *(ebraeus* clade) have wide distributions and a high degree of sympatry. With the possible exception of the Western Australian endemic *C. doreensis,* members of this clade may have speciated sympatrically. This might be the mode of speciation between the sister species *C. ebraeaus* and *C. chadeaus.* These species overlap in range with *C. chaldeaus,* occupying a lower intertidal habitat than *C. ebraeus* (Röckel et al. 1995). *C. chaldaeus* has the largest node height, and thus diverged earlier than other members of the clade.

Members of Clade 1 conform to a prediction of sympatric speciation. In the absence of obvious geographical barriers to speciation, if species with overlapping ranges are monophyletic and are habitat specific, then they have likely speciated sympatrically. Range overlap or sympatry is negatively correlated with node height in sympatric speciation This prediction is shown by Figure 7.4 and shows a pattern similar to that predicted by the sympatric speciation model shown in Figure 7.1.

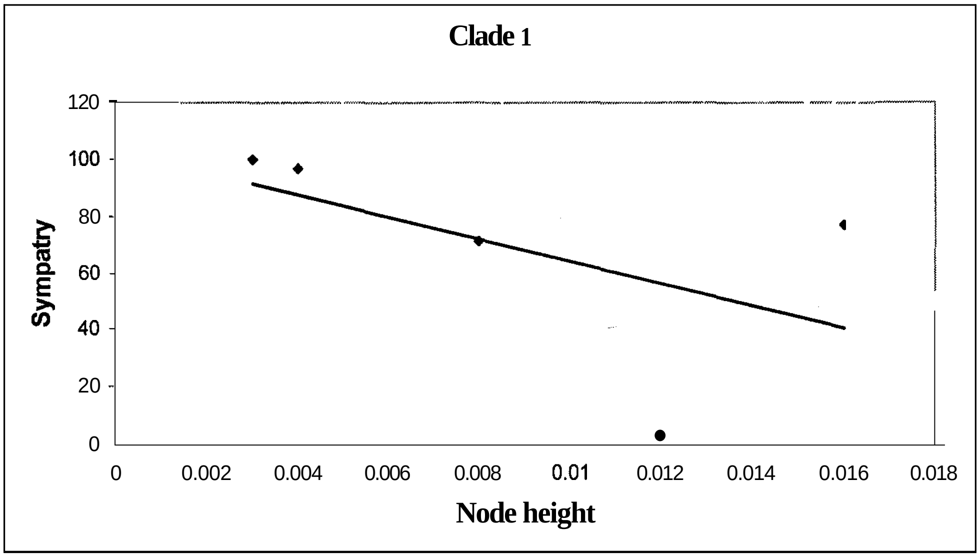


Figure 7.4. Decrease in sympatry with increasing node height in members of Clade 1 (the *ebraeaus* clade). This trend is consistent with a prediction of sympatric speciation.. (r^2 =0.3, p= 0.56)

7.3.2 Sympatry and habitat characteristics

Non habitat-specific species (species that can live in two or more kinds of microhabitat) exhibit a greater degree of sympatry than habitat-specific species. The regression lines in both classes are non-significant (p = 0.52 for habitat specific and p = 0.63 for non habitat-specific). There are habitat-specific low sympatry species with a low node height. The regressions do show weak positive and negative relationships. This suggests that there has been range changes after speciation and that the geographic mode of speciation in the species has been obscured. The lack of a relationship indicates that one cannot infer either allopatric or sympatric speciation.

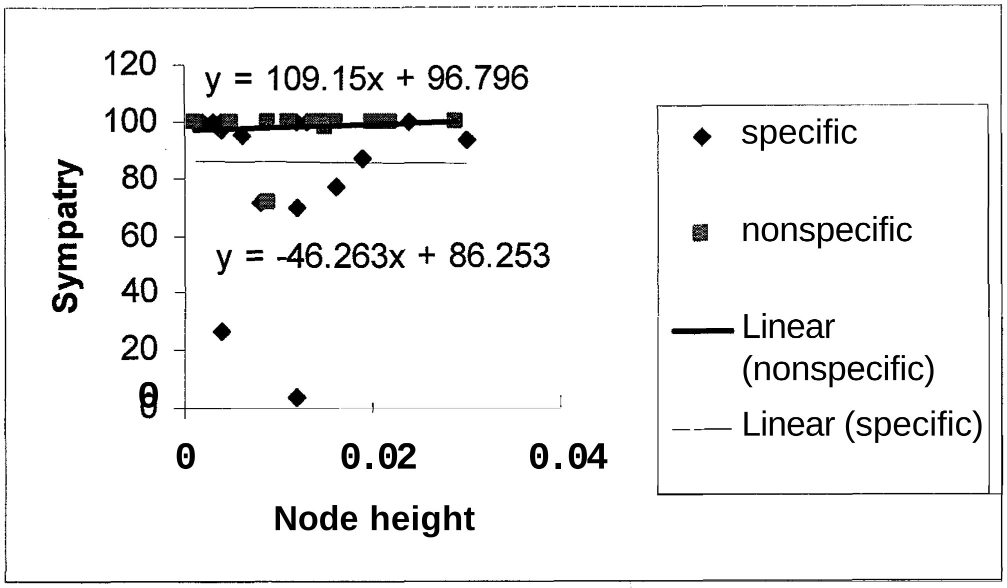


Figure 7.5. Trends in sympatry and node height among habitat-specific and non-habitat-specific *Conus*

7.3.3 Pelagic stage and node height

As node height increased, there was an increase in the length of the pelagic larval stage in *Conus* species. This relationship is not statistically significant (P=0.22) (Figure 7.6)

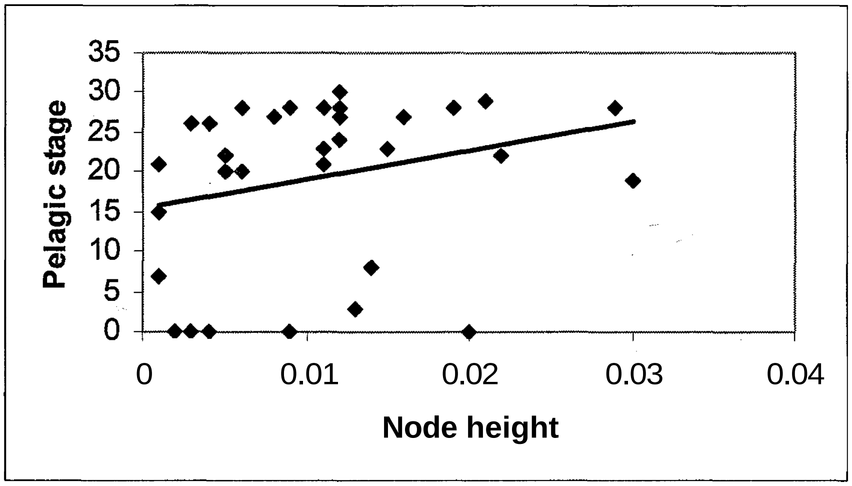


Figure 7.6. Positive relationship between length of pelagic stage and node height. (r^2 = 0.14, P=0.22)

7.4 DISCUSSION

The low endemism and high species diversity in the IWP island arc are difficult to explain. The processes that shape this observed pattern are not fully understood (Bellwood and Hughes 2001). This contrasts with the terrestrial environment, where isolation of biotas has promoted rapid species diversification in numerous taxa (Wallace 1859; Wallace 1880; Heaney 1986; Simberloff and Martin 1991; Rosenzweig 1995; Heaney 1998; Heaney and Regalado 1998; McKinney 1998; Heaney 1999). Species diversification as a result of isolation is demonstrated clearly in the Philippine archipelago (Oosterzee 1997; Heaney 1998) where the age of each of the major islands corresponds to the phylogenetic age of the plant and animal taxa on each island.

The model of species diversification in the terrestrial flora and fauna of the Philippines has been repeated colonization by chance events and subsequent isolation due to vicariant events such as Pleistocene sea level changes (Heaney 1986). Pleistocene sea level changes have been proposed as the main mechanism of speciation in shallow water coral reef taxa in the Philippines and the marginal oceanic basins of Indonesia (McManus 1985). The Philippine archipelagic sea of

Sibuyan remains as the centre of species diversity in *Conus* (Vallejo 1999) in the IWP, and other Philippine archipelagic seas are centres of species diversity in other marine vertebrate and invertebrate taxa (Vallejo 2001; Aliño et al. 2002).

This pattern of high species diversity in different taxa would suggest that speciation occurred in these archipelagic seas. However this hypothesis may be investigated only by inferring the mode of speciation.. *Conus* is an excellent taxon to investigate the hypothesis of species origin in the IWP island arc. The taxonomy, ecology, reproductive biology, phylogeny and biogeography of *Conus* has been described (Kohn 1967; Kohn 1969; Kohn and Nybakken 1975; Kohn 1980; Kohn 1990; Kohn 1990; Kohn 1994; Kohn and Perron 1994; Röckel, Korn et al. 1995; Kohn 1997; Duda and Palumbi 1999; Duda et al. 2001). There is abundant information on the natural history of *Conus* to infer the direction of its evolutionary history.

The results of this study confirm the hypothesis that planktotrophy in the genus is probably of ancient origin. This characteristic is lost in a few species that have recently speciated on the outer edge of IWP. In species with a distribution that includes the IWP island arc (C. magus, C. cineareus), the distributional ranges do not extend beyond the western Pacific. Non-planktotrophy has evolved in different clades. There are no clades that are purely non- planktotrophic (Duda and Palumbi 1999) The mode of speciation in the genus cannot be ascertained, as the slope of the sympatry versus node height plots are not significant. If sympatric speciation did occur, the historical information on these events has been obscured. The possibility of sympatric speciation is greatest in Clade 1 (the ebraeus clade). Members of the clade fulfil some of the predictions of sympatric speciation, as most members have wide distributional ranges and are habitat-specific. This implies that there had not been geographical barriers to distribution. Diversification in this clade cannot be inferred from the allopatric model. In other clades, this prediction cannot be investigated since they have both habitat-specific or non-specific species.

It is easier to detect allopatric than sympatric speciation. Low node height and very low sympatry suggest allopatric speciation. This is seen in *Conus*, especially for species with parapatric ranges. However this is not very informative. Rapid dispersal as planktonic larvae via ocean currents is a characteristic of many members of the genus. This life history strategy has been largely conserved in the evolution of the genus. This probably contributed to the large degree of sympatry regardless of node height in the genus. The process of dispersal operates in ecological time.

Non-informative relationships between sympatry and node height have been demonstrated in the taxa modelled by Barraclough and Vogler (2000). Widely dispersive birds such as auks, and warblers, insects such as fruitflies and leafhoppers show non-informative relationships because of increasing sympatry among recently split clades. In fruitflies that are host-specific, some clades show a sympatric speciation pattern. If this pattern occurs in higher frequencies, sympatric speciation may be detected (Barraclough and Vogler 2000). Nevertheless, when the models are considered together, there is a signal of allopatric speciation. The same study also presents models that show clear signals of allopatric speciation. In the freshwater fish *Xiphophorus*, birds such as cranes and fairy wrens, the models show clear patterns of vicariant speciation. Platnick and Nelson (1978) earlier examined speciation in platies and swordtails as a case in vicariance biogeography. With the exception of cranes, members of the taxa are not dispersive. However cranes require specialised wetland habitats (Kennedy et al. 2000) that may isolate populations and promote allopatric speciation.

Barraclough and Vogler (2000) suggest that non-informative relationships are due to range changes after speciation. If these changes are so great, the model becomes unreliable. The non-informativeness of the models may be due to differing rates of speciation, post-speciational range changes that include extinction, ecological displacement, rapid dispersal at very short timescales (Barraclough and Nee 2001) and climate and geological factors (Barraclough and Vogler 2000). The accuracy of the phylogenetic trees may also affect the information content of models especially for trees that reconstruct relationships in higher taxonomic groups (Barraclough and Nee 2001). The main problem in reconstructing phylogenetic history is that all members of a group need to be sampled for maximum accuracy (Barraclough and Nee 2001).

Because the modem ranges of *Conus* are not historically informative, it is not possible to determine exactly where cladogenesis and consequent speciation occurred in the genus. Thus, the hypothesis that speciation occurred in the IWP island arc cannot be verified nor falsified with this approach. The hypothesis of speciation on the Pacific plate cannot be supported by this data, since there is no evidence to show that there are clades composed of endemics with a central Pacific distribution. The probable solution to the problem of species origins is to apply the principle of parsimony in order to choose a model that conserves the greatest historical information (Sober 1991).

This would require a comparative approach among coral reef taxa. The rapid developments of sequencing techniques in DNA analysis provide the opportunity to propose species-level phylogenies as historical hypotheses (Barraclough and Nee 2001). When these are properly examined, and if similar evolutionary trajectories are revealed in various taxa, then a more robust hypothesis to account for the origin and dimensions of marine biodiversity in the IWP arc, especially in the Philippines, may be proposed.

This hypothesis will have a specific historical approach. This should take account of vicariant events in a clade's history and relevant historical events. The relationship of a modern phenomenon such as a distribution with history needs to be established (Blalock 1961) in order to derive inferences. Historical biogeography has a genetic explanation. This can explain a present system by describing how it evolved from an ancestral one (Anderson 1996). This explanation is probabilistic in nature. Genetic explanations are appropriate for “what if' analysis (Shermer 2002). The most parsimonious "what-if' should be congruent with the present observed pattern. This then implies an accurate historical reconstruction.

The models presented here have limited explanatory power for inferring the history of speciation in IWP *Conus*. However the models provide interesting approaches to investigate probable modes of speciation in coral reef biota. There will be a limit to certainty in determining the evolutionary history of a marine taxon. But with a consideration of phylogeny and patterns in species distribution, an empirical understanding of how species diversity evolves can be achieved.

CHAPTER 8.

General Discussion, Synthesis and Hypotheses

"It has always been easier in biogeography to devise explanations than to test them. There can be few subjects that have offered so much scope for so many people to speculate at such length on so little evidence"- B.R. Rosen, 1988

"Severe criticisms are severe empirical tests"
Karl Popper, 1974

8.1 INTRODUCTION

Numerous hypotheses have been proposed to explain how the arcuate distribution of some marine taxa in the Indo-West Pacific (IWP) developed, and how such patterns are maintained in time (Rosen 1988). An understanding of how these patterns are maintained will give insight into the nature of species diversity in the IWP.

Three general hypotheses have been proposed in the last 40 years to account for the origin of high species diversity in the IWP. These three hypotheses are the centre of origin, peripheral speciation models (Rosen 1988) and refuge hypotheses (Wilson and Rosen 1998; Bellwood and Wainwright 2002). The first postulates that based on decreasing taxonomic diversity across the Indian and Pacific Oceans, especially in gastropods and scleractinian corals, the Indo-West Pacific and Southeast Asia are the centre of speciation (Briggs 1992; Veron 1995; Briggs 1996; Briggs 2000). The major mechanism for vicariant speciation is through tectonics and sea level changes that result in the fragmentation of geographical ranges. The second hypothesis is the peripheral speciation model, in which speciation is greatest on the Pacific Plate (Jokiel and Martinelli 1992, Springer 1982). The third hypothesis presumes that the numerous environments in the IWP island arc have provided refuges from extinction (Wilson and Rosen 1998; Bellwood and Wainwright 2002) Presumably the source populations of these speciation events are from species with wide geographical ranges. Tectonic changes and changes in ocean circulation fragment and divide these geographical ranges. The end result is genetic differentiation that eventually results in new species. The major difference between the models is in the role of dispersal. The role of dispersal is more significant in the peripheral speciation model. While the various hypotheses propose explanations for species origins, some hypotheses

(McCoy and Kenneth L. Heck 1976; McManus 1985) also have an ecological timeframe. Changes in environmental conditions that may have resulted in distributional changes in ecological time are reviewed in Rosen (1988) and Veron(1995).

Since knowledge of the geology, paleoclimatology and paleooceanography of Southeast Asia is limited, it is impossible at present to decide which of the competing hypotheses is more likely correct. Genetic evidence produces contrasting explanations that either favour the centre of origin or peripheral speciation models (Palumbi 1996). Unless a larger suite of species is assessed for genetic evidence at a variety of geographical scales, this approach is unlikely to favour either hypothesis.

This chapter discusses the general issues of the patterns of marine biodiversity in the IWP. It draws upon the available evidence from modem faunas: patterns of distribution, patterns of endemism, and the geometry and structure of species ranges, geology and molecular phylogenies.

8.2 THE HISTORICAL NATURE OF THE IWP AS THE CENTRE OF MARINE SPECIES DIVERSITY

The Philippines, eastern Indonesia, New Guinea, the eastern coast of tropical Australia, the Great Barrier Reef and the Solomon Islands form the Indo-Pacific centre of marine biological diversity. As one goes further eastwards or westwards from the centre, taxonomic diversity decreases. This arcuate spatial pattern of distributions of many marine species is somewhat unique to the Indo-West Pacific. Such distributions are not found in comparable island arcs, such as in the Caribbean. Several hypotheses have been proposed to explain the maintenance of this spatial pattern.

The arcuate distribution is a panbiogeographical track that follows the IWP island arc. It was first recognised by Croizat (1958), and used by McManus (1985) to support an argument about the existence of barriers to marine fauna in Southeast Asia. The panbiogeographical track links occurrences of fauna and flora. Such concepts were first applied to describe distributions of terrestrial plants, birds and mammals (Croizat

1958). It has been used to interpret the distributions of Australasian flora and fauna (Craw 1990) and the global distribution of cyprinid fish (Croizat 1958). If two or more tracks representing endemic species distributions are congruent, this suggests dispersion. Panbiogeography is a theory proposed before plate tectonics became a paradigm (Brown and Lomolino 1998; Grehan 2001). It does not account for the possible mixing of floras and faunas by plate tectonics.

McManus argues that if terrestrial biota have similar arcuate distributions to marine biota in SE Asia, then dispersion probably occurred via land bridges that then served as barriers to marine fauna during periods of low sea level. While land bridges did connect the Philippine island of Palawan with greater Southeast Asia, there remained significant water barriers that reduced mammal dispersion from Asia into the Philippines (Heaney 1986). The same is true for Australia and the Maluku islands of Indonesia.

If incomplete land bridges existed, then the isolation of the region's marginal ocean basins was not complete. Thus possibilities for biotic exchange between oceanic basins did exist, but possibly not at levels observed today. While the basins may have been isolated, this isolation may not have given rise to levels of speciation of marine fauna expected of truly isolated oceanic archipelagos such as Hawaii, the Galapagos and the Abrolhos islands of Brazil.

The endemism of marine mollusc species of the Galapagos is estimated at 20-22% (Kay 1991), Hawaii 20% (Kay and Palumbi 1987) and the 9-16% for the Brazilian Albrolhos Islands (Leal 1991). In contrast the estimated total marine mollusc endemism of the Philippines is 4% (Springsteen and Leobrera 1986). A high degree of genetic connectivity by larval dispersal, as is likely in the Philippines, can lead to smaller evolutionary divergence (Kay 1991). Endemism could be an index of speciation rate, since a taxon with higher rates of speciation is more prone to produce endemics (Stanley 1986). Thus if rapid speciation does not account for much of the high species diversity in the arcuate "centre of diversity", then what could have?

There is evidence of persistence of relict species in the Indo West Pacific. Wallace (1997) hypothesises that the predominance of plesiomorphic traits in endemic

Indonesian *Acropora* suggests that these species are Tethys Sea relicts. The region could then have served as refuges (Bellwood and Hughes 2001) during massive extinction events that are hypothesized to have produced the modern gastropod – bivalve ratio of 2:1 in the Philippines (Springsteen and Leobrera 1986). Paulay (1990) suggests that oceanic islands suffered massive extirpations of bivalve faunas because of the loss of lagoon habitats favourable for bivalves. Paulay (1990) did not suggest that this occurred in the Philippines or in Indonesia, areas with marginal oceanic basins.

Paulay (1990) concludes that sea level changes were selective in causing extinctions. Inner reef areas and the sandy intertidal suffered the greatest extinctions, and the shallow forereef slopes may have served as refuges. The rocky intertidal gastropods on the other hand are believed to be somewhat resistant to extinction, and susceptible to founder speciation when changes in oceanic circulation cut gene flow between populations (Vermeij 1987). Marine biota on atoll islands probably suffered the greatest extinction rates, having lost their lagoons during periods of low sea level, and having no significant rocky intertidal zones such as those found on high islands.

Phylogenetic studies of the species-rich genus *Conus* have confirmed that several characteristics such as lecithotrophy and piscivory have evolved independently in several clades (Duda and Palumbi 1999; Duda et al. 2001). Lecithotrophy would suggest restricted ranges, since larval dispersal would be limited. The modem ranges of lecithotrophic species of *Conus* cover the western Pacific. Although this is considerably less than the ranges of many other *Conus* species, these lecithotrophic species are not endemic to the IWP island arc, or to the Philippines. Relating the molecular phylogeny to modern ranges (Chapter 7) suggests that there is a weak signal of allopatric speciation that is parapatric in nature. The evidence for this is however, weak. Nevertheless, the evidence in Chapter 7 does support the peripheral speciation model. However the hypothesis that evolutionary radiation occurred on the Pacific plate is questionable, since there are no clades that occur in the central Pacific alone. At best, the analysis of phylogeny and modern ranges is not very informative. The most parsimonious explanation for species richness in the IWP island arc is species persistence from species that originated from either side of the island arc, the Indian Ocean and the Pacific Ocean. This explanation is supported by Brooks'

Parsimony Analysis of IWP coral reef biota (Santini and Winterbottom 2002). In this study, the authors conclude that the lineages of diverse coral reef biota originated through vicariant events resulting from the break-up of Gondwana. This is also supported by the Terminal Tethyan Event hypothesis that is reflected in area cladograms for parrotfishes (Bellwood and Wainwright 2002). It is important to note that complete Tethyan closure occurred in the Miocene, when *Conus* and *Oliva* radiations were believed to have started (Duda and Palumbi 1999, Tursch and Greifeneder 2001). This is noteworthy because there was no paleontological record for reef development before the Miocene (Wilson and Rosen 1998).

Therefore there is no clear evidence that the IWP island arc, that includes the Philippines, was the site of species diversification that resulted in the present high species diversity. The IWP has enhanced species persistence due to the availability of a wide variety of habitats, climatic insulation from the extremes in the Pleistocene, and the specific pattern of oceanic circulation. The latter may likely have enhanced species persistence, as suggested by the vortex model of coral biogeography (Jokiel and Martinelli 1992). The basins also were viable environments for most shallow water taxa. There were no significant regions of anaerobiosis typical of land locked seas like the Black Sea (Exon et al. 1981).

8.3 THE NATURE OF BASIN ISOLATION: GEOGRAPHICAL RANGE AND MORPHOLOGICAL DIVERSITY OF REEF GASTROPODS

The geographical ranges of gastropods observed in this study, and those documented by earlier studies of coral reefs, mangroves and seagrasses, indicate narrow distributions often centred within the Philippines (Fortes 1986). These distributions are likely a product of geographic constraints, and the effects of macroecological factors such as rainfall, temperature, current, tides etc. Narrow distributions are more common in carnivorous than herbivorous taxa, suggesting trophic status may be an important influence on range shape. This may be correlated with the distribution of favoured prey items of the carnivores. The correlation of species compositions and ranges with longitude and monsoon variables suggests that the prevailing climate may be important in maintaining species distributions. While the paleoclimate of Southeast Asia is not fully understood, Houle (1998) suggests that the monsoon climate has existed since the Tethys Sea closure. However, the intensity of paleomonsoons is not known.

In *Conus*, life history is not a significant predictor of range size at the scale of resolution of this study. Range of habitat types predicts both range size and species diversity far better than life history in this taxon. In the Philippines, the frequency of habitat types is a significant predictor of species diversity. The frequency of sandy habitats, which have variable composition and diversity, is the most significant predictor of species diversity in *Conus*.

In ***Oliva,*** the morphological diversity of monotopic (occupying on one substrate type) species is related to the basin in which they occur. Polytopic species (occupying multisubstrates) have no such patterns. Thus, particular environments in the basins may be favourable to some species. The monotopic species are usually found in the central Philippine basins of Sibuyan, Visayas and Sulu Sea. Polytopic species are found throughout the country. Morphological diversity may be due to local scale environmental processes (Tursch 1994; Tursch 1998; Tursch and Greifeneder 2001).

The unique geography of the Southeast Asian land masses and ocean basins, and the prevailing monsoon climate provide a spatially heterogenous environment (Aliño 1994). This may allow for the maintenance of high species diversity. Reversing currents, driven by monsoons, should not constrain distributions of marine organisms. However, historical and ecological factors appear to have constrained many distributions, and many of these distributions have an arcuate shape. The distribution of habitats in the Philippine islands may have played a key role in constraining distributions of marine organisms in this way.

8.4 THE SPECIES-AREA RELATIONSHIP AND CONSTRAINTS TO DISTRIBUTION

Species-area relationships may suggest how isolation or connectivity has determined the structure of species assemblages. The z value, or the slope of the species-area relationship, is a useful indicator of assemblage structure. Biotic isolates tend to have a low z value. Larger areas composed of such isolates (e.g. archipelagos), or continents, tend to have higher z values. Larger, non-isolated, areas tend to have constant immigration. This pattern of z values is confounded if speciation occurs by adaptive radiation in isolates.

In the Philippines the high z values observed between provinces suggest that species pools are not well mixed. This implies that ecological factors operating at local scales (1 to 100 km) may be important in determining assemblage structure and even ranges of species. For example, in stenotopic (species with narrow ecological tolerances or niches) *Conus,* habitat, life history and macroecological factors (e.g climate, rainfall, landscape factors etc) determine diversity. How a species utilises habitat heterogeneity will be variable in geographic space, due to local scale influences. Thus, patchiness in diversities will result in the observed high z values. This may also indicate a de-coupling of species diversity with area, or an area independence effect (Rosenzweig 1995). This phenomenon was first noted in studies of island biogeography. Macarthur and Wilson (1967) called it as the "small island effect". Thus, each centre of diversity is a province (Rosenzweig 1995). Larval connectivity patterns will be critical in maintaining such patterns in ecological time, and affecting speciation in evolutionary time. The biogeographical regions defined for reef fishes are defined by peaks of species richness, oceanic currents and basin geography (Aliiio 1994; Aliiio et al. 2002).

The Sibuyan and Visayan marginal basins have high z values relative to the total fauna of the Philippines. This suggests historical isolation that continues to the present. The positive correlation of z with the basin isolation index supports this hypothesis. These basins are the centres of diversity for several of the taxa investigated in this thesis.

8.5 THE CENTRE OF ORIGIN HYPOTHESIS RE-EXAMINED: THE POSSIBLE SIGNIFICANCE OF DUAL DISTRIBUTIONS AND ENDEMIC SPECIES.

The centre of origin hypothesis for the Indo-West Pacific (IWP) is based on speciation through allopatry. Molecular evidence suggests that both peripheral and "centre of origin" speciation in the IWP were likely important mechanisms generating biological diversity in the region (Palumbi 1994). Centre of origin hypotheses are based on Pliocene and Pleistocene sea level regressions and associated climate and oceanographic changes that allowed for allopatric speciation to occur. Dual distribution refers to the occurrence of morphologically similar, but genetically distinct, Indian and Pacific Ocean species. Such species pairs have been reported for fish (Endriga 2001), echinoderms and molluscs(Tursch and Greifeneder 2001).

In Chaetodon, a genus of coral reef fish, capacity for larval dispersal is large. This genus has several species-pairs with non-overlapping distributions (McMillan and Palumbi 1995). Furthermore, mtDNA evidence suggests that species differentiation in this genus in the IWP occurred in the Pliocene and Pleistocene (McMillan and Palumbi 1995). The lack of endemics, except in peripheral basins and regions such as the Red Sea and Hawaii, suggests that the IWP was not completely partitioned by Pliocene and Pleistocene sea level regressions.

Major ocean currents and the monsoon driven regional current systems like those seen today, were likely present in the Pleistocene (Houle 1998). The western boundary currents may have been more intense (Houle 1998) and the monsoon was probably drier and more intense than at present (Rosseau 2001). ENSO events were probably less frequent than in the present (Houle 1998). Thus the weak eastward currents could have been a significant vicariance mechanism (Veron 1995) that allowed for central and eastern Pacific speciation to occur.

Some distributions of marine gastropod species in the Philippines are not overlapping and have different spatial orientations. These may have historical explanations. For example, *Echininus* and *Tectarius* are found in the South China Sea, Bashi Channel, Celebes and the Philippine Sea, but not in the central Philippine basins. Similarly, some Nerita species have a distribution that largely excludes the central basin islands of the Philippines. Some of these species may be relicts. The significance of such distributions to the centre of origin hypothesis is unknown. However, such distributions were recognised by Wallace (1997) in an analysis of Indonesian Acropora. This pattern is likely to result from partial isolation of the Pacific and Indian Oceans, as well as isolation of the marginal oceanic basins of the IWP. This basin isolation has provided an opportunity for species to survive as relicts, and the possible generation of new species in the IWP through allopatry and subsequent sympatry.

Wallace (1997) provides insight on the nature of endemism of marine species in the IWP. Endemic species within the high species diversity IWP centre are not likely to persist over time. The evolutionary constraint of a dispersive larval phase forces new species to have wide dispersal. Thus the paradoxical low endemism of the IWP diversity centre may be accounted for. This is the exact opposite of terrestrial models of speciation, where high endemism is the hallmark of rapid speciation.

The persistence of relict species within the IWP island arc is strong evidence for the refuge from extinction hypothesis (Bellwood and Wainwright 2002) and may partially explain East-West isolation type of distributions. McManus (1985) suggests that marginal basins in the IWP arc allowed species to persist due to the presence of numerous habitats. Species with arcuate distributions follow the geography of the island arc. Indian and Pacific Ocean species may overlap on the IWP island arc or show observable disjunctions.

The capacity for wide dispersal is also a characteristic of IWP intertidal muricids belonging to the apomorphic ergalataxine and rapanine clades (Shuto 1983; Middlefart 1997a). The IWP rapanine clade is mainly planktotrophic (Kool 1993) although some species exhibit non-planktotrophy (Middlefart 1997a). The clades have diversified without loss of planktotrophy. Loss of planktotrophy may result in limited distribution. With a few exceptions, none of the IWP tropical species are endemic to a single region. Even in the habitat-specialised, non-planktotrophs such as Murex (Shuto 1983), wide distributions and a capacity for dispersal is the norm. Most muricid Western Pacific endemics occur only as cool water representatives at higher latitudes (Kool 1993). Thus, the capacity to disperse widely and to reduce endemism in modern species is likely to be a general characteristic of IWP species. Planktotrophy has allowed persistence in geological time (Scheltema 1983). With the Miocene radiation of most IWP mollusc taxa, this capacity for wide spread dispersal has not been lost. This suggestion is supported by this thesis. Modern ranges and phylogenetics have confounded the historical patterns attributed to allopatric and sympatric speciation.

8.6 PHILIPPINE MARINE BIOGEOGRAPHICAL REGIONS: DEFINED BY EAST-WEST SEPARATION, OCEANIC BASINS AND MACROECOLOGICAL FACTORS

The results of this study support the division of the Philippines into marine biogeographic regions based on faunal similarity, species richness and provinciality (Gomez et al. 1994; Aliño et al. 2002). The archipelago can be divided into the following regions 1) Western Luzon and Palawan, 2) Calamian Islands 3) Sulu Sea, 4) Visayan and Camotes Sea 5) Sibuyan Sea *6)* Eastern Philippine Province and 7) North Luzon and Batanes Province (Figure 8.1). These divisions are based on previous delimitations by Aliño et *al* (1994). The Eastern Philippine Province may be divided into two regions defined by the bifurcation of the North Equatorial Current (Licuanan, personal communication). Southern Mindanao and Palawan are insufficiently surveyed to allow for biogeographic classification, although there is evidence that these are distinct biogeographic regions. The regions are defined mainly by the east-west separation of gastropod assemblages probably due to the monsoons. These regions are also largely congruent with the geography of the ocean basins. This proposed division is similar to those proposed by Gomez et al (1994). However, there is one major difference.

In earlier biogeographical classifications, the central Philippines (Visayas) was considered one region. However, species diversity and provinciality of gastropods suggests that the Sibuyan Sea and the Visayan Seas are separate biogeographical regions. This is more consistent with geography, historical isolation and evidence from faunal provinciality.

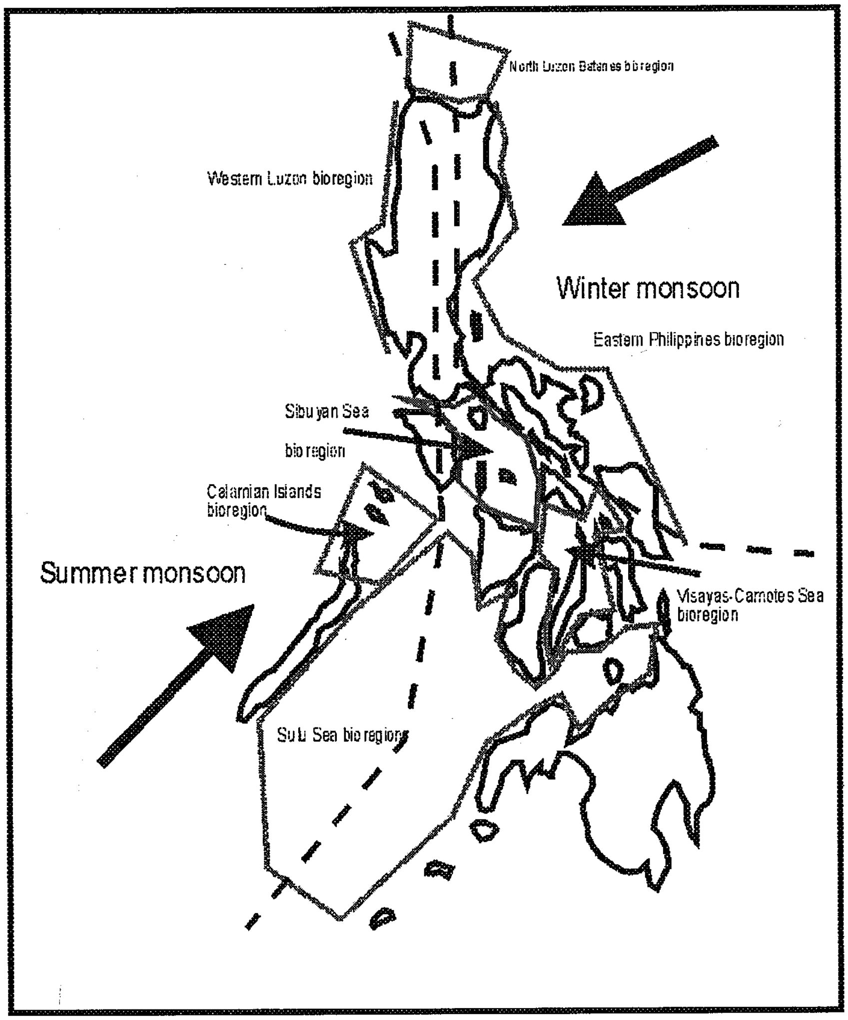


Figure 8.1 Proposed biogeographical regions of the Philippines. The dotted line indicates the regions influenced by the summer and winter monsoons. Southern Mindanao and Palawan are not sufficiently surveyed to allow for biogeographical classification.

8.7 GENERAL CONCLUSIONS

The validity of scientific evidence rests on its capacity to falsify as well as to support various hypotheses (McManus 1985). The historical sciences can rarely, if ever, utilise experimental approaches to test hypotheses. Since biogeography is an historical science, it can suggest a description of the evolution of the present state from an ancestral one (Andersson 1996). Genetic explanations (e.g. phylogenies) are probabilistic, with various states possibly evolving from the ancestral state. It is therefore necessary to determine which explanation is the most likely to explain the current situation. In this thesis I have attempted to present various approaches to examine the nature of species diversity in the Philippines, a region in the Indo-West Pacific centre of species diversity.

The approach taken does not confirm or deny the centre of origin paradigms, of which McManus' (1985) hypothesis is a part. I present methodological approaches that would enable readers to propose and test hypotheses. The methodological approaches help address the following questions and I discuss alternative explanations and propose other approaches to address these questions

Can modern species distributions and diversity provide historically recoverable information?

The answer to this question is unclear. There are a number of possible explanations of why the present pattern of distributions of marine species in the Philippines is observed. Some may have evolutionary significance and some may be explained in purely ecological time scales. I used the species-area relationship analysis proposed by Rosenzweig (1995) as a measure of historical biotic isolation that continues into the present. Species diversity and provinciality estimates suggest high diversity basins had separate evolutionary histories. However, this provinciality may be due to patchiness of diversities resulting from a de-coupling of species diversity with area. This may be a result of the presence of a large number of heterogenous habitats in a small area. Other explanations involve differences in colonization dynamics and possibly differences in marine productivity. While it can be inferred that basin isolation could have resulted in this high diversity, there is low endemism.

Circumstantial evidence, in the form of distributions of endemics and near-endemics within Philippine and nearby basins, supports the historical nature of basin isolation. These factors suggest that evolutionary constraints on speciation in the marine environment were different from that on land. Furthermore, the role of habitats in affecting the present biogeography cannot be ignored

There is a need to quantify the modern distribution of diverse taxa of coral reef gastropods within the Philippines. Distributions of mixed substrate and rock dwelling Cypraea may be arcuate, overlapping or disjunct, depending on their habitat preferences. Cypraea is most diverse in the Visayan basins (Springsteen and Leobrera 1986). The larvae of tropical Cypraea are usually planktotrophic. A similar "constraint" of planktotrophy of larvae was noted as a possible deterrninanant of the species diversity of *Conus* in this study. In Cypraea, the planktonic veliger stage is 1.5 to 2 weeks in duration (Kay 1990). Habitat availability may affect the distribution of this taxon, and may explain why some widespread IWP species are either absent or have restricted ranges within the Philippines.

Differential extinction rates and degrees of species persistence may account for the large number of species of coral reef organisms in the IWP. This is supported by geological evidence that suggests that coral reefs existed during sea level regressions, and may have provided refuges from extinction. Further evidence for species persistence may come from studies of geographical heterochrony or the co-existence of modern species assemblages with relict ones. Geographically heterochronic assemblages are often associated with coastal upwelling features (Petuch 1987). In the Philippines, such assemblages may be found in areas where upwelling is driven by monsoonal winds. These upwelling systems were believed to be more intense in the Pleistocene, and may have been dispersal barriers (Fleminger 1985).

It is difficult to separate historical and ecological explanations using Rosenzweig’s approach, since biotic isolation cannot be adequately demonstrated. However the observed patterns of species distribution and diversity warrant further investigation.

Can information on phylogeny and modern distribution provide an alternative explanation to the McManus hypothesis?

To answer this question, the nature of endemism in the IWP needs to be assessed by further systematic sampling. How plesiomorphic relicts and derived species may have contributed to this endemicity and should provide insight into speciation in the region. An initial approach is to examine the taxonomic structure of biota in the IWP and compare this with the biota of oceanic islands (Jablonski and Flessa 1986). This may determine where in the region speciation may have occurred. While genetic and phylogenetic evidence supports speciation adjacent to Southeast Asia in the Indian and Pacific Oceans (Fleminger 1985; Benzie 1998), there is no conclusive evidence on the location of speciation of *Conus* in the IWP. Allopatric speciation may have occurred in Indonesia and the Philippines, especially with temperature sensitive clades, or clades with non-dispersive larvae. However, the most parsimonious explanation at present is speciation and evolutionary radiation outside the IWP island arc, possibly related to the Terminal Tethyan Event and the breakup of Gondwana. This is supported by a number of explanations not consistent with a centre of origin hypothesis. A general theory of marine biogeography of the IWP is still required.

8.8 RECAPITULATION

McManus (1985) provided a theoretical framework to examine the nature, dimension, origin and fate of marine species diversity in the Philippines, and the IWP in general. McManus provides empirical evidence for the origin and maintenance of species diversity that were considerations of this thesis

As in all science, these results are preliminary. Additional work will likely change the inferences presented. There is a need for systematic research into all aspects of marine biodiversity, from descriptive natural history to the unravelling of complex evolutionary and ecological patterns. These will be well served by standardised methods of local-scale ecological research, and will involve integrating processes in ecological and geological time (Heaney 1999). As knowledge increases, our ability to determine which hypothesis is most parsimonious will increase. However in order to achieve this objective, a strong well-funded programme of continuing biological surveys, taxonomic and phylogenetic research, and support to natural history museums, need to be addressed.

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APPENDIX 1: DESCRIPTIONS OF FIELD COLLECTING SITES

Philippines

Palaui, Fuga Moro and Escucha Islands, Cagayan Province, northeastern Luzon 18°35' N; 122°10 E

This is the northernmost extension of the Sierra Madre Mountains of eastern Luzon that were formed in Paleocene . Palaui and Fuga Moro islands are volcanic and plutonic in origin with steep cliffs and numerous embayments. These embayments are fringed with wide coral reefs on the east, the largest of which is Robo Reef. The western side of Palaui Island has narrow fringing coral reefs and numerous embayments. The shoreline is composed of basalt boulders, and wide intertidal platforms with a carbonate base. Shore angle ranges from 5 degrees to 35 degrees.

Pagudpud-Patapat Coast, Ilocos Norte Province, northern Luzon
18°38' N; 120°49' E

The coastline forms the edge of the Cordillera Central Mountains of northern Luzon. Steep cliffs drop to the seacoast. The shoreline is composed of basalt boulders ranging from 1 metre to 3 metres in diameter. The coast is exposed to swells generated by the winter monsoon. Little fringing reef development is noted on these exposed shores. Shore angle is 20 degrees.

Bolinao, Pangasinan Province, northwestern Luzon
16°19' - 16°28' N; 119°52'-120°02 E

Bolinao is a limestone cape headland facing the South China Sea at the northwestern boundary of Lingayen Gulf. Immediately north of the cape is Santiago Island. It is surrounded by a wide fringing reef system.

Subic Bay, Subic Bay Freeport, western Luzon

14°47' N; 120°17' E

Subic Bay sites were on the strict nature preserve on the southwest shore of the bay 30 kilos from the freeport. The area including Miracle Beach is fringed with massive corals, relatively protected from the summer monsoon. The nearby land area is covered with primary growth rainforest.

Ligpo Point, Balayan Bay, Batangas Province

13°37' N; -120°53' E

The shore is at the edge of an ancient volcano and is composed of lava flows from a prehistoric eruption of Taal Volcano. A highly embayed coastline, it is fringed by coral reefs in an incipient stage of development. A narrow veneer reef fringes Ligpo Point, where the classic fringing reef structure is seen at the southwest edge of the point. . The shoreline is composed of interspersed limestone blocks and basalt boulders. It is likely that the limestone blocks are due to reef structures being raised onto the beach during intense tropical cyclones. The cliff edge is composed of conglomerates embedded in volcanic ash, a result of the prehistoric catastrophic eruption of Taal. Shore angle is 25 degrees.

Maricaban, Sombrero, Caban Islands, Verde Island Passage, Batangas Province

13°36' N; 120°56 E

This group of islands is composed of conglomerates embedded in volcanic ash and represents the edge of a collapsed volcano. Numerous headlands and embayments characterise the coast. Sombrero Island is the remnants of a volcanic cone. At present the islands are fringed by non-reef coral communities or reefs at an early stage of development. The island shorelines are composed of basalt boulders and coral rubble.

Tilted and overturned *Porites* microatolls suggest the effects of tropical cyclones. This is likely the source of limestone boulders on the beach.

Bacacay, Albay Province, southeastern Luzon
13°12' N; 123°47' E

The island coastlines are composed of volcanic headlands composed of basalt interspersed with hardened volcanic ash. Bacacay is fringed by coral reefs in a high sedimentary environment. On sheltered shores, mangroves are present. The area is 35 kilos from the composite cone of Mayon Volcano. The shore angle is 20 degrees.

Rizal Beach, Sorsogon Province, southeastern Luzon
12°40' N;124°10' E

A single volcanic headland is adjacent to a wide sandy beach exposed to Pacific Ocean swells. A wide reef is adjacent the headland and is composed primarily of massive *Porites, Favia* and *Favites*. *Thallasia hemprichii* and *Enhalus* seagrass cover the reef flat. Shore angle is 15 degrees.

Calauit, Dimakya, Walang Lang-aw Islands, Calamian Group, Palawan Province
12°14' N;-120°11' E

These islands are geologically distinct from other islands of the Philippines. They represent a displaced terrane of the Asian continent derived from southeastern China. The islands are composed of granitic intrusions and marble. All islands are fringed by well-developed coral reefs and have rocky shores on the exposed sides. Relatively sheltered sites have sandy beaches or mangrove forests. Rocky shore angle is 30 degrees.

UsUsan, Nagarao, Inampulugan Islands, Panay Gulf, Guimaras Province
10°23' N;122°39 E

These islands are of volcanic origin and are fringed by coral reefs. UsUsan has two volcanic headlands on the exposed side and a wide sandy beach on the sheltered side. Inampulugan has volcanic headlands on the southwestern to western sides and mangroves on the eastern side facing the larger island of Guimaras. The headlands are exposed to the south or summer monsoon. The shoreline consists of basaltic blocks and boulders. Shore angle is 35 degrees.

Southern Bohol and Panglao Island, Bohol Province
09°30' N; 123°56' E

Panglao Island and the larger island of Bohol are composed of uplifted coral limestone. Wide scale uplift occurred in the Pliocene to the Pleistocene. Wide fringing reefs and sandy beaches surround these islands. On the exposed headlands, wave action has scoured the base of the limestone cliffs into a characteristic overhang shape. Shore angle is 20 degrees.

Camiguin Island, Camiguin Province
09°13' N; 124°42E

Camiguin is a true oceanic island that emerged from the sea within the last 2 million years. Composed of the volcanoes, Hibok-Hibok, Camiguin and Mambajao that are still active, the island lies off the coast of northern Mindanao. Its shoreline is composed of volcanic boulders and basaltic cliffs. Shore angle is 20-45 degrees. Narrow coral reefs fringe the coastline. It has never been connected to Mindanao.

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OGU	Basin	Island	Coastal area	*Clypeomorus*	Littorinidae	Muricidae	*Nerita*	*Conus*
Batanes	Philippine Sea	Yes	162	4	5	NS	NS	NS
Catanduanes	Philippine Sea	Yes	119.62	3	NS	2	3	NS
east Luzon	Philippine Sea	No	255	3	NS	NS	NS	NS
Eastern Samar	Philippine Sea	No	247.28	2	NS	3	3	18
north Luzon	Philippine Sea	No	376.71	7	5	9	9	NS
southeast Luzon	Philippine Sea	No	133.47	2	1	2	3	7
east Cebu	Visayan –Camotes	No	277.19	8	NS	NS	4	48
west Cebu	Visayan-Camotes	No	269	2	NS	NS	NS	NS
Danajon Reef Cays	Visayan-Camotes	Yes	25	NS	NS	2	1	4
Samar	Visayan-Camotes Sea	No	194.7	4	NS	NS	NS	26
Masbate	Sibuyan Sea	No	175	4	2	NS	NS	NS
Ragay Gulf	Sibuyan Sea	No	65	5	NS	NS	NS	NS
Sibuyan Sea islands	Sibuyan Sea	Yes	31.9	1	2	NS	7	9
Tayabas Bay	Sibuyan Sea	No	210.56	5	NS	8	10	70
Southwestern Luzon	Sibuyan Sea	No	268.66	7	7	8	7	13
Verde Island Passage	Sibuyan Sea	Yes	58	2	2	2	3	7
north Panay	Sibuyan Sea	No	198.99	NS	NS	NS	7	21
Calamian Islands	Sulu Sea	Yes	150	6	3	6	3	4
south Palawan	Sulu Sea	Yes	83.34	3	2	NS	3	NS
southern Panay	Sulu Sea	No	247.85	5	3	8	9	31
Sulu Sea Islands	Sulu Sea	Yes	144.2	6	3	2	2	10
Camiguin	Sulu Sea	Yes	94	1	1	2	6	2
east Palawan	Sulu Sea	No	235	NS	NS	NS	NS	16
southwest Bohol	Sulu Sea	Yes	127.33	1	NS	1	NS	12
west Luzon	South China Sea	No	280.38	8	2	8	6	6
west Palawan islands	South China Sea	Yes	138	8	NS	4	2	NS
northwest Luzon	South China Sea	No	380.3	NS	2	4	8	31

APPENDIX 2. TABLE A: Summary table of Philippine operating geographical unit (OGU) recorded species diversity and area in the 5 coral reef and rocky intertidal shore taxa in this thesis. NS- OGU not sufficiently surveyed for the taxon.

Basin	OGU	area	*Oliva* Species number
Celebes Sea	Davao Gulf	40	2
Philippine Sea	Eastern Luzon (Baler)	5	3
Philippine Sea	Surigao del Sur	185	16
Philippine Sea	Eastern Samar	247.78	4
Philippine Sea	Northern Luzon	135	11
Philippine Sea	Surigao del Norte	215	2
Philippine Sea	Sorsogon	158	4
Philippine Sea	Southeastern Luzon (Bicol)	133.47	5
South China Sea	Zambales	62.8	13
South China Sea	Western Luzon (Ilocos)	375	10
South China Sea	Mindoro Occidental	457	9
Sibuyan Sea	Northern Panay	54	18
Sibuyan Sea	Masbate	175	12
Sibuyan Sea	Marinduque	110	7
Sibuyan Sea	Mindoro Oriental	514	5
Sibuyan Sea	Southewestern Luzon (Batangas)	268.66	3
Sibuyan Sea	Western Quezon (Ragay)	340	4
Sulu Sea	Zamboanga del Norte	10	17
Sulu Sea	Calamian Islands	74.66	10
Sulu Sea	Southern Panay (Iloilo)	247.85	8
Sulu Sea	Southern Palawan (Balabac)	83.4	6
Sulu Sea	Cuyo Islands	23	3
Sulu Sea	Western Palawan	235	3
Sulu Sea	Sulu and Tawi Tawi	44.2	13
Sulu Sea	Bohol	13	6
Sulu Sea	Zamboanga	90	4
Visayan-Camotes Sea	Eastern Panay	45	13
Visayan-Camotes Sea	Negros Oriental	14	18
Visayan-Camotes Sea	Samar	194.7	12
Visayan-Camotes Sea	Leyte	235	9
Visayan-Camotes Sea	Cebu East (Mactan)	277.19	1
Philippines		5062.71	

APPENDIX 2B. B. Summary table of Philippine operating geographical unit (OGU) recorded species diversity and area in *Oliva*.

Basin	Island	z
Sulu Sea	50	0.4324
Sibuyan Sea	17	1.446
VIS	13	1.309
Philippine Sea	29	0.7339
South China Sea	30	0.7521

Z and island plot data

	MREEF	z
Sulu Sea	73.5	0.4324
Sibuyan Sea	43.125	1.446
VIS	58.75	1.309
Philippine Sea	55	0.7339
South China Sea	75	0.7521

Percent reef and z plot data

Basin	index	z
Sulu Sea	0.041379	0.4324
Sibuyan Sea	0.078947	1.446
Visayan-Camotes Sea	0.033333	1.309
Philippine Sea	0.0005	0.7339
South China Sea	0.001724	0.6294

Basin isolation index and z plot data

BASIN	P	z
Philippine Sea	0.926338	0.733
VIS	1.786655	1.309
Sibuyan Sea	1.864419	1.446
Sulu Sea	0.693009	0.4329
South China Sea	0.893933	0.6294
PH	1	0.6308

Basin z plot and Provinciality data

Basin	MCOMP	Z
Sulu Sea	0.09	0.4324
Sibuyan Sea	0.046	1.446
VIS	0.04	1.309
Philippine Sea	0.076	0.7339
South China Sea	0.03	0.7521

Coastal complexity and z plot data

Appendix 2C. Data used in evaluating basin isolation in Chapter 6.

APPENDIX 3

Vallejo, B. (1999). Distribution and range of rocky shore gastropods in the Philippines: Comparisons between mainland and island coastlines. In *Symposium on Marine Biodiversity in the Visayas and Mindanao* (ed. W. L. Campos), pp. 21-42. University of the Philippines in the Visayas, Miag-ao, Iloilo, Philippines: University of the Philippines in the Visayas.

OGU or Bioregion	Species diversity	H1	H2	H3	H4	H5	H6	H7	H8	H9	TOTAL
Philippines											
East Cebu	48	4	1	2	0	1	0	0	3	0	11
East Palawan	16	3	1	0	0	0	0	1	1	0	6
East Samar	18	1	3	0	0	1	0	0	2	0	7
Northern Panay	27	11	23	1	2	3	2	8	9	0	59
NW Luzon	29	14	8	5	0	2	0	13	50	0	92
Samar	26	3	6	0	0	0	1	2	0	0	12
Southern Panay	31	16	19	2	3	6	2	6	13	0	67
Sibuyan Sea Islands	9	1	0	0	1	1	0	1	1	0	5
Sulu Sea Islands	10	1	0	0	0	0	0	0	0	0	1
SW Bohol	12	1	1	0	0	0	0	2	1	0	5
SW Luzon	8	2	0	0	1	0	0	0	0	0	3
Tayabas Bay	69	67	68	3	17	14	6	33	46	0	254
Western Luzon	6	0	0	0	0	2	0	0	0	0	2
Totals		124	130	13	24	30	11	66	126	0	524

APPENDIX 4. Frequencies of *Conus* habitats in 9 habitat classes in the Philippines.

APPENDIX 5 Cone shells of the Philippines

Cone Shells of the Philippines					
ConeID	GENUS	SPECIES	AUTHOR DATE	Endemic	Habitat
1	*Conus*	*marmoreus*	Linné, 1758	No	7
2	*Conus*	*imperialis*	Linné, 1758	No	7
3	*Conus*	*litteratus*	Linné, 1758	No	7
4	*Conus*	*tessulatus*	Born, 1778	No	
5	*Conus*	*eburneus*	Hwass, 1792	No	2
7	*Conus*	*chaldeus*	(Röding, 1798)	No	1
8	*Conus*	*ebraeus*	Linné, 1758	No	2
9	*Conus*	*coronatus*	(Röding, 1798)	No	2
11	*Conus*	*musicus*	Hwass, 1792	No	4
12	*Conus*	*sponsalis*	Hwass, 1792	No	2
13	*Conus*	*lividus*	Hwass, 1792	No	8
14	*Conus*	*moreleti*	Crosse, 1858	No	7
15	*Conus*	*distans*	Hwass, 1792	No	8
17	*Conus*	*arenatus*	Hwass, 1792	No	1
18	*Conus*	*stercusmuscarum*	Linné, 1758	No	7
19	*Conus*	*varius*	Linné, 1758	No	8
20	*Conus*	*achatinus*	Gmelin, 1791	No	4
21	*Conus*	*catus*	Hwass, 1792	No	2
22	*Conus*	*striatellus*	Link, 1807	No	1
24	*Conus*	*planorbis*	Born, 1778	No	8
25	*Conus*	*furvus*	Reeve, 1843	No	1
26	*Conus*	*magus*	Linné, 1758	No	1
27	*Conus*	*subulatus*	Kiener, 1849	No	5
28	*Conus*	*stramineus*	Lamarck, 1810	No	5
29	*Conus*	*consors*	Sowerby, 1833	No	1
30	*Conus*	*australis*	Holten, 1802	No	5
31	*Conus*	*radiatus*	Gmelin, 1791	No	5
32	*Conus*	*parius*	Reeve, 1843	No	1
33	*Conus*	*vexillum*	Gmelin, 1791	No	7
34	*Conus*	*capitaneus*	Linné, 1758	No	2
35	*Conus*	*rattus*	Hwass, 1792	No	8
36	*Conus*	*mustelinus*	Hwass, 1792	No	8
37	*Conus*	*miles*	Linné, 1758	No	2
38	*Conus*	*virgo*	Linné, 1758	No	6
39	*Conus*	*emaciatus*	Reeve, 1849	No	2
40	*Conus*	*flavidus*	Lamarck, 1810	No	2
41	*Conus*	*frigidus*	Reeve, 1848	No	2
42	*Conus*	*pennaceus*	Born, 1778	No	3
43	*Conus*	*textile*	Linné, 1758	No	7
44	*Conus*	*telatus*	Reeve, 1848	Yes	1
45	*Conus*	*figulinus*	Linné, 1758	No	5
46	*Conus*	*quercinus*	(Lightfoot, 1786)	No	1
47	*Conus*	*striatus*	Linné, 1758	No	1

Cone Shells of the Philippines

ConeID	GENUS	SPECIES	AUTHOR DATE	Endemic	Habitat
49	*Conus*	*nussatella*	Linné, 1758	No	8
50	*Conus*	*terebra*	Born, 1778	No	2
51	*Conus*	*glans*	Hwass, 1792	No	2
53	*Conus*	*muriculatus*	Sowerby I, 1833	No	8
54	*Conus*	*sulcatus*	Hwass, 1792	No	1
55	*Conus*	*moluccensis*	Küster,1838	No	1
56	*Conus*	*insculptus*	Kiener, 1845	No	5
57	*Conus*	*mucronatus*	Reeve, 1843	No	1
59	*Conus*	*acutangulus*	Lamarck, 1810	No	1
60	*Conus*	*floridulus*	Adams & Reeve, 1849	No	1
61	*Conus*	*alabaster*	Reeve, 1849	No	
62	*Conus*	*furvus*	Reeve, 1843	No	
63	*Conus*	*ammiralis*	Linné, 1758	No	
64	*Conus*	*aphrodite*	Petuch, 1979	No	
66	*Conus*	*armadillo*	Shikama,1971	No	
67	*Conus*	*articulatus*	Sowerby III,1873	No	
68	*Conus*	*asiaticus*	da Motta, 1975	No	
69	*Conus*	*aulicus*	Linné, 1758	No	1
70	*Conus*	*auratinus*	da Motta, 1982	No	
72	*Conus*	*auricomus*	Hwass, 1792	No	
73	*Conus*	*aurisiacus*	Linné, 1758	No	
74	*Conus*	*baileyi*	Röckel & DaMotta, 1979	No	
75	*Conus*	*balteatus*	Sowerby I, 1833	No	
76	*Conus*	*grangeri*	Sowerby III, 1900	No	
77	*Conus*	*betulinus*	Linné, 1758	No	
78	*Conus*	*sulcatus*	Hwass, 1792	No	
79	*Conus*	*boeticus*	Reeve, 1843	No	3
80	*Conus*	*boholensis*	Petuch, 1979	No	
81	*Conus*	*broderippi*	Reeve, 1843	No	
82	*Conus*	*bullatus*	Linné, 1758	No	
83	*Conus*	*canonicus*	Hwass, 1792	No	
85	*Conus*	*caracteristicus*	Fischer, 1807	No	
89	*Conus*	*cervus*	Lamarck, 1822	No	
90	*Conus*	*chiangi*	(Azuma, 1982)	No	1
91	*Conus*	*cinereus*	Hwass, 1792	No	3
92	*Conus*	*circumactus*	Iredale, 1929	No	
93	*Conus*	*circumcisus*	Born, 1778	No	3
94	*Conus*	*coccineus*	Gmelin, 1791	No	
95	*Conus*	*collisus*	Reeve, 1849	No	
96	*Conus*	*neptunus*	Reeve, 1843	Yes	
97	*Conus*	*comatosa*	Pilsbry, 1904	No	5

Cone Shells of the Philippines

ConeID	GENUS	SPECIES	AUTHOR DATE	Endemic	Habitat
98	*Conus*	*corallinus*	Kiener, 1845	No	
100	*Conus*	*cylindraceus*	Broderip & Sowerby, 1833	No	
101	*Conus*	*dayriti*	Röckel & da Motta, 1983	No	
103	*Conus*	*dondani*	Kosuge, 1981	Yes	
104	*Conus*	*dusaveli*	(H. Adams, 1872)	No	
106	*Conus*	*episcopatus*	da Motta, 1982	No	
108	*Conus*	*excelsus*	Sowerby III, 1908	No	
109	*Conus*	*eximius*	Reeve, 1849	No	
110	*Conus*	*fischoederi*	Röckel & da Motta, 1983	No	
111	*Conus*	*floccatus*	Sowerby II, 1839	No	
112	*Conus*	*miliaris*	Hwass, 1792	No	2
114	*Conus*	*generalis*	Linné, 1767	No	1
115	*Conus*	*geographus*	Linné, 1758	No	1
116	*Conus*	*glaucus*	Linné, 1758	No	
117	*Conus*	*gloriamaris*	Chemnitz, 1777	No	5
119	*Conus*	*hirasei*	(Kuroda, 1956)	No	5
121	*Conus*	*ichinoseana*	(Kuroda, 1956)	No	
122	*Conus*	*ione*	Fulton, 1938	No	
123	*Conus*	*kimioi*	(Habe, 1965)	No	
124	*Conus*	*kinoshitai*	(Kuroda, 1956)	No	
125	*Conus*	*kintoki*	Habe & Kosuge, 1970	Yes	
126	*Conus*	*kuroharai*	(Habe, 1965)	No	
127	*Conus*	*eugrammatus*	Bartsch & Rehder, 1943	No	
128	*Conus*	*laterculatus*	Sowerby III, 1870	No	
129	*Conus*	*legatus*	Lamarck, 1810	No	
130	*Conus*	*lenavati*	da Motta & Röckel 1982	Yes	
131	*Conus*	*leobrerai*	da Motta & Martin, 1982	No	
132	*Conus*	*leopardus*	(Röding, 1798)	No	3
133	*Conus*	*litoglyphus*	Hwass, 1792	No	
134	*Conus*	*luteus*	Sowerby I, 1833	No	
135	*Conus*	*lynceus*	Sowerby II, 1858	No	1
136	*Conus*	*tulipa*	Linné, 1758	No	
137	*Conus*	*obscurus*	Sowerby, 1833	No	
139	*Conus*	*suratensis*	Hwass, 1792	No	
140	*Conus*	*thomae*	Gmelin, 1791	Yes	
141	*Conus*	*teramachii*	(Kuroda, 1956)	No	
142	*Conus*	*pertusus*	Hwass, 1792	No	
143	*Conus*	*sulcocastaneus*	Kosuge, 1981	No	
147	*Conus*	*tenuistriatus*	Sowerby II, 1858	No	
148	*Conus*	*viola*	Cernohorskyi, 1977	No	

Cone Shells of the Philippines

ConeID	GENUS	SPECIES	AUTHOR DATE	Endemic	Habitat
149	*Conus*	*monachus*	Linné, 1758	No	
150	*Conus*	*mitratus*	Hwass,1792	No	1
151	*Conus*	*proximus*	Sowerby II, 1859	No	
154	*Conus*	*spectrum*	Linné, 1758	No	
157	*Conus*	*samiae*	da Motta, 1982	No	
158	*Conus*	*pagodus*	Kiener, 1845	No	
159	*Conus*	*thalassiarchus*	Sowerby I, 1834	Yes	
163	*Conus*	*sanguinolentus*	Quoy & Gaimard, 1834	No	
165	*Conus*	*retifer*	Menke, 1829	No	
166	*Conus*	*nobilis*	Linné, 1758	No	
169	*Conus*	*tribblei*	Walls, 1977	No	
170	*Conus*	*sugimotonis*	Kuroda, 1928	No	
171	*Conus*	*sp.*		No	
172	*Conus*	*recluzianus*	Bernardi, 1857	No	
173	*Conus*	*voluminalis*	Reeve, 1843	No	
175	*Conus*	*sp.*		No	
176	*Conus*	*magnificus*	Reeve, 1843	No	
177	*Conus*	*omaria*	Hwass, 1792	No	3
178	*Conus*	*praecellens*	A. Adams, 1854	No	1
180	*Conus*	*memiae*	(Habe & Kosuge, 1960)	No	
181	*Conus*	*sp.*		No	
182	*Conus*	*sp.*		No	
183	*Conus*	*pseudorbignyi*	Röckel & Lan, 1981	No	
184	*Conus*	*orbignyi*	Audouin, 1831	No	
185	*Conus*	*vimineus*	Reeve, 1849	No	
186	*Conus*	*montillai*	Röckel, 1985	Yes	1
187	*Conus*	*scalptus*	Reeve, 1843	Yes	
188	*Conus*	*wakayamensis*	(Kuroda, 1956)	No	
189	*Conus*	*polongimarumai*	Kosuge, 1980	No	
190	*Conus*	*saecularis*	Melvill, 1898	No	
191	*Conus*	*sazanka*	Shikama, 1972	No	
192	*Conus*	*saecularis*	Melvill, 1898	No	
193	*Conus*	*pulicarius*	Hwass, 1792	No	3
194	*Conus*	*litoglyphus*	Hwass, 1792	No	
197	*Conus*	*vexillum*	Gmelin, 1791	No	7
198	*Conus*	*obscurus*	Sowerby, 1833	No	
200	*Conus*	*tulipa*	Linné, 1758	No	
201	*Conus*	*suratensis*	Hwass, 1792	No	
202	*Conus*	*longurionis*	Kiener, 1845	No	1
203	*Conus*	*pseudokimioi*	da Motta & Martin, 1982	No	

Cone Shells of the Philippines					
ConeID	**GENUS**	**SPECIES**	**AUTHOR DATE**	**Endemic**	**Habitat**
207	*Conus*	*rolani*	Röckel, 1986	No	
209	*Conus*	*zapatosensis*	Röckel, 1987	Yes	
210	*Conus*	*blandifordianus*	Crosse, 1867	No	
211	*Conus*	*cordigera*	Sowerby II, 1866	No	
212	*Conus*	*shikamai*	Coomans, Moolenbeck & Wils, 1985	No	
213	*Conus*	*stupa*	(Kuroda, 1959)	No	
214	*Conus*	*darkini*	Röckel, Korn & Richard, 1992	No	
215	*Conus*	*axelrodi*	Walls, 1978	No	
216	*Conus*	*crocatus*	Lamarck, 1810	No	1

APPENDIX 6. *Oliva* species recorded from the Philippines based on DMNH material.

	Oliva SPECIES	Range size (sq km)	Frequency of occurrence	Habitat Code	Distribution type
1	*athenia*	480000	9	6	2
2	*amethystina*	1672000	60	3	1,4
3	*bulbiformis*	1027200	20	1	3,4
4	*caerulea*	208000	8	1	5
5	*carneola*	1952000	44	6	3,4
6	*concavospira*	320000	6	6	2
7	*dactyliola*	832000	29	6	3,4
8	*dubia*	192000	8	7	2
9	*elegans*	880000	14	9	3
10	*hirasei*	48000	1	1	5
11	*lacanientai*	48000	1	6	5
12	*mantichora*	720000	5	3	1
13	*miniacea*	2168000	62	3	1,4
14	*mustelina*	80000	2	1	5
15	*oliva*	2880000	60	1	3,4
16	*"ornata"**	1027200	14	1	3,4
17	*reticulata*	1096000	66	9	3
18	*rufofulgurata*	160000	5	1	2
19	*rufula*	48000	8	7	2
20	*sericea*	512000	31	3	3,4
21	*tigridella*	240000	15	3	2
22	*tigrina*	112000	4	1	2
23	*todosina*	1344000	7	1	3
24	*tricolor*	1000000	19	2	1
25	*vidua*	1988800	59	9	1,4
26	*tesselata*	1025600	12	3	1
27	*lecoquiana*	48000	1	1	5
28	*irisans*	160000	1	1	5
29	Unidentified species Possibly *parkinsoni*	160000	1		5

Distribution type: 1) Straddle the central Philippines basins, 2) Found on the edges of basins (Sibuyan Sea) 3) Central basins with northward extension to the South China Sea, 4) Eastern Philippines, 5) Recorded from one locality only

Habitat code: 1) Sand, 2) Coarse sand, 3) Coral sand, 4) Coral-volcanic sand, 5) Fine sand, 6) Muddy sand, 7) Mud, 8) Gravelly sand, 9) Multisubstrate, 10) Sand and rubble

* *Oliva "ornata"* may resemble *O. irisans*. However the aperture in the DMNH specimens is white that is diagnostic for *O. irisans*. All other conchological diagnostics described and Tursch and Greifeneder (2001) and observed in the DMNH material are for the Australian endemic *O. ornata.*

APPENDIX 7. Philippine *Oliva* species as recorded in Tursch and Greifeneder (2001)

	GENUS	SPECIES	AUTHORDATE
1	*Oliva*	*amythestina*	(Röding,1798)
2	*Oliva*	*athenia*	Duclos, 1835
3	*Oliva*	*buelowi*	Sowerby, 1890
4	*Oliva*	*bulbiformis*	Duclos, 1840
5	*Oliva*	*brettinghami*	Bridgman, 1909
6	*Oliva*	*caerulea*	(Röding, 1798)
7	*Oliva*	*carneola*	(Gmelin, 1791)
8	*Oliva*	*chrysoplecta*	Tursch and Greifeneder, 1989
9	*Oliva*	*concavospira*	Sowerby, 1914
10	*Oliva*	*dactyliola*	Duclos, 1840
11	*Oliva*	*dubia*	Schepman, 1904
12	*Oliva*	*elegans*	Lamarck, 1811
13	*Oliva*	*hirasei*	Kira, 1959
14	*Oliva*	*irisans*	Lamarck, 1811
15	*Oliva*	*lacanientai*	Greifeneder and Blöcher, 1985
16	*Oliva*	*lecoquiana*	Duclos de St. Germaine, 1857
17	*Oliva*	*mantichora*	Duclos,1840
18	*Oliva*	*miniacea*	(Röding, 1798)
19	*Oliva*	*multiplicata*	Reeve, 1850
20	*Oliva*	*mustelina*	Lamarck, 1811
21	*Oliva*	*oliva*	(Linné, 1758)
22	*Oliva*	*ornata**	Marrat,1867
23	*Oliva*	*parkinsoni*	Prior, 1975
24	*Oliva*	*reticulata*	(Röding, 1798)
25	*Oliva*	*rufofulgurata*	Schepman, 1911
26	*Oliva*	*rufula*	Duclos, 1840
27	*Oliva*	*sericea*	(Röding, 1798)
28	*Oliva*	*semmilinki*	Schepman, 1891
29	*Oliva*	*tessellata*	Lamarck, 1811
30	*Oliva*	*tigridella*	Duclos, 1835
31	*Oliva*	*tigrina*	Lamarck, 1811
32	*Oliva*	*todosina*	Duclos, 1840
33	*Oliva*	*tricolor*	Lamarck, 1811
34	*Oliva*	*vicdani***	Da Motta, 1982
35	*Oliva*	*vidua*	(Röding, 1798)

*possibly *O. irisans*
** Philippine endemic

ConeID	Species	KohnHabit	Locality	OGU	Endemic	Near Ende	Habitat	Remarks
115	geographus		Albay Gulf	SELUZ	FALSE	FALSE		
136	tulipa		E. Samar	ESAM	FALSE	FALSE		
137	obscurus		E. Samar	ESAM	FALSE	FALSE		
39	emaciatus	2	Bohol	SWBOH	FALSE	FALSE		
94	coccineus		Samar	SAM	FALSE	FALSE		
85	caracteristicus		Manila	WLUZ	FALSE	FALSE		
36	mustelinus	8	Cebu	CEBE	FALSE	FALSE		
34	capitaneus	2	Cebu	CEBE	FALSE	FALSE		
116	glaucus		Baler	ELUZ	FALSE	FALSE		
46	quercinus	1		SWLUZ	FALSE	FALSE		
4	tessulatus		Batangas	SWLUZ	FALSE	FALSE		
49	nussatella	8	Cebu	CEBE	FALSE	FALSE		
77	betulinus		Manila Bay	WLUZ	FALSE	FALSE		
139	suratensis		Pangasina	WLUZ	FALSE	FALSE		
45	figulinus	5	Pangasina	WLUZ	FALSE	FALSE		
73	aurisiacus		Southern	SSIS	FALSE	TRUE	20-80 m	Celebes S
104	dusaveli		Cebu	CEBE	FALSE	FALSE		
140	thomae		Davao	DAV	TRUE	FALSE	celebes sea endemic	
66	armadillo		S. Mindana	SSIS	FALSE	FALSE		
126	kuroharai		S. Mindana	SSIS	FALSE	TRUE		
135	lynceus	1	Manila	WLUZ	FALSE	TRUE		
216	crocatus	1	Samar	SAM	FALSE	FALSE		
141	teramachii		Mindoro	EMIN	FALSE	FALSE		
142	pertusus		Cebu	CEBE	FALSE	FALSE		
143	sulcocastaneus		Cebu	CEBE	FALSE	FALSE		
93	circumcisu	3	Cebu	CEBE	FALSE	FALSE		
96	neptunus		Bohol	SWBOH	TRUE	FALSE	120-240 m	
89	cervus		S. Mindana	SMIN	FALSE	FALSE		
82	bullatus		Samar	SAM	FALSE	FALSE		
111	floccatus		Sulu Archi	SSIS	FALSE	FALSE		
108	excelsus		S. Mindana	SMIN	FALSE	TRUE	100-400 m	
145	ochroleucus		Batangas	SWLUZ	FALSE	FALSE		
145	ochroleucus		Batangas	SWLUZ	FALSE	FALSE		synonym o
19	varius	8	Marinduqu	SIBIS	FALSE	FALSE		
96	neptunus		Cebu	CEBE	FALSE	FALSE		
57	mucronatu	1	Sorsogon	SELUZ	FALSE	FALSE		
52	scabriuscu	2	Samar	SAM	FALSE	FALSE		
51	glans	2	Eastern Sa	SAM	FALSE	FALSE		
147	tenuistriatus		E. Samar	ESAM	FALSE	FALSE		
148	viola		Cebu	CEBE	FALSE	FALSE		
134	luteus		Cebu	CEBE	FALSE	FALSE		
57	mucronatu	1	Cebu	CEBE	FALSE	FALSE		
149	monachus		Marinduqu	SIBIS	FALSE	FALSE		
150	mitratus	1	Samar	SAM	FALSE	FALSE		
100	cylindraceus		Samar	SAM	FALSE	FALSE		
20	achatinus	4	Marinduqu	SIBIS	FALSE	FALSE		
32	parius	1	Batangas	SWLUZ	FALSE	FALSE		
151	proximus		Cebu	CEBE	FALSE	FALSE		
153	molluccens	1	Cebu	CEBE	FALSE	FALSE		
114	generalis		Samar	CEBE	FALSE	FALSE		
25	furvus	1	Palawan	EPAL	FALSE	FALSE		

133	litoglyphus		Samar	SAM	FALSE	FALSE		
31	radiatus	5	Manila Bay	WLUZ	FALSE	FALSE		
154	spectrum		Palawan	EPAL	FALSE	FALSE		synonym o
79	boeticus		Samar	SAM	FALSE	FALSE		
95	collisus		Marinduqu	SIBIS	FALSE	FALSE		
7	chaldeus	1	E. Samar	ESAM	FALSE	FALSE		
81	broderippi		Sulu	SSIS	FALSE	TRUE		
28	stramineus	5	Marinduqu	SIBIS	FALSE	FALSE		
8	ebraeus	2	Samar	SAM	FALSE	FALSE		
35	rattus	8	E. Samar	ESAM	FALSE	FALSE		
91	cinereus	3	Sulu	SSIS	FALSE	FALSE		
91	cinereus		Marinduqu	SIBIS	FALSE	FALSE		
17	arenatus	1	Palawan	EPAL	FALSE	FALSE		
193	pulicarius	6	Samar	SAM	FALSE	FALSE		
21	catus	2	Samar	SAM	FALSE	FALSE		
5	eburneus	2	Samar	SAM	FALSE	FALSE		
18	stercusmus	7	Samar	SAM	FALSE	FALSE		
5	eburneus		Camarines	SELUZ	FALSE	FALSE		synonym o
37	miles	2	E. Samar	ESAM	FALSE	FALSE		
15	distans	8	Bohol	SWBOH	FALSE	FALSE		
2	imperialis	7	Bohol	SWBOH	FALSE	FALSE		
33	vexillum	7	Samar	SAM	FALSE	FALSE		
54	sulcatus	1	Cebu	CEBE	FALSE	FALSE		
78	sulcatus		Cebu	CEBE	FALSE	FALSE		
157	samiae		S. Mindana	SMIN	FALSE	FALSE		
47	striatus	1	Samar	SAM	FALSE	FALSE		
128	laterculatus		Tayabas B	TB	FALSE	TRUE		
30	australis	5	E. Samar	ESAM	FALSE	TRUE		
50	terebra	2	E. Samar	ESAM	FALSE	FALSE		
68	asiaticus		Tayabas B	TB	FALSE	TRUE		
76	grangeri		Punta Enga	CEBE	FALSE	FALSE		
158	pagodus		Tayabas B	TB	FALSE	FALSE		
109	eximius		Cebu	CEBE	FALSE	FALSE		
159	thalassiarchus		Palawan	EPAL	TRUE	FALSE	shallow	
26	magus	1	Albay Gulf	SELUZ	FALSE	FALSE		
26	magus		Albay Gul,	SELUZ	FALSE	FALSE		
26	magus		Palawan	EPAL	FALSE	TRUE		
29	consors	1	Samar	SAM	FALSE	FALSE		
14	moreleti	7	Marinduqu	SIBIS	FALSE	FALSE		
53	muriculatus		Marinduqu	SIBIS	FALSE	FALSE		synonym o
40	flavidus	2	E. Samar	ESAM	FALSE	FALSE		
13	lividus	8	E Samar.	ESAM	FALSE	FALSE		
53	muriculatus	8	Cebu	CEBE	FALSE	FALSE		
102	achatinus	4	Palawan	EPAL	FALSE	FALSE		
41	frigidus	2	Palawan	EPAL	FALSE	FALSE		
22	striatellus	1	Samar	SAM	FALSE	FALSE		
75	balteatus		Samar	SAM	FALSE	FALSE		
163	sanguinolentus		E. Samar	ESAM	FALSE	FALSE		
16	biliosus	1	Marinduqu	SIBIS	FALSE	FALSE		
24	planorbis		Palawan	EPAL	FALSE	FALSE		
24	planorbis	8	Palawan	EPAL	FALSE	FALSE		
23	planorbis	8	Samar	SAM	FALSE	FALSE		

92	circumactus		Sulu Archip	SSIS	FALSE	FALSE		
117	gloriamaris	5	Punta Enga	CEBE	FALSE	FALSE		
69	aulicus	1	E. Samar	ESAM	FALSE	FALSE		
72	auricomus		E. Samar	ESAM	FALSE	FALSE		
165	retifer		E. Samar	ESAM	FALSE	FALSE		
44	telatus	1	Palawan	EPAL	TRUE	FALSE		
63	ammiralis		Sulu Archip	SSIS	FALSE	FALSE		
129	legatus		E. Samar	ESAM	FALSE	FALSE		
43	textile	7	Palawan	EPAL	FALSE	FALSE		
83	canonicus		Samar	SAM	FALSE	FALSE		
1	marmoreus	7	Albay Gulf,	SELUZ	FALSE	FALSE		
166	nobilis		Palawan	EPAL	FALSE	FALSE		
114	generalis		Punta Enga	CEBE	FALSE	FALSE		
61	alabaster		Tayabas B	TB	FALSE	FALSE		
168	areonosus		Coron Is.,	CALAMIAN	FALSE	FALSE		
125	kintoki		Punta Enga	CEBE	TRUE	FALSE	100-400m	
122	ione		Cebu	CEBE	FALSE	TRUE	200-240	
3	litteratus	7	Bohol	SWBOH	FALSE	FALSE		
132	leopardus		Cebu	CEBE	FALSE	FALSE		
169	tribblei		Tayabas B	TB	FALSE	FALSE		
130	lenavati		Punta Enga	CEBE	TRUE	FALSE	100-240 m	
170	sugimotonis		Bohol	SWBOH	FALSE	FALSE		
124	kinoshitai		Panglao, B	SWBOH	FALSE	FALSE		
112	miliaris		Samar	SAM	FALSE	FALSE		
112	miliaris	2	Batangas	SWLUZ	FALSE	FALSE		
171	sp.		Cebu	CEBE	FALSE	FALSE		
172	recluzianus		Tayabas B	TB	FALSE	TRUE	25-240 m	
173	voluminalis		Turtle Is., S	SSIS	FALSE	FALSE		
174	voluminalis		Tayabas B	TB	FALSE	FALSE		
175	sp.		Cebu	CEBE	FALSE	FALSE		
69	aulicus	1	Albay Gulf,	SELUZ	FALSE	FALSE		
176	magnificus		Samar	ESAM	FALSE	FALSE		
177	omaria	3	Mactan Is.,	CEBE	FALSE	FALSE		
70	auratinus		E. Samar	ESAM	FALSE	FALSE		
106	episcopatus		Samar	ESAM	FALSE	FALSE		
178	praecellens		Tayabas B	TB	FALSE	FALSE		synomym c
178	praecellens		Punta Enga	CEBE	FALSE	FALSE		
59	acutangulu	1	Cebu	CEBE	FALSE	FALSE		
180	memiae		Punta Enga	CEBE	FALSE	FALSE		
123	kimioi		Punta Enga	CEBE	FALSE	FALSE		
97	comatosa	5	Cebu	CEBE	FALSE	FALSE		
102	aculeiformis		Punta Enga	CEBE	FALSE	FALSE		
181	sp.		Punta Enga	CEBE	FALSE	FALSE		
182	sp.		Cebu	CEBE	FALSE	FALSE		
121	ichinoseana		Punta Enga	CEBE	FALSE	TRUE		
183	pseudorbignyi		Punta Enga	CEBE	FALSE	TRUE		
184	orbignyi		Tayabas B	TB	FALSE	FALSE		
185	vimineus		Punta Enga	CEBE	FALSE	FALSE		
60	floridulus	1	Mactan Is.,	CEBE	FALSE	FALSE		
186	montillai	1	Palawan	EPAL	TRUE	FALSE		
187	scalptus		Punta Enga	CEBE	TRUE	FALSE		
11	musicus	4	Batangas	SWLUZ	FALSE	FALSE		

12	sponsalis	2	Batangas	SWLUZ	FALSE	FALSE		
9	coronatus		Samar	SAM	FALSE	FALSE		
9	coronatus	2	Samar	SAM	FALSE	FALSE		
64	aphrodite		Bohol	SWBOH	FALSE	FALSE		
119	hirasei	5	S. Mindana	SMIN	FALSE	TRUE	100-240 m	
98	corallinus		Sulu Archi	SSIS	FALSE	FALSE		
26	magus		Palawan	EPAL	FALSE	FALSE		
131	leobrerai		Visayan Se	NWBOH	FALSE	FALSE		
127	eugrammatus		Punta Enga	CEBE	FALSE	FALSE		
67	articulatus		Punta Enga	CEBE	FALSE	FALSE		
101	dayriti		Palawan	EPAL	FALSE	FALSE		
90	chiangi	1	Panglao, B	SWBOH	FALSE	FALSE		
74	baileyi		Panglao, B	SWBOH	FALSE	FALSE		
80	boholensis		Panglao, B	SWBOH	FALSE	FALSE		
127	eugrammatus		Visayan Se	NWBOH	FALSE	FALSE		
103	dondani		Panglao, B	SWBOH	TRUE	FALSE		
188	wakayamensis		Visayan Se	NWBOH	FALSE	FALSE		30-140 m
189	polongimarumai		Punta Enga	CEBE	FALSE	FALSE		
62	furvus		Samar	SAM	FALSE	FALSE		
30	australis		Visayan Se	NWBOH	FALSE	FALSE		
190	saecularis		Punta Enga	CEBE	FALSE	FALSE		
191	sazanka		Davao	DAV	FALSE	FALSE		
110	fischoederi		Samar	SAM	FALSE	TRUE	30 m coral rubble	
192	saecularis		Punta Enga	CEBE	FALSE	FALSE		
1	marmoreus	7	Pagbilao	TB	FALSE	FALSE		
1	marmoreus	7	Matandang	TB	FALSE	FALSE		
1	marmoreus	7	Unisan	TB	FALSE	FALSE		
1	marmoreus	7	Agdangan	TB	FALSE	FALSE		
1	marmoreus	7	Ibabang Su	TB	FALSE	FALSE		
1	marmoreus	7	Amang Cal	TB	FALSE	FALSE		
1	marmoreus	7	Busdak	TB	FALSE	FALSE		
1	marmoreus	7	Kawayan	TB	FALSE	FALSE		
1	marmoreus	7	Gatasan	TB	FALSE	FALSE		
2	imperialis	7	Hacupan Is	TB	FALSE	FALSE		
2	imperialis	7	Imelda	TB	FALSE	FALSE		
2	imperialis	7	Amang Cal	TB	FALSE	FALSE		
3	litteratus	7	Mayao	TB	FALSE	FALSE		
3	litteratus	7	Matandang	TB	FALSE	FALSE		
3	litteratus	7	Imelda	TB	FALSE	FALSE		
3	litteratus	7	Bagong Sil	TB	FALSE	FALSE		
4	tesullatus	1	Laiya	TB	FALSE	FALSE		
4	tesullatus	1	Mayao	TB	FALSE	FALSE		
4	tesullatus	1	S Marinduc	TB	FALSE	FALSE		
5	eburneus	2	Cabuyo	TB	FALSE	FALSE		
6	caracterisc	1	Mongpong	TB	FALSE	FALSE		
7	chaldeus	1	Hacupan Is	TB	FALSE	FALSE		
35	rattus	8	Pasaleng E	NWLUZ	FALSE	FALSE		
35	rattus	8	Darara Poi	NWLUZ	FALSE	FALSE		
37	miles	2	Cadalian	NWLUZ	FALSE	FALSE		
37	miles	2	Maglasi	NWLUZ	FALSE	FALSE		
37	miles	2	Delavis	NWLUZ	FALSE	FALSE		
37	miles	2	Salomaque	NWLUZ	FALSE	FALSE		

11	musicus	7	Salomaque	NWLUZ	FALSE	FALSE
11	musicus	7	Pagatpat	NWLUZ	FALSE	FALSE
11	musicus	7	Currimao	NWLUZ	FALSE	FALSE
11	musicus	7	Maglasi	NWLUZ	FALSE	FALSE
11	musicus	7	Sabang	NWLUZ	FALSE	FALSE
37	miles	2	Salomaque	NWLUZ	FALSE	FALSE
11	musicus	7	Pasaleng E	NWLUZ	FALSE	FALSE
112	miliaris	2	Pasaleng E	NWLUZ	FALSE	FALSE
14	moreleti	7	Bantoc	NWLUZ	FALSE	FALSE
11	musicus	7	Pagsanaar	NWLUZ	FALSE	FALSE
112	miliaris	2	Centro	NWLUZ	FALSE	FALSE
11	musicus	7	Pagsanaar	NWLUZ	FALSE	FALSE
53	muriculatu	8	Dardarat	NWLUZ	FALSE	FALSE
26	magus		Daclapan	NWLUZ	FALSE	FALSE
53	muriculatu	8	Gubat Nort	NWLUZ	FALSE	FALSE
36	mustelinus	8	Parana Poi	NWLUZ	FALSE	FALSE
37	miles	2	Sulvec	NWLUZ	FALSE	FALSE
37	miles	2	Surngit	NWLUZ	FALSE	FALSE
37	miles	2	Sulvec	NWLUZ	FALSE	FALSE
14	moreleti	7	Dirigue Ba	NWLUZ	FALSE	FALSE
37	miles	2	Bangui Ba	NWLUZ	FALSE	FALSE
21	catus	1	Liwi	NWLUZ	FALSE	FALSE
21	catus	1	Cadalian	NWLUZ	FALSE	FALSE
21	catus	1	Maglawi	NWLUZ	FALSE	FALSE
21	catus	1	Apatot	NWLUZ	FALSE	FALSE
21	catus	1	Sulvec	NWLUZ	FALSE	FALSE
21	catus	1	Santiago	NWLUZ	FALSE	FALSE
21	catus	1	Maglasi	NWLUZ	FALSE	FALSE
21	catus	1	Sabang	NWLUZ	FALSE	FALSE
21	catus	1	Pagsanaar	NWLUZ	FALSE	FALSE
198	obscurus		Saud	NWLUZ	FALSE	FALSE
145	ochroleucus		Dirigue Ba	NWLUZ	FALSE	FALSE
24	planorbis	8	Liwis	NWLUZ	FALSE	FALSE
193	pulicarius	3	Cadalian	NWLUZ	FALSE	FALSE
193	pulicarius	3	Maglasi	NWLUZ	FALSE	FALSE
24	planorbis	8	Bateria	NWLUZ	FALSE	FALSE
193	pulicarius	3	Sulvec	NWLUZ	FALSE	FALSE
24	planorbis	8	Badoc Isla	NWLUZ	FALSE	FALSE
193	pulicarius	3	Badoc Isla	NWLUZ	FALSE	FALSE
151	proximus		Tamunong	NWLUZ	FALSE	FALSE
193	pulicarius	3	Bobon	NWLUZ	FALSE	FALSE
12	sponsalis	2	Salomaque	NWLUZ	FALSE	FALSE
47	striatus	1	Pasaleng E	NWLUZ	FALSE	FALSE
16	biliosus	1	Salomaque	NWLUZ	FALSE	FALSE
201	suratensis		Barangay	NWLUZ	FALSE	FALSE
47	striatus	1	Maglaoi	NWLUZ	FALSE	FALSE
12	sponsalis	2	Sulvec	NWLUZ	FALSE	FALSE
12	sponsalis	2	Salomaque	NWLUZ	FALSE	FALSE
12	sponsalis	2	Sulvec	NWLUZ	FALSE	FALSE
8	ebreaus	2	Hacupan I	TB	FALSE	FALSE
8	ebreaus	2	Hacupan I	TB	FALSE	FALSE
8	ebreaus	2	Maniuaya I	TB	FALSE	FALSE

11	musicus	4	Talaotalao	TB	FALSE	FALSE
11	musicus	4	Calancan	TB	FALSE	FALSE
11	musicus	4	Panambo	TB	FALSE	FALSE
11	musicus	4	Mancarang	TB	FALSE	FALSE
11	musicus	4	Pagbilao G	TB	FALSE	FALSE
11	musicus	4	Mongpong	TB	FALSE	FALSE
11	musicus	4	Mongpong	TB	FALSE	FALSE
11	musicus	4	Kawayan	TB	FALSE	FALSE
11	musicus	4	Inabuan	TB	FALSE	FALSE
11	musicus	4	Busdak	TB	FALSE	FALSE
11	musicus	4	Ajos	TB	FALSE	FALSE
11	musicus	4	Santa Rosa	TB	FALSE	FALSE
11	musicus	4	Ajos	TB	FALSE	FALSE
11	musicus	4	Ajos	TB	FALSE	FALSE
12	sponsalis	2	Hacupan Is	TB	FALSE	FALSE
13	lividus	8	Laiya	TB	FALSE	FALSE
14	moreleti	7	Bacong Iba	TB	FALSE	FALSE
14	moreleti	7	Imelda	TB	FALSE	FALSE
14	moreleti	7	Calancan	TB	FALSE	FALSE
15	distans	8	Tuhian Poi	TB	FALSE	FALSE
16	biliosus	1	Tigwi	TB	FALSE	FALSE
17	arenatus	1	Pulong	TB	FALSE	FALSE
17	arenatus	1	Laiya	TB	FALSE	FALSE
17	arenatus	1	Calancan	TB	FALSE	FALSE
18	stercusmus	7	Subukin	TB	FALSE	FALSE
18	stercusmus	7	Patabog	TB	FALSE	FALSE
18	stercusmus	7	Hacupan Is	TB	FALSE	FALSE
18	stercusmus	7	Cabuyo	TB	FALSE	FALSE
18	stercusmus	7	Kawayan	TB	FALSE	FALSE
18	stercusmus	7	Busdak	TB	FALSE	FALSE
18	stercusmus	7	Ajos	TB	FALSE	FALSE
19	varius	8	Tayabas	TB	FALSE	FALSE
19	varius	8	Patabog	TB	FALSE	FALSE
20	achatinus	4	Cabuyo	TB	FALSE	FALSE
20	achatinus	4	Inabuan	TB	FALSE	FALSE
20	achatinus	4	Ajos	TB	FALSE	FALSE
21	catus	1	Cabuyo	TB	FALSE	FALSE
21	catus	1	Cabuyo	TB	FALSE	FALSE
22	striatellus	1	Kalutan	TB	FALSE	FALSE
23	planorbis	8	Catanauan	TB	FALSE	FALSE
23	planorbis	8	Sandoval F	TB	FALSE	FALSE
24	planorbis	8	Laiya	TB	FALSE	FALSE
24	planorbis	8	Ibabang Pu	TB	FALSE	FALSE
24	planorbis	8	Panambo	TB	FALSE	FALSE
24	planorbis	8	Matandang	TB	FALSE	FALSE
24	planorbis	8	Kalutan	TB	FALSE	FALSE
24	planorbis	8	Pagbilao G	TB	FALSE	FALSE
24	planorbis	8	Sandoval F	TB	FALSE	FALSE
24	planorbis	8	Kawayan	TB	FALSE	FALSE
24	planorbis	8	Inabuan	TB	FALSE	FALSE
25	furvus	1	Punta1	TB	FALSE	FALSE
26	magus	1	Talaotalao	TB	FALSE	FALSE

26	magus	1	Pagbilao G	TB	FALSE	FALSE
26	magus	1	Matandang	TB	FALSE	FALSE
26	magus	1	Bacong Iba	TB	FALSE	FALSE
12	sponsalis	2	Bago	NWLUZ	FALSE	FALSE
44	telatus	1	Dadalaquit	NWLUZ	TRUE	FALSE
50	terebra	2	Pagsanaar	NWLUZ	FALSE	FALSE
50	terebra	2	Sulvec	NWLUZ	FALSE	FALSE
50	terebra	2	Capurpurai	NWLUZ	FALSE	FALSE
200	tulipa		Burgos	NWLUZ	FALSE	FALSE
200	tulipa		Tamunong	NWLUZ	FALSE	FALSE
197	vexillum	7	Salomaque	NWLUZ	FALSE	FALSE
23	planorbis	8	Paraoir	NWLUZ	FALSE	FALSE
23	planorbis	8	Maglawi	NWLUZ	FALSE	FALSE
19	varius	8	Narvacan	NWLUZ	FALSE	FALSE
197	vexillum	7	Bateria	NWLUZ	FALSE	FALSE
23	planorbis	8	Bobon	NWLUZ	FALSE	FALSE
19	varius	8	Torre	NWLUZ	FALSE	FALSE
23	planorbis	8	Dirigue Bay	NWLUZ	FALSE	FALSE
23	planorbis	8	Maglasi	NWLUZ	FALSE	FALSE
13	lividus	8	Dirigue Bay	NWLUZ	FALSE	FALSE
13	lividus	8	Cabugao	NWLUZ	FALSE	FALSE
2	imperialis	7	Sabang	NWLUZ	FALSE	FALSE
13	lividus	8	Sulvec	NWLUZ	FALSE	FALSE
13	lividus	8	Pasuquin	NWLUZ	FALSE	FALSE
13	lividus	8	San Roque	NWLUZ	FALSE	FALSE
13	lividus	8	Imelda Par	NWLUZ	FALSE	FALSE
13	lividus	8	Santiago C	NWLUZ	FALSE	FALSE
13	lividus	8	Bobon	NWLUZ	FALSE	FALSE
13	lividus	8	Bobon	NWLUZ	FALSE	FALSE
13	lividus	8	Bolanos	NWLUZ	FALSE	FALSE
13	lividus	8	Sulvec	NWLUZ	FALSE	FALSE
13	lividus	8	Carpurpura	NWLUZ	FALSE	FALSE
13	lividus	8	Tamunong	NWLUZ	FALSE	FALSE
13	lividus	8	Delavu	NWLUZ	FALSE	FALSE
194	litoglyphus		Bulalo	NWLUZ	FALSE	FALSE
13	lividus	8	Pagnasaar	NWLUZ	FALSE	FALSE
13	lividus	8	Tamunong	NWLUZ	FALSE	FALSE
13	lividus	8	Batil	NWLUZ	FALSE	FALSE
13	lividus	8	Poro Point	NWLUZ	FALSE	FALSE
13	lividus	8	Pasaleng E	NWLUZ	FALSE	FALSE
13	lividus	8	Padalaquit	NWLUZ	FALSE	FALSE
46	quercinus	1	Tulnaga	NWLUZ	FALSE	FALSE
35	rattus	8	Pinget Islai	NWLUZ	FALSE	FALSE
35	rattus	8	Salomaque	NWLUZ	FALSE	FALSE
35	rattus	8	Liwis	NWLUZ	FALSE	FALSE
35	rattus	8	Pasaleng E	NWLUZ	FALSE	FALSE
35	rattus	8	Saud	NWLUZ	FALSE	FALSE
35	rattus	8	Badoc Islai	NWLUZ	FALSE	FALSE
35	rattus	8	Badoc Islai	NWLUZ	FALSE	FALSE
35	rattus	8	Capurpurai	NWLUZ	FALSE	FALSE
35	rattus	8	Dalaui	NWLUZ	FALSE	FALSE
35	rattus	8	Dalaui	NWLUZ	FALSE	FALSE

31	radiatus	5	Marcos Sa	NWLUZ	FALSE	FALSE
31	radiatus	5	Lingayen G	NWLUZ	FALSE	FALSE
35	rattus	8	Butol	NWLUZ	FALSE	FALSE
35	rattus	8	Tamunong	NWLUZ	FALSE	FALSE
35	rattus	8	Burgos	NWLUZ	FALSE	FALSE
35	rattus	8	Saloge	NWLUZ	FALSE	FALSE
35	rattus	8	Torre	NWLUZ	FALSE	FALSE
26	magus	1	Pagbilao G	TB	FALSE	FALSE
26	magus	1	Pagbilao G	TB	FALSE	FALSE
26	magus	1	Abung	TB	FALSE	FALSE
26	magus	1	Subukin	TB	FALSE	FALSE
26	magus	1	Subukin	TB	FALSE	FALSE
26	magus	1	Ibabang Su	TB	FALSE	FALSE
26	magus	1	Hacupan Is	TB	FALSE	FALSE
26	magus	1	Cabuyo	TB	FALSE	FALSE
26	magus	1	Matandang	TB	FALSE	FALSE
26	magus	1	Sandoval F	TB	FALSE	FALSE
26	magus	1	Punta	TB	FALSE	FALSE
26	magus	1	Busdak	TB	FALSE	FALSE
26	magus	1	Busdak	TB	FALSE	FALSE
26	magus	1	Busdak	TB	FALSE	FALSE
26	magus	1	Maalat	TB	FALSE	FALSE
26	magus	1	Busdak	TB	FALSE	FALSE
26	magus	1	Maalat	TB	FALSE	FALSE
26	magus	1	Busdak	TB	FALSE	FALSE
26	magus	1	Kawayan	TB	FALSE	FALSE
26	magus	1	Ajos	TB	FALSE	FALSE
26	magus	1	Ajos	TB	FALSE	FALSE
26	magus	1	Ajos	TB	FALSE	FALSE
26	magus	1	Gatasan	TB	FALSE	FALSE
26	magus	1	Gatasan	TB	FALSE	FALSE
26	magus	1	Gatasan	TB	FALSE	FALSE
27	subulatus	5	Laiya	TB	FALSE	TRUE
27	subulatus	5	Bacong Iba	TB	FALSE	TRUE
28	stramineus	5	Matandang	TB	FALSE	FALSE
29	consors	1	Matandang	TB	FALSE	FALSE
29	consors	1	Catanauan	TB	FALSE	FALSE
29	consors	1	Cabuyo	TB	FALSE	FALSE
30	australis	5	Tayabas	TB	FALSE	TRUE
31	radiatus	5	Talaotalao	TB	FALSE	FALSE
31	radiatus	5	Matandang	TB	FALSE	FALSE
31	radiatus	5	Punta	TB	FALSE	FALSE
31	radiatus	5	Mulanay	TB	FALSE	FALSE
31	radiatus	5	Parales	TB	FALSE	FALSE
31	radiatus	5	Ibabang Su	TB	FALSE	FALSE
31	radiatus	5	Matandang	TB	FALSE	FALSE
31	radiatus	5	Bagong Sil	TB	FALSE	FALSE
32	parius	1	Cabuyo	TB	FALSE	FALSE
33	vexillum	7	Ibabang Pu	TB	FALSE	FALSE
197	vexillum	7	Amang Cal	TB	FALSE	FALSE
34	capitaneus	2	Talaotalao	TB	FALSE	FALSE
34	capitaneus	2	Laiya	TB	FALSE	FALSE

34	capitaneus	2	Matandang	TB	FALSE	FALSE
34	capitaneus	2	Catanauan	TB	FALSE	FALSE
34	capitaneus	2	Busdak	TB	FALSE	FALSE
34	capitaneus	2	Sandoval F	TB	FALSE	FALSE
35	rattus	8	Laiya	TB	FALSE	FALSE
35	rattus	8	Maniuaya I	TB	FALSE	FALSE
35	rattus	8	Bagong Sil	TB	FALSE	FALSE
36	mustelinus	8	Talaotalao	TB	FALSE	FALSE
36	mustelinus	8	Laiya	TB	FALSE	FALSE
36	mustelinus	8	Ibabang Pu	TB	FALSE	FALSE
36	mustelinus	8	Matandang	TB	FALSE	FALSE
36	mustelinus	8	Punta	TB	FALSE	FALSE
36	mustelinus	8	Putting Bul	TB	FALSE	FALSE
36	mustelinus	8	Catanauan	TB	FALSE	FALSE
36	mustelinus	8	Bacong Iba	TB	FALSE	FALSE
36	mustelinus	8	Imelda	TB	FALSE	FALSE
36	mustelinus	8	Sandoval F	TB	FALSE	FALSE
36	mustelinus	8	Ajos	TB	FALSE	FALSE
37	miles	2	Hacupan Is	TB	FALSE	FALSE
37	miles	2	Laiya	TB	FALSE	FALSE
37	miles	2	San Franci	TB	FALSE	FALSE
38	virgo	6	Ibabang Pu	TB	FALSE	FALSE
38	virgo	6	Pagbilao G	TB	FALSE	FALSE
38	virgo	6	Matandang	TB	FALSE	FALSE
38	virgo	6	Bacong Iba	TB	FALSE	FALSE
38	virgo	6	Silag	TB	FALSE	FALSE
38	virgo	6	Matandang	TB	FALSE	FALSE
39	emaciatus	2	Hacupan Is	TB	FALSE	FALSE
39	emaciatus	2	Panambo	TB	FALSE	FALSE
39	emaciatus	2	Hacupan Is	TB	FALSE	FALSE
40	flavidus	2	Hacupan Is	TB	FALSE	FALSE
41	frigidus	2	Tigwi	TB	FALSE	FALSE
42	pennaceus	3	Sta Cruz	TB	FALSE	FALSE
42	pennaceus	3	Laiya	TB	FALSE	FALSE
42	pennaceus	3	Cabuyo	TB	FALSE	FALSE
43	textile	7	Laiya	TB	FALSE	FALSE
43	textile	7	Hacupan Is	TB	FALSE	FALSE
43	textile	7	Cabuyo	TB	FALSE	FALSE
43	textile	7	Cabuyo	TB	FALSE	FALSE
43	textile	7	Santa Rosa	TB	FALSE	FALSE
44	telatus	1	Mongpong	TB	TRUE	FALSE
45	figulinus	5	Matandang	TB	FALSE	FALSE
46	quercinus	1	Maniuaya I	TB	FALSE	FALSE
46	quercinus	1	Silag	TB	FALSE	FALSE
47	striatus	1	Banot Islar	TB	FALSE	FALSE
47	striatus	1	Putting Bul	TB	FALSE	FALSE
47	striatus	1	Catanauan	TB	FALSE	FALSE
47	striatus	1	Amang Cal	TB	FALSE	FALSE
47	striatus	1	Cabuyo	TB	FALSE	FALSE
47	striatus	1	Mongpong	TB	FALSE	FALSE
47	striatus	1	Gatasan	TB	FALSE	FALSE
48	anemone	1	Tayabas	TB	FALSE	FALSE

48	anemone	1	Laiya	TB	FALSE	FALSE
49	nussatella	8	Maniuaya I	TB	FALSE	FALSE
49	nussatella	8	Laiya	TB	FALSE	FALSE
50	terebra	2	Laiya	TB	FALSE	FALSE
50	terebra	2	Bacong Iba	TB	FALSE	FALSE
50	terebra	2	Mongpong	TB	FALSE	FALSE
51	glans	2	Mongpong	TB	FALSE	FALSE
51	glans	2	Laiya	TB	FALSE	FALSE
52	scabriuscu	2	Mongpong	TB	FALSE	FALSE
53	muriculatus	8	Talaotalao	TB	FALSE	FALSE
53	muriculatus	8	Laiya	TB	FALSE	FALSE
53	muriculatus	8	Ibabang Pu	TB	FALSE	FALSE
53	muriculatus	8	Patabog	TB	FALSE	FALSE
53	muriculatus	8	Ibabang Pu	TB	FALSE	FALSE
53	muriculatus	8	Patabog	TB	FALSE	FALSE
53	muriculatus	8	Abung	TB	FALSE	FALSE
53	muriculatus	8	Subukin	TB	FALSE	FALSE
53	muriculatus	8	Ibabang Su	TB	FALSE	FALSE
53	muriculatus	8	Pacatin	TB	FALSE	FALSE
53	muriculatus	8	Cabuyo	TB	FALSE	FALSE
53	muriculatus	8	Matandang	TB	FALSE	FALSE
53	muriculatus	8	Ajos	TB	FALSE	FALSE
53	muriculatus	8	Santa Rosa	TB	FALSE	FALSE
53	muriculatus	8	Cabuyo	TB	FALSE	FALSE
54	sulcatus	1	Tayabas	TB	FALSE	FALSE
55	moluccens	1	Cabuyo	TB	FALSE	FALSE
55	moluccens	1	Tigwi	TB	FALSE	FALSE
55	moluccens	1	Tigwi	TB	FALSE	FALSE
55	moluccens	1	Tigwi	TB	FALSE	FALSE
56	insculptus	5	Tayabas	TB	FALSE	FALSE
57	mucronatus	1	Busdak	TB	FALSE	FALSE
178	praecellens	1	Tayabas	TB	FALSE	FALSE
59	acutangulu	1	Laiya	TB	FALSE	FALSE
60	floridulus	1	Tigwi	TB	FALSE	FALSE
20	achatinus	4	Guimaras I	SPANAY	FALSE	FALSE
17	arenatus	1	Tangalan	NPANAY	FALSE	FALSE
17	arenatus	1	Anini-Y	SPANAY	FALSE	FALSE
17	arenatus	1	Tangalan	SPANAY	FALSE	FALSE
17	arenatus	1	Pandan	NPANAY	FALSE	FALSE
17	arenatus	1	Malay	NPANAY	FALSE	FALSE
79	boeticus	3	Concepcion	SPANAY	FALSE	FALSE
34	capitaneus	2	Guimaras S	SPANAY	FALSE	FALSE
34	capitaneus	2	Tangalan	NPANAY	FALSE	FALSE
34	capitaneus	2	Concepcion	SPANAY	FALSE	FALSE
34	capitaneus	2	Guimaras I	SPANAY	FALSE	FALSE
34	capitaneus	2	Malay	NPANAY	FALSE	FALSE
34	capitaneus	2	Tangalan	NPANAY	FALSE	FALSE
34	capitaneus	2	Tangalan	NPANAY	FALSE	FALSE
34	capitaneus	2	Guimaras I	SPANAY	FALSE	FALSE
21	catus	2	Nabus	NPANAY	FALSE	FALSE
21	catus	2	Tobias Fer	SPANAY	FALSE	FALSE
7	chaldeus	1	Caluya	SPANAY	FALSE	FALSE

7	chaldeus	1	Anini-Y	SPANAY	FALSE	FALSE
7	chaldeus	1	Anini-Y	SPANAY	FALSE	FALSE
7	chaldeus	1	Malay	NPANAY	FALSE	FALSE
7	chaldeus	1	Anini-Y	SPANAY	FALSE	FALSE
95	collisus		Guimaras I	SPANAY	FALSE	FALSE
95	collisus		Carles	SPANAY	FALSE	FALSE
15	distans	8	Tangalan	NPANAY	FALSE	FALSE
8	ebraeus	2	Sapian Ba	NPANAY	FALSE	FALSE
8	ebraeus	2	Culasi	NPANAY	FALSE	FALSE
8	ebraeus	2	Tobias Fer	NPANAY	FALSE	FALSE
8	ebraeus	2	Guimaras I	SPANAY	FALSE	FALSE
8	ebraeus	2	Anini-Y	NPANAY	FALSE	FALSE
8	ebraeus	2	Caluya	NPANAY	FALSE	FALSE
8	ebraeus	2	Carles	SPANAY	FALSE	FALSE
8	ebraeus	2	Malay	NPANAY	FALSE	FALSE
8	ebraeus	2	Buruanga	NPANAY	FALSE	FALSE
8	ebraeus	2	Guimaras I	SPANAY	FALSE	FALSE
8	ebraeus	2	Anini-Y	SPANAY	FALSE	FALSE
8	ebraeus	2	Anini-Y	SPANAY	FALSE	FALSE
8	ebraeus	2	Concepcio	SPANAY	FALSE	FALSE
8	ebraeus	2	Tangalan	NPANAY	FALSE	FALSE
8	ebraeus	2	Tangalan	NPANAY	FALSE	FALSE
8	ebreaus	2	Manulao	TB	FALSE	FALSE
8	ebreaus	2	Maniuaya I	TB	FALSE	FALSE
8	ebreaus	2	Busdak	TB	FALSE	FALSE
8	ebreaus	2	Busdak	TB	FALSE	FALSE
8	ebreaus	2	Maalat	TB	FALSE	FALSE
9	coronatus	2	Talaotalao	TB	FALSE	FALSE
9	coronatus	2	Banot Isla	TB	FALSE	FALSE
9	coronatus	2	Laiya	TB	FALSE	FALSE
9	coronatus	2	Matandan	TB	FALSE	FALSE
9	coronatus	2	Patabog	TB	FALSE	FALSE
9	coronatus	2	Bacong Ib	TB	FALSE	FALSE
9	coronatus	2	Bacong Ib	TB	FALSE	FALSE
9	coronatus	2	Subukin	TB	FALSE	FALSE
9	coronatus	2	Abung	TB	FALSE	FALSE
9	coronatus	2	Subukin	TB	FALSE	FALSE
9	coronatus	2	Hacupan I	TB	FALSE	FALSE
9	coronatus	2	Cabuyo	TB	FALSE	FALSE
9	coronatus	2	Calancan	TB	FALSE	FALSE
9	coronatus	2	Matandan	TB	FALSE	FALSE
9	coronatus	2	Tayabas B	TB	FALSE	FALSE
9	coronatus	2	Punta	TB	FALSE	FALSE
9	coronatus	2	Busdak	TB	FALSE	FALSE
9	coronatus	2	Maalat	TB	FALSE	FALSE
9	coronatus	2	Busdak	TB	FALSE	FALSE
9	coronatus	2	Kawayan	TB	FALSE	FALSE
9	coronatus	2	Inabuan	TB	FALSE	FALSE
9	coronatus	2	Inabuan	TB	FALSE	FALSE
9	coronatus	2	Ajos	TB	FALSE	FALSE
9	coronatus	2	Ajos	TB	FALSE	FALSE
9	coronatus	2	Ajos	TB	FALSE	FALSE

9	coronatus	2	Ajos	TB	FALSE	FALSE
9	coronatus	2	Ajos	TB	FALSE	FALSE
9	coronatus	2	Santa Ros	TB	FALSE	FALSE
9	coronatus	2	Ajos	TB	FALSE	FALSE
9	coronatus	2	Ajos	TB	FALSE	FALSE
9	coronatus	2	Ajos	TB	FALSE	FALSE
9	coronatus	2	Gatasan	TB	FALSE	FALSE
9	coronatus	2	Gatasan	TB	FALSE	FALSE
9	coronatus	2	Gatasan	TB	FALSE	FALSE
9	coronatus	2	Gatasan	TB	FALSE	FALSE
9	coronatus	2	Gatasan	TB	FALSE	FALSE
9	coronatus	2	Bagong Sil	TB	FALSE	FALSE
112	miliaris	2	Laiya	TB	FALSE	FALSE
8	ebraeus	2	Santander	NPANAY	FALSE	FALSE
8	ebraeus	2	Anini-Y	SPANAY	FALSE	FALSE
5	eburneus	2	Tangalan	NPANAY	FALSE	FALSE
39	emaciatus	2	Caluya	NPANAY	FALSE	FALSE
39	emaciatus	2	Culasi	NPANAY	FALSE	FALSE
45	figulinus	5	Tangalan	SPANAY	FALSE	FALSE
40	flavidus	2	Anini-Y	SPANAY	FALSE	FALSE
40	flavidus	2	Caluya	SPANAY	FALSE	FALSE
112	miliaris		Pilar	NPANAY	FALSE	FALSE
51	glans	2	Malay	NPANAY	FALSE	FALSE
51	glans	2	Anini-Y	SPANAY	FALSE	FALSE
51	glans	2	Tobias Fer	SPANAY	FALSE	FALSE
51	glans	2	Tangalan	NPANAY	FALSE	FALSE
51	glans	2	Anini-Y	SPANAY	FALSE	FALSE
51	glans	2	Tangalan	NPANAY	FALSE	FALSE
114	generalis		Pilar	NPANAY	FALSE	FALSE
114	generalis		Tibiao	NPANAY	FALSE	FALSE
8	ebraeus	2	Guimaras I	SPANAY	FALSE	FALSE
2	imperialis	7	Anini-Y	SPANAY	FALSE	FALSE
2	imperialis	7	Malay	NPANAY	FALSE	FALSE
2	imperialis	7	Tangalan	NPANAY	FALSE	FALSE
132	leopardus	3	Malay	NPANAY	FALSE	FALSE
132	leopardus	3	Tibiao	SPANAY	FALSE	FALSE
3	litteratus	7	Guimaras I	SPANAY	FALSE	FALSE
3	litteratus	7	Tangalan	NPANAY	FALSE	FALSE
3	litteratus	7	Malay	NPANAY	FALSE	FALSE
13	lividus	8	Pandan	SPANAY	FALSE	FALSE
13	lividus	8	Makato	NPANAY	FALSE	FALSE
13	lividus	8	Anini-Y	SPANAY	FALSE	FALSE
13	lividus	8	Guimaras I	SPANAY	FALSE	FALSE
13	lividus	8	Guimaras I	SPANAY	FALSE	FALSE
26	magus	1	Caluya	SPANAY	FALSE	FALSE
26	magus	1	Concepcio	SPANAY	FALSE	FALSE
26	magus	1	Concepcio	SPANAY	FALSE	FALSE
26	magus	1	Pilar	NPANAY	FALSE	FALSE
26	magus	1	Tangalan	NPANAY	FALSE	FALSE
26	magus	1	San Dionis	SPANAY	FALSE	FALSE
26	magus	1	Tangalan	NPANAY	FALSE	FALSE
26	magus	1	Concepcio	SPANAY	FALSE	FALSE

26	magus	1	Libertad	SPANAY	FALSE	FALSE
26	magus	1	Carles	SPANAY	FALSE	FALSE
26	magus	1	Tangalan	NPANAY	FALSE	FALSE
26	magus	1	Guimaras I	SPANAY	FALSE	FALSE
26	magus	1	Concepcio	SPANAY	FALSE	FALSE
26	magus	1	Guimaras I	SPANAY	FALSE	FALSE
26	magus	1	Guimaras I	SPANAY	FALSE	FALSE
37	miles	2	Concepcio	SPANAY	FALSE	FALSE
37	miles	2	Tangalan	NPANAY	FALSE	FALSE
37	miles	2	Nabus	NPANAY	FALSE	FALSE
37	miles	2	Pandan	SPANAY	FALSE	FALSE
37	miles	2	Malay	NPANAY	FALSE	FALSE
37	miles	2	Guimaras I	SPANAY	FALSE	FALSE
37	miles	2	Tangalan	NPANAY	FALSE	FALSE
37	miles	2	Anini-Y	SPANAY	FALSE	FALSE
37	miles	2	Carles	SPANAY	FALSE	FALSE
14	moreleti	7	Anini-Y	SPANAY	FALSE	FALSE
14	moreleti	7	Anini-Y	SPANAY	FALSE	FALSE
53	muriculatu	8	Guimaras I	SPANAY	FALSE	FALSE
11	musicus	4	Anini-Y	SPANAY	FALSE	FALSE
11	musicus	4	Anini-Y	SPANAY	FALSE	FALSE
11	musicus	4	Pandan	SPANAY	FALSE	FALSE
11	musicus	4	Tangalan	NPANAY	FALSE	FALSE
11	musicus	4	Tangalan	NPANAY	FALSE	FALSE
11	musicus	4	Malay	NPANAY	FALSE	FALSE
11	musicus	4	Anini-Y	SPANAY	FALSE	FALSE
36	mustelinus	8	Ibayang	NPANAY	FALSE	FALSE
36	mustelinus	8	Carles	SPANAY	FALSE	FALSE
36	mustelinus	8	Tangalan	NPANAY	FALSE	FALSE
36	mustelinus	8	Concepcio	SPANAY	FALSE	FALSE
36	mustelinus	8	Guimaras I	SPANAY	FALSE	FALSE
36	mustelinus	8	Sapian Ba	NPANAY	FALSE	FALSE
26	magus	1	Concepcio	SPANAY	FALSE	FALSE
21	catus	1	Culasi	SPANAY	FALSE	FALSE
21	catus	1	Anini-Y	SPANAY	FALSE	FALSE
21	catus	1	Buruanga	NPANAY	FALSE	FALSE
21	catus	1	Malay	NPANAY	FALSE	FALSE
177	omaria	3	Caluya	SPANAY	FALSE	FALSE
177	omaria	3	Caluya	SPANAY	FALSE	FALSE
24	planorbis	8	Libertad	SPANAY	FALSE	FALSE
24	planorbis	8	Concepcio	SPANAY	FALSE	FALSE
24	planorbis	8	Concepcio	SPANAY	FALSE	FALSE
24	planorbis	8	Caluya	SPANAY	FALSE	FALSE
24	planorbis	8	Tangalan	NPANAY	FALSE	FALSE
24	planorbis	8	Tangalan	NPANAY	FALSE	FALSE
24	planorbis	8	Tangalan	NPANAY	FALSE	FALSE
24	planorbis	8	Malay	NPANAY	FALSE	FALSE
151	proximus		Guimaras I	SPANAY	FALSE	FALSE
193	pulicarius	6	Pandan	SPANAY	FALSE	FALSE
193	pulicarius	6	Tangalan	NPANAY	FALSE	FALSE
31	radiatus	5	Caluya	SPANAY	FALSE	FALSE
31	radiatus	5	Guimaras I	SPANAY	FALSE	FALSE

31	radiatus	5	Roxas City	NPANAY	FALSE	FALSE	
31	radiatus	5	Sapian Ba	NPANAY	FALSE	FALSE	
31	radiatus	5	Guimaras I	SPANAY	FALSE	FALSE	
31	radiatus	5	Guimaras I	SPANAY	FALSE	FALSE	
35	rattus	8	Ibayang	NPANAY	FALSE	FALSE	
35	rattus	8	Tobias Fer	SPANAY	FALSE	FALSE	
35	rattus	8	Caluya	SPANAY	FALSE	FALSE	
35	rattus	8	Anini-Y	SPANAY	FALSE	FALSE	
35	rattus	8	Tangalan	NPANAY	FALSE	FALSE	
12	sponsalis	2	Anini-Y	SPANAY	FALSE	FALSE	
12	sponsalis	2	Malay	NPANAY	FALSE	FALSE	
12	sponsalis	2	Buruanga	NPANAY	FALSE	FALSE	
12	sponsalis	2	Anini-Y	SPANAY	FALSE	FALSE	
12	sponsalis	2	Guimaras I	SPANAY	FALSE	FALSE	
12	sponsalis	2	Anini-Y	SPANAY	FALSE	FALSE	
12	sponsalis	2	Santander	NPANAY	FALSE	FALSE	
28	stramineus	5	Anini-Y	SPANAY	FALSE	FALSE	
28	stramineus	5	Anini-Y	SPANAY	FALSE	FALSE	
28	stramineus	5	Anini-Y	SPANAY	FALSE	FALSE	
28	stramineus	5	Estancia	SPANAY	FALSE	FALSE	
28	stramineus	5	na	NPANAY	FALSE	FALSE	
47	striatus	1	Anini-Y	SPANAY	FALSE	FALSE	
47	striatus	1	Tangalan	NPANAY	FALSE	FALSE	
47	striatus	1	Pandan	SPANAY	FALSE	FALSE	
47	striatus	1	Libertad	SPANAY	FALSE	FALSE	
216	crocatus	1	Bantayan	CEBE	FALSE	FALSE	Intertidal
202	longurionis	1	Philippines	NA	FALSE	FALSE	
203	pseudokimioi		Philippines	NA	FALSE	TRUE	
189	polongimarumai		Philippines	NA	FALSE	TRUE	
103	dondani		Philippines	NA	TRUE	FALSE	
206	otohimaea		Philippines	NA	FALSE	FALSE	
207	rolani		Philippines	NA	FALSE	TRUE	
208	sculpturatus		Philippines	NA	TRUE	TRUE	
210	blandifordianus		Philippines	NA	FALSE	TRUE	
211	cordigera		Philippines	SSIS	FALSE	TRUE	mud
209	zapatosensis		Philippines	MASBATE	TRUE	FALSE	
212	shikamai		Philippines	NA	FALSE	TRUE	
213	stupa		Philippines	NA	FALSE	TRUE	150-430m
214	darkini		Balut	SAR	FALSE	TRUE	325 m mud
215	axelrodi		Coron	CALAMIAN	FALSE	TRUE	shallow water
186	montillai	1	Coron	CALAMIAN	TRUE	FALSE	Shallow water