



A Review of the Marine Soft-Sediment Assemblages of New Zealand
New Zealand Aquatic Environment and Biodiversity Report No 96

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EXECUTIVE SUMMARY

Rowden, A.A.; Berkenbusch, K.; Brewin, P.E.; Dalen, J.; Neill, K.F.; Nelson, W.A.; Oliver, M.D.; Probert, P.K.; Schwarz, A-M.; Sui, P.H.; Sutherland, D. (2012) A review of the marine soft-sediment assemblages of New Zealand.

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Soft sediments are unconsolidated substrata such as mud, sand and gravels that form extensive areas of habitat in the coastal and offshore areas of the New Zealand marine environment. Diverse biotic assemblages are associated with these habitats that are integral to the functioning of the soft sediment ecosystem. Some of these assemblages are currently threatened by anthropogenic activities.

The availability of sufficient and suitable data frequently restricts the spatial extent over which patterns of diversity and threats can be assessed, and as a consequence, the suggestions made concerning the need for further research that will allow for a better understanding of biodiversity and management of the environment. To facilitate the best utilisation, and collection, of past and new biodiversity data it is wise to undertake a thorough and documented review of information already available. Such a review will provide a useful synthesis of current knowledge and can include the identification of particular issues of interest or concern.

The objectives of the present project were to review existing published and unpublished sources of information on soft-sediment marine assemblages around New Zealand; to thereby identify hotspots of biodiversity, areas of particular vulnerability, and gaps in knowledge and make recommendations on areas or assemblages that could be the subject of directed research in future years.

A database: The Marine Soft Sediment Biodiversity Bibliographic Database, was constructed to house over 700 references for reports, journal papers, theses, video material, conference proceedings and databases. The vast majority (95%) of the references are post-1960 and the subject of these articles spatially concentrated. These findings probably reflect the distribution of on-going land and coastal development and population growth; mussel farms; science researchers and institutes (via their proximity to study sites). Areas where there were relatively few records probably reflect the distance of these locations from human population centres; their inaccessibility; and their relative lack of soft-sediment habitats.

The written review was conducted separately for seagrass and mangroves, macroalgae, intertidal, and subtidal macroinvertebrate assemblages. These extensive and comprehensive reviews addressed the project's objectives and thereby addressed some of the objectives of New Zealand's Biodiversity Strategy.

The reviews include a series of recommendations that indicate the types of research that is considered necessary in order to address perceived shortfalls in knowledge of biodiversity, its importance to ecosystem function, and the threats and consequences of disturbance by anthropogenic activities.

More studies are recommended than can be presently supported by the biodiversity research funds that the Ministry of Fisheries administers. It is proposed that there now follow a formal and rigorous procedure to prioritise the recommendations, in order that important and scarce national biodiversity funds are directed towards a research agenda that will best deliver on New Zealand's commitment to the Convention on Biological Diversity.

1. INTRODUCTION

1.1 Overview

Soft sediments are unconsolidated substrata such as mud, sand and gravels that constitute one of the largest ecosystems on Earth in areal coverage (Snelgrove 1999), and around New Zealand form extensive areas of habitat in the estuaries, beaches and bays of the coast (Goff et al. 2003) and offshore on the continental shelf, slope and deep-sea (Mitchell et al. 1989). Many organisms live in association with marine soft sediments, including macrophytes such as seagrass, mangroves and algae, and macroinvertebrates such as polychaetes, molluscs, crustaceans, echinoderms and many other taxa (e.g. Snelgrove 1998). Assemblages of organisms in or on soft sediments can be species diverse (Gray 2002) and are integral to the functioning of the soft sediment ecosystem (Snelgrove et al 1997).

Globally, areas of seagrass (often known as ‘meadows’ or ‘beds’) have been described as being one of the most valuable coastal ecosystems in terms of the value-added benefits of the services they provide (Costanza et al. 1997). Both seagrasses and mangroves are important primary producers, stabilize the substrata and serve as nursery habitat for juvenile fish. They provide structure and a direct and indirect source of food for a diverse fauna thereby locally enhancing diversity (see review for seagrass and fish, Jackson et al. 2001). More recently the role of seagrass in the oceanic carbon budget has been described as being proportionally more significant than expected from their relatively modest 1% contribution to global ocean primary production. Duarte & Chiscano (1999) suggested that globally, seagrasses are responsible for 15% of the net CO₂ uptake by oceanic biota.

Macroalgae occur much less frequently in soft sediment environments than on rocky reefs, normally requiring hard substrata for attachment, although a number of taxa are able to grow on small cobbles and shell fragments (Adams 1994). Relatively few species of macroalgae are tolerant of varying salinity although the contribution these species make to estuarine and harbour biomass and productivity may be very significant in certain locations and/or at particular times of the year (see review by Raffaelli et al. 1998). Unattached macroalgae may accumulate intertidally and subtidally over soft sediments (often known as ‘algal mats’) and in some areas they continue to grow and to photosynthesise, and in some situations provide refuge for invertebrates (Raffaelli et al. 1998). Rhodolith or maerl ‘beds’ (made up of free living non-geniculate coralline red algae) are widely distributed in polar, temperate and tropical oceans, and are habitats of high biodiversity, serving as important refuge sites and nursery areas for many fish and invertebrate species, including commercially valuable species (Foster 2001).

Macroinvertebrates, variously defined as animals large enough to be retained on a 300 µm, 500 µm or 1 mm sieve, usually constitute the dominant organism biomass of marine soft sediments (Snelgrove 1998). Of the known non-symbiont phyla all but one are found in the marine environment, with most being represented in marine sediments (Grassle et al. 1991). Consequently species diversity of benthic macroinvertebrates can be very high and the macroinvertebrates of marine sediments play a very important role in ecosystem processes such as nutrient cycling and secondary production (Snelgrove et al. 1997).

Organisms associated with soft sediment habitats are currently threatened by anthropogenic activities. Both seagrass (Duarte 1999) and mangrove (ITTO 2002) ecosystems have been markedly reduced in area on a global scale and remain under threat through coastal development and anthropogenic impacts including impacts on water clarity and quality. Maerl beds are being disturbed by dredging for fertilisers and trawling on a worldwide scale, (e.g., Hall-Spencer & Moore 2000) which has led them to be included in a European Union Directive for environment protection (BIOMAERL team 1998). Macroinvertebrate assemblages of soft sediments are also threatened by human activities e.g. fishing activity via associated habitat disturbance (see reviews by Dayton 1995, Thrush et al. 1998, Collie et al. 2000). Thus, evaluating and understanding the processes that generate and maintain patterns of diversity in marine soft sediments is both important and challenging (Snelgrove 1998).

The availability of sufficient and suitable data frequently restricts the spatial extent over which patterns of diversity, status and threats can be assessed, and as a consequence, suggestions made concerning the need for further research that will allow for a better understanding of biodiversity and management of the environment. Considering the cost-implications of gathering additional information, it is becoming increasingly necessary to exploit sources of data that have hitherto been under-utilised (Whitehouse 1998). In relation to this need, there are now many initiatives to ensure that marine faunal and floral data are well documented, archived and made accessible (e.g. Rees & Finney 2000). Properly constructed and maintained databases, including bibliographic databases, will provide quality data in a format that will aid both descriptive and hypothesis-testing biodiversity research to be conducted (Grassle 2000). To facilitate the collection, and best utilisation, of such data it is wise to undertake a thorough and documented review of information already available (Underwood 2000). Such a review will provide a useful synthesis of current knowledge and can include the identification of particular issues of interest (e.g. apparent ‘hotspots’ of biodiversity) or concern (e.g. areas or taxa threatened, or likely to be threatened, by anthropogenic activities).

1.2 Objectives

There was one overall objective in the project ‘Biodiversity of New Zealand’s soft-sediment communities’ (ZBD2001/06):

- To review the current knowledge of the biodiversity of macroinvertebrates and macrophytes living in and on soft-sediment substrates in New Zealand’s harbours, estuaries, beaches and to 1000 m water depth.

Within the overall objective of the project there were two specific objectives:

- To review existing published and unpublished sources of information on soft-sediment marine assemblages around New Zealand.
- Using the results of the first specific objective, identify gaps in the knowledge, hotspots of biodiversity, areas of particular vulnerability, and make recommendations on areas or assemblages that could be the subject of directed research in future years.

1.3 Definitions and approach

‘Soft-sediment’ is defined as unconsolidated sediments that range from silt to pebble size (0.0039 mm – 64 mm). Included in this definition are ‘biogenic sediments’ that are unconsolidated (e.g., those made from bryozoan/coral fragments or calcareous red algae). For the purposes of this review, sediments that have become consolidated to form essentially hard-structures, sometimes known as ‘biogenic reefs’, were also considered. Marine macrophytes are taxonomically defined thus; Avicennaceae (mangroves), Zosteraceae (seagrasses) and the Rhodophyta, Chlorophyta and Phaeophyceae (macroalgae). Macroinvertebrates considered by the review are those contained by the smallest sieve size most commonly used during sampling (i.e. 0.5 mm is the standard mesh size for estuarine studies). The 1000 m water depth limit stipulated by the overall project objective was not applied, in order that a more complete review of the marine soft-sediment assemblages of the New Zealand region could be undertaken.

Since the early species association schemes to describe macroinvertebrate (Petersen 1914, Thorson 1957) and macrophyte assemblages (Braun-Blanquet 1932), and thereby consider their distribution, statistical techniques have been developed to recognise ‘communities’. In marine ecology, a community is commonly thought of as “... a group of organisms occurring in a particular environment, presumably interacting with each another and with the environment, and separable by means of ecological survey

from other groups.” (Mills 1969). Relatively few investigations of soft-sediment macroinvertebrate and macrophyte assemblages have objectively defined communities (even if the word ‘community’ is used), which would mean that a review of communities alone would be very limited. Thus, the present review was conducted with reference to the more inclusive term ‘assemblage’. An assemblage is simply a group of organisms occurring at a particular place at a particular time, with no assumption that these organisms are interacting with each another nor their environment, and the group has not necessarily been defined by any objective means. Thus, with the wholesale exception of seagrass and mangrove (there being in New Zealand only one species of each occurring in the subject environment), literature that relates to the occurrence of single species is not generally included here in the written review or the bibliographic database (there are also a few isolated exceptions for macroalgae).

The review was conducted, at the request of the Ministry of Fisheries, according to somewhat arbitrary taxonomic and water depth subdivisions. That is, macrophytes and macroinvertebrates were reviewed separately; within which subdivision seagrass and mangrove were considered together and apart from macroalgae. Macroinvertebrates of the intertidal and subtidal were also reviewed separately. The chapters of this report, that review these subdivisions, have been written by their particular authors to stand alone, with the intention that a version of these reviews will eventually be submitted for publication in the primary scientific literature.

In the main, references included in the review are up to the end of 2004. Exceptions exist where some additional references were added during revision and for Chapter 5 which was completed later and therefore contains references up to 2007.

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2. INFORMATION DATABASE

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2.1 Introduction

Electronic databasing of museum collections, species distributions, biodiversity hotspots, and publications has improved the ease and speed with which information can be retrieved, both locally and globally (Ponder 1999). Electronic databases can provide an historical perspective, many can be accessed and updated by numerous specialists and can be validated at any time in the future. Emerging fields, such as Biodiversity Informatics, use databases to study spatial patterns of biological diversity, often using massive global data sets (Soberon & Peterson 2004).

An increasingly important application of electronic databases is as bibliographic repositories for published papers, popular articles, unpublished theses, reports, and visual media. This assembly of references can be used to detect areas where research effort is good or deficient, and to direct future funding priorities (Harvey 1999).

One such research area deemed worthy of specific attention is the study of marine soft sediment communities (Ministry of Fisheries, Draft Medium Term Research Plan). New Zealand has a variety of soft sediment habitats in coastal (estuaries, embayments, mangroves, seagrass beds) and offshore waters (shelf, slope, deep-sea) for which there is a perceived lack of biodiversity and ecosystem-function information. In addition, the New Zealand Biodiversity Strategy (2000), conceived to halt the decline of indigenous biodiversity, requires the documentation of marine species, their taxonomy, distribution and the mapping of habitats and ecosystems. Therefore, an assembly of literature pertaining to research of soft sediment macrophytes and macroinvertebrates will make a contribution to the fulfilment of a number of the strategy's objectives.

The **Marine Soft Sediment Biodiversity Bibliographic Database** is intended to usefully summarise existing published and unpublished papers, reports and theses, as well as other bibliographic and distributional databases, and visual media for the New Zealand region. The database is intended as an online, user-friendly system for quickly assessing where research priorities have historically been focused within New Zealand and for aiding decisions about future research directions.

This chapter describes the construction, population and initial evaluation of the Marine Soft Sediment Biodiversity Bibliographic Database. That is, how the database was created, including a description of the main data structures accompanied by an Entity Relationship Diagram (ERD) and a listing of all the main database tables; how the relevant publications was assembled; and provides a summary of results based on the spatial, temporal and biological nature of the literature.

Chapters 3-6 of this report discuss and provide a detailed summary of the literature for seagrass, mangroves, macroalgae, intertidal and subtidal macroinvertebrates.

2.2 Methods

2.2.1 Database description and design

The design and management of the information database was developed by The National Institute of Water and Atmospheric Research (NIWA) in consultation with the Ministry of Fisheries (MFish) Data Manager, and Biodiversity science staff. The database software Microsoft Access was selected to house the reference information. NIWA is the Data Manager and Custodian for the research data owned by MFish.

Any requests for data should, in the first instance, be directed to the Ministry of Fisheries.

This database contains several tables. The ERD (Figure 2.1) shows the logical structure of the database and its entities (each entity is implemented as a database *table*) and relationships between these tables. Each table represents an object, event, or concept (in the real world) that is selected for representation in the database. Each *attribute* of a table is a defining property or quality of the table.

All of the tables' attributes are shown in the ERD. The attributes in bold represent the table's primary key (a primary key is an attribute or a combination of attributes that contains a unique value to identify that record). This schema is valid regardless of the database system chosen, and it can remain correct even if the Database Management System (DBMS) is changed. Most of the tables in the database have some attributes, called foreign keys. These attributes provide links to supporting tables within the database.

The database is implemented as a relational database. That is, each table is a special case of the mathematical construct known as a *relation*. Elementary relation theory is used to deal with the data within tables and the relationships between them. There are both one-to-many and many-to-many relationships in the database.

One-to-many relationships can be either mandatory or optional. These relationships are enforced in the database by the use of referential constraints (also known as integrity checks). Foreign key constraints do not allow *orphans* to exist in any table; i.e., where a 'child' record exists without a related 'parent' record. This may happen when:

- i) a parent record is deleted;
- ii) the parent record is altered so the relationship is lost;
- ii) a child record is entered without a parent record.

All constraints in the database prevent the latter from occurring.

As shown in the ERD, the main table of the database is the individual reference record table, *reference*. Each reference is uniquely identified by an integer, stored as the attribute *reference_id*.

For all tables, each record is identified by one or two unique integers that make up the table's primary key(s).

In order to determine the spatial distribution of references and allow spatially defined searches, it was necessary to include several tables with spatial categories. One such category is the pre-defined MFish Fisheries Management Areas (Figure 2.2) or FMAs. These are stored in the *FMA* table. Multiple geographic areas can be selected from FMA 1 to 10 and are associated with a reference through the linking table *ref_FMA*. General details of FMA are recorded in the *FMA* table, such as north ordinate, east ordinate, west ordinate, south ordinate, and region name.

The NIWA coastal areas (Figure 2.3) provide a more detailed spatial record of where research has been conducted within New Zealand's coastal region and are stored in the *NIWA_coastal_area* table.

Multiple NIWA coastal areas can be associated with a reference through the linking table *ref_coastal_area*. There are 37 coastal areas associated with the New Zealand region.

The NIWA oceanic areas (Figure 2.3) permit the inclusion of references for deep-sea offshore research. There are nine of these large geographical areas and they are stored in the *NIWA_oceanic_area* table. Multiple NIWA oceanic areas can be associated with a reference through the linking table *ref_oceanic_area*.

The phyla sampled table stores information about which taxa are studied in each reference. References gave varying levels of detail about what plants or animals were sampled so the gross groupings of order, class and family were chosen. Multiple choices could be made from 25 available options. Details for individual phyla sampled are stored in the *phyla_sampled* table. Multiple phyla sampled can be associated with a reference through the linking table *ref_phyla*.

The table *purpose* gives four options describing the overall purpose of the research described in the reference. The options for the purpose of the research were environmental impact assessment, descriptive, experiment and monitoring. Each reference can be associated with only one purpose.

The tables *ref_coastal_area*, *ref_FMA*, *ref_oceanic_area*, *ref_phyla*, *ref_sampling_type*, and *ref_water_depth*, are examples of how to resolve many-to-many relationships in a relational database. In each of these cases, one defined coastal_area/FMA/oceanic_area/phyla/sampling_type/water_depth can be represented in many references, and one reference can have many defined coastal_area/FMA/oceanic_area/phyla/sampling_type/water_depths. To resolve this, these intermediate tables have been created to explicitly store each instance of a reference and defined coastal_area/FMA/oceanic_area/phyla/sampling_type/water_depth relation.

The table *reference_type* contains a list of available types for an associated reference. All references must be associated with only one reference type. Options for reference type include report, journal article, article, thesis, book, video, conference proceedings, information series and electronic database.

The sampling equipment types are stored in the table *sampling_type*. Multiple sampling types can be associated with a reference through the linking table *ref_sampling_type*. This table details the way samples were collected and includes 13 options which are dredge, grab, hand-placed core, mechanical core, trawl, video, camera, hand collection, traps, side-scan sonar, sled, observation, and suction sampler.

The table *target_assemblage* contains two values; macroinvertebrates and macrophytes. This gives a quick and simple indicator of the target group for each reference. All references must be associated with one or the other.

The database asks for the lowest taxonomic level of identification. These are stored in the *taxonomic_level* table. There are six options; phylum, class, order, family, genus, species. Only one selection can be made. This information is useful for determining the level of detail contained within a document.

The final table is *water_depth*. This table stores categories or bands of water depth associated with the reference. Multiple water depths can be associated with a reference through the linking table *ref_water_depth*. Options include intertidal, shallow 1–30 m, shelf 30–200 m, slope 200–700 m, deep-sea 700 m or greater.

2.2.2 Literature search

The literature for entry into the database was initially compiled using NIWA and university library database search engines to locate published documents, theses, and popular articles with quantitative information on soft-sediment macrobiota using a variety of key word phrases. In addition, regional and district councils were contacted to obtain bibliographic references for all client and government commissioned reports containing quantitative soft sediment macrobiota assemblage information. Permission to obtain, review and cite documents/databases identified as 'restricted access' (e.g., client reports, museum databases) was sought where appropriate.

The main purpose of the literature search was to find papers that describe assemblages of the groupings under consideration (see Chapter 1). Publications describing the distribution or abundance of one or a limited number of taxa were generally excluded from the database (e.g. MFish shellfish stock assessments). Most of the distributional information contained in this latter type of literature will be summarised in the National Aquatic Biodiversity Information System (NABIS). The obvious exception to this general omission of single-species references was literature that pertained to seagrass and mangroves (for which there is only one species of each in New Zealand but these provide habitat for assemblages of other species) and also a few references for macroalgae species where the availability of assemblage data was more limited.

All forms of reference were borrowed or copied and viewed with an aim of extracting information according to the pre-determined tables within the database.

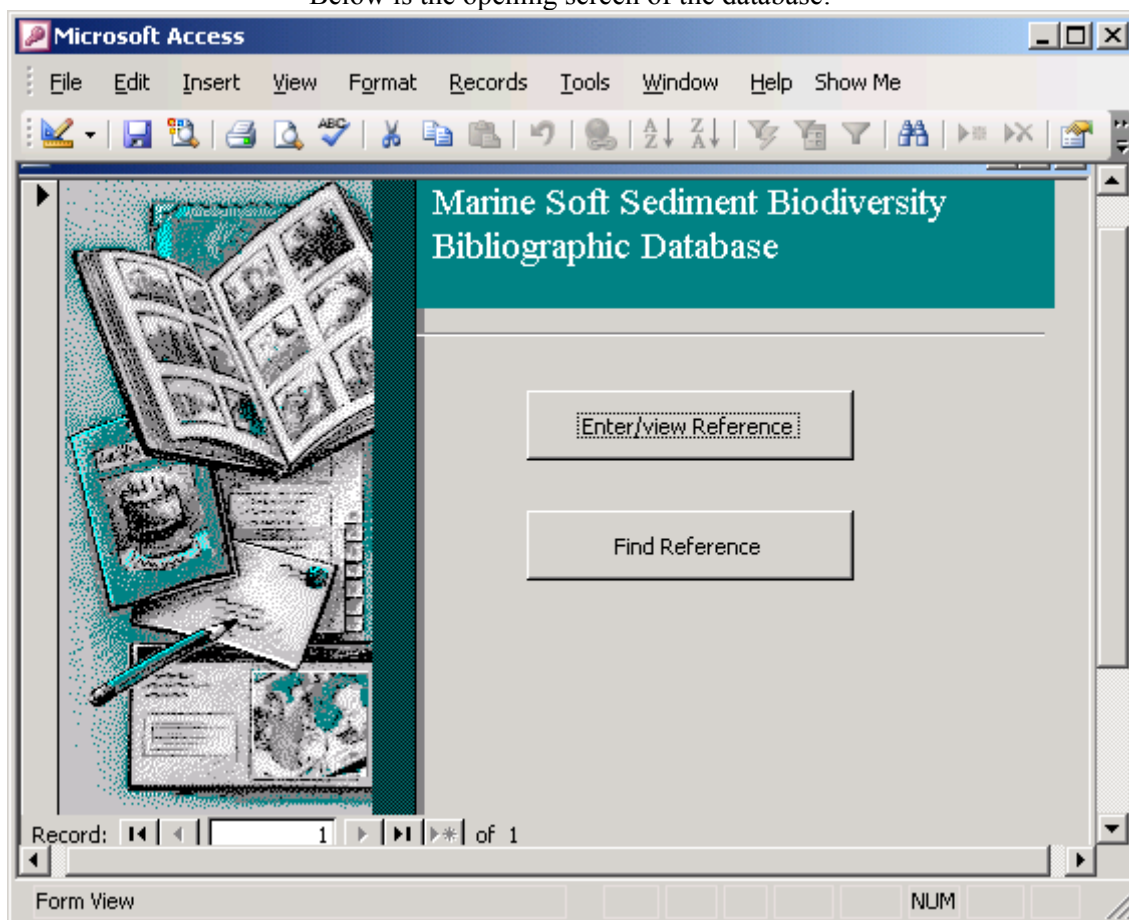
2.2.3 Entering the data and searching the database

The key functions of this Access database are to:

- Enter and maintain soft sediment review records
- Search soft sediment review records

The database forms are designed in a user-friendly tabbed interface. The database is infinitely expandable and can output various reports, export search results and so on.

Below is the opening screen of the database:



Currently, only the following buttons are utilised in the current form of the database. Other buttons can be added to expand the database functionality if required.

- Enter/View Reference
- Find Reference

A key function of the database is the ability to enter new reference records. This next screen facilitates adding new records:

Microsoft Access

File Edit Insert View Format Records Tools Window Help Show Me

Type a question for help

MS Sans Serif 8 B I U

reference

Reference ID: 144

Reference Type: Article

Authors: Poole, A.L.

Year of Publication: 1966

Title: Mangrove or Manawa.

Journal/report/book Name: An encyclopedia of New Zealand.

Volume Number:

Series Number:

Pages: p 397

Editors: A.H. McLintock

Publisher: Government Printer

Target Assemblage: macrophytes

Lowest Taxonomic Level:

Sediment Sample Taken:

Additional Info:

Notes: Briefly describes aspects of the biology of Avicennia resinifera

Reviewer Notes:

Place of Publication: Wellington

University of Thesis:

Type of Thesis:

Purpose: descriptive

Location Name: NZ wide

sampling_unit_m²:

sieve_mesh_size_mm:

NIWA Coastal Area(s):

Oceanic Area(s):

FMA:

Phyla Sampled:

Sampling Equipment Type(s):

Water Depth(s):

Record: 1 of 781

Form View

NUM

From the above form, the user can enter all reference information and the database is immediately updated. A reference ID number is issued automatically for each new entry.

The next form allows the user to search for a particular reference record:

Microsoft Access

File Edit Insert View Format Records Tools Window Help Show Me

Find Matching Records

Search Reference

title contains

Search

Cancel

Record: 1 of 781

Form View

NUM

The summary results of this database, described in the next section, were obtained by querying the database. With knowledge of the database structure, it is possible to design a query that searches the database for matching information. For instance, a query might summarise the number of publication types present in the database or the number of times each coastal area appears. Queries can be designed to search single or multiple tables and extract quite explicit information about the location and content of references. In certain cases, only nominated personnel may have access to the query function.

2.3 Results

The bibliographic database contains 782 references to 449 reports (57%), 200 journal articles (26%), 65 theses (8%), 21 books (3%), and smaller numbers of popular articles (2%), conference proceedings (1.5%), information series (1.3%), videos (0.2%) and electronic databases (1%). At least two of the eight databases are themselves bibliographic and cite in excess of 2000 references.

2.3.1 Database records

One database, ECODATA, was produced by and is held by Davidson Environmental Ltd of Nelson. ECODATA contains 1956 references to studies conducted in the Marlborough region and contains very general descriptions of the phyla found at various locations. This database was prepared for the Marlborough District Council and will be in the public domain. There are likely to be numerous overlaps with this reference database with respect to Marlborough Sounds marine farm reports.

The Cawthron Marine Database contains 96 reports with over 100,000 records of macrobiota and their locations. The majority of these data are for the Marlborough/Tasman region, but some data have been supplied by University of Otago and refer to hard substrate biota of Fiordland.

NABIS, sponsored by the Ministry of Fisheries, uses GIS technology to illustrate the distributional ranges of marine mammal, invertebrate and fish species. This database includes species from hard and soft shore communities and from all water depths.

INMARC, created and maintained by the Department of Conservation is a GIS based database in development, and includes marine literature references for each biogeographic region of New Zealand.

The Auckland Regional Council oversees the remaining four databases and these are the result of collaborative research with NIWA and the University of Auckland. These databases contain several thousand records from impact assessments and descriptive sampling of harbours and estuaries in the Auckland region. These databases contain mostly presence-absence data for macroinvertebrates and some additional sediment and core analyses information.

2.3.2 Literature records

The reviewed literature provides 2111 records of benthic soft-sediment taxa from 35 of New Zealand's coastal regions. These taxa span 25 phyla, with 56% of the records representing 4 main taxonomic groups: Mollusca (18%), Arthropoda (14%), Echinodermata (14%), and Annelida (10%) (Table 2.1). The total number of records of flora and fauna is likely to be much higher because some publications did not contain complete species lists, or the database entries are incomplete. In addition, the commercially sensitive nature of some impact assessment reports prevented them from being included in the review.

The references range in publication date from 1875 to June 2004, when the literature search was completed. Five publications remain in press or submitted and their publication dates may succeed the June 2004 cut-off. The literature is largely limited to post-1960s publications and these comprise 95% of the database entries.

Forty-five percent of the references were published between 1991 and 2002 and these, for the most part, represent studies that relate to the massive expansion in marine farm development, particularly in the late 1990s. Marlborough experienced the greatest growth in this area and more than 150 biological reports on proposed marine farm sites were published between 1999 and 2000 for this region.

The majority of the publications were descriptive (66%) reports of studies that have surveyed a location and described the species present. This reference category includes a large number of reports that are related to proposed Marlborough marine farms. Another 20% of the publications were classified as environmental impact assessments, followed by experiments (12%) and monitoring studies (2%).

2.3.3 Geographic spread of records

Of the 35 coastal areas (Figure 2.3) recorded within the database as having information records, Hauraki, Cook Strait and Bay of Plenty coastal sections of the North Island contain the largest number of records (Table 2.2). In fact, the North Island represents over 71% of all records.

In several cases, if a reference was considered relevant to most of New Zealand's coastal areas it was deemed a New Zealand-wide reference and assigned multiple coastal and oceanic areas. This may mean that for some areas, the database will overestimate the geographical range covered by a particular reference. However, this will only apply in approximately 16 cases or 2% of the total records.

Given the concentration of records in the North Island, it is not surprising, that the NIWA Oceanic Area, "Cook", was represented by 65% of the database entries (Table 2.3) (Figure 2.3). This area encompasses the majority of the North Island and the very northern tip of the South Island. Fifteen percent of the records were included the Bounty oceanic area and 12% in the Three Kings. Resolution, encompassing Fiordland, Southland and Stewart Island, was represented by 6% of the database entries. Less than 1% of the records were from Campbell, Chatham, Bellona, Lord Howe or Auckland oceanic areas (Table 2.3). These latter offshore areas records do not have corresponding coastal areas (i.e. the NIWA oceanic area does not abut a coastal area).

Coastal New Zealand is represented by seven of the ten Fisheries Management Areas (FMAs) (Figure 2.2). FMA 1 includes the Hauraki Gulf, Coromandel and the Bay of Plenty, and has the largest proportion of records (29.5%), followed by FMA 7 (23%), FMA 9 (15%) and FMA 3 (12.5%) (Table 2.4). FMA s 4, 6 and 10 cover deep offshore areas and the Chatham Islands and are cited less frequently than all other areas (Table 2.4).

Of the total number of references cited in the database, 75% have recorded the target assemblage as macroinvertebrates. The remaining 25% targeted macrophytes.

Macroinvertebrate records are most prevalent in the Cook Strait coastal area (18%), followed closely by the Hauraki area (16%) (Table 2.5, Figure 2.4). There is a relative paucity of records along the entire South Island West Coast with no more than 2% of records occurring in any one coastal area (Table 2.5).

Macrophyte records are reported mostly from Hauraki (18%) and the Bay of Plenty (11%) (Table 2.5, Figure 2.4). Also in the North Island, the coastal areas of Poor Knights, Hokianga, Kaipara, and Raglan contain 6%, 8%, 8.5% and 8.5% of macrophyte records respectively. Mangrove studies form the majority of records for these areas and may slightly overestimate the geographical range of the references cited.

The Hauraki coastal area dominates the records for intertidal macroinvertebrates (27%) (Table 2.6, Figure 2.5). Cook Strait has the greatest number of subtidal records (18%) followed by Hauraki (8.5%). There are generally lower numbers of records for both intertidal and subtidal habitats along the South Island West Coast, and the lower east coast of both the North and South Islands (Table 2.6, Figure 2.5).

2.4 Discussion

The Marine Soft Sediment Biodiversity Bibliographic Database includes over 700 references for reports, journal papers, theses, video material, conference proceedings and databases. Within the eight cited databases there are in excess of 2000 further references to the animals and plants of soft sediment communities of the marine region of New Zealand.

The majority (95%) of the references are post-1960. However, 36 earlier publications potentially provide useful information about the distribution of plants and animals prior to anthropogenic changes in what are now highly developed regions.

The concentration of records in the Hauraki, Bay of Plenty and Cook Strait coastal areas probably reflects two issues; the on-going land and coastal development and population growth in Auckland and Bay of Plenty regions (Statistics New Zealand), and the rapid expansion of the Marlborough Sounds mussel farm industry in the late 1990s having elicited numerous surveys of the seabed biota.

In addition, there is a concentration of marine researchers and institutes in the main North Island urban centres, such as Auckland, Hamilton and Wellington, which conduct research in the surrounding coastal areas. The aforementioned, combined with university laboratories and field stations, such as the Auckland University Leigh Marine Laboratory at Goat Island, that produce numerous theses and published articles based on local research, further add to the number of publications reported for these North Island areas.

The extreme paucity of records for the South Island west coast, the Southland coast and Stewart Island probably reflect the distance of these areas from human population centres, combined with inaccessibility. Scientific research has been and is undertaken in these areas, for example Deep Cove in Doubtful Sound, but studies in these environments predominantly addresses hard bottom assemblages. Clearly very little study of soft sediment assemblages has been conducted in these locations.

The lower east coast of the North Island including East Cape, Mahia and Turnagain coastal areas also have relatively low numbers of records. Again, this paucity of records may reflect the relatively small populations in these areas.

The number of records indicating macroinvertebrates as the target assemblage over macrophytes is greatest in the Cook Strait coastal area, followed by Hauraki coastal area. This finding is probably due to the Cook Strait coastal area including the Marlborough Sounds and thus, a concentration of marine

farm studies. Over 150 marine farm reports have been produced for the Marlborough Sounds, representing almost 80% of the Cook Strait coastal area records.

Macrophyte record numbers are greatest for the Hauraki and Bay of Plenty coastal area. The majority of these records are mangrove studies and may, in some instances, overestimate the geographical range of the references because of the clumped nature of mangrove distribution.

The Cook Strait coastal area has the largest number of records for subtidal studies, followed by Hauraki coastal area. Again, it is worth pointing out that the Cook Strait area includes the Marlborough Sounds marine farm studies and this contributes to the large number of subtidal records.

Records for intertidal studies are greatest in the Hauraki coastal area. This situation is probably because there are numerous estuarine and mangrove ecosystems in this area and many of these are subject to anthropogenic impacts which have required monitoring and assessment.

The above summary and initial evaluation of the records contained within the database makes the value of such a tool immediately apparent. The database allows a quick synopsis of research hotspots and areas where research effort is minimal or likely to be required. Furthermore it can highlight the nature of previous research in particular areas and pinpoint what groups or species may have been overlooked.

The following chapters provide more detailed analyses of the research and references included in the database for seagrass, mangroves, macroalgae, intertidal and subtidal macroinvertebrates. The chapters also give more detail on the geographical distribution of the studies and provide recommendations for where further research should be directed.

2.5 Recommendations

- Given the large amount of literature, the task of entering information into the database involved 8 individuals. The fact that many people were involved in entering the information made the eventual grooming of the database for consistency and completeness a time-consuming job. In the future it would be sensible to constrain the entry of data with the use of compulsory fields. This constraint would mean that someone entering data could not advance to the next form until these compulsory fields are filled in. In addition, changes to the attributes within tables of the database should be controlled by one designated person and not updated or changed by individuals as they deemed fit or required. The latter created unnecessary duplication of categories.
- An essential part of maintaining useful databases is keeping them up-to-date. Many databases fail in this respect because they cease to be interactive and become obsolete. Updates of the database need to be periodically contracted and managed and/or the database could be open access and available via the internet for continual updating by authorised people.

2.6 Acknowledgments

The references contained within the bibliographic database were gathered, reviewed and/or entered into the database by Anne-Marie Schwarz, Donna Sutherland (seagrass and mangrove), Wendy Nelson, Kate Neill, Jennifer Dalen (macroalgae), Kay Vopel, Jane Halliday, (intertidal invertebrates), Megan Oliver, Kate Neill, Ashley Rowden, Keith Probert and Paul Brewin (subtidal macroinvertebrates).

2.7 References

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Soberon, J.; Peterson, A.T. (2004). Biodiversity Informatics: managing and applying primary biodiversity data. *Philosophical Transactions of the Royal Society of London* 359, 689–698.

The New Zealand Biodiversity Strategy (2000). Department of Conservation and the Ministry of Fisheries. Wellington, New Zealand, 146 p.

Table 2.1: Number of publications in the Marine Soft Sediment Biodiversity Bibliographic Database containing records for each phylum.

Phyla	Number of records	% of cited records
Mollusca	398	18.72
Arthropoda	295	13.96
Echinodermata	294	13.91
Annelida	210	9.95
Cnidaria	165	7.78
Porifera	116	5.47
Ascidacea	114	5.37
Nemertea	83	3.96
Brachiopoda	79	3.72
Tracheophyta/Avicennaceae	78	3.68
Bryozoa	70	3.35
Chlorophyta/Ulvophyceae	56	2.64
Anthophyta/Zosteraceae	25	1.18
Sipuncula	23	1.13
Chordata	22	1.08
Heterokontophyta/Phaeophyceae	20	0.99
Pycnogonida	12	0.57
Rhodophyta/Rhodophyceae	11	0.52
Phoronida	10	0.47
Platyhelminthes	8	0.42
Echiura	7	0.33
Priapulida	7	0.33
Nematoda	5	0.24
Hemichordata	4	0.19
Aschelminthes	1	0.05
TOTAL	2111	100.00

Table 2.2: Number of records in the Marine Soft Sediment Biodiversity Bibliographic Database for each coastal area by reference type. Here the category “Other” includes the reference types conference proceedings, popular articles, information series, videos and electronic databases.

Coastal Area	Journal					TOTAL
	Paper	Report	Book	Thesis	Other	
Banks	1	1	0	0	0	2
Bay of Plenty	26	38	18	8	24	114
Campbell	3	14	14	0	8	39
Cook Strait	19	166	15	1	8	209
Cuvier	4	2	0	0	0	6
Dusky	2	0	1	0	0	3
East Cape	4	5	14	0	6	29
Egmont	1	1	0	0	0	2
Ellesmere	2	24	14	4	7	51
Foulwind	2	5	14	0	6	27
Foveaux	12	5	1	3	0	21
Hauraki	100	105	18	33	35	291
Hokianga	14	14	18	3	23	72
Hokitika	5	8	14	0	6	33
Jackson	2	5	13	0	6	26
Kaipara	15	12	18	4	23	72
Karamea	2	5	14	0	6	27
Mahia	9	11	14	2	6	42
Mernoo	1	0	0	0	0	1
Milford	4	2	1	0	1	8
Mokau	6	13	14	0	8	41
North Cape	4	11	0	0	0	15
Nuggets	2	4	14	0	6	26
Oamaru	7	6	14	1	7	35
Otago	17	10	14	5	8	54
Palliser	17	21	15	2	6	61
Patea	7	13	14	0	7	41
Pegasus	9	44	16	6	8	83
Poor Knights	13	12	4	3	17	50
Puysegur	1	0	0	0	0	1
Raglan	16	17	17	5	25	80
Snares	1	0	0	0	0	1
Tasman	9	24	14	0	9	56
Three Kings	4	7	0	0	0	11
Turnagain	6	9	14	1	6	36
TOTAL	347	613	351	81	272	1665

Table 2.3: Absolute number and percentage of records in the Marine Soft Sediment Biodiversity Bibliographic Database for each NIWA Oceanic Area.

NIWA Oceanic Area	Number of records cited	Proportion of records cited (%)
Cook	595	64.96
Bounty	139	15.17
Three Kings	105	11.57
Resolution	56	6.11
Campbell	9	0.98
Chatham	6	0.66
Bellona	2	0.22
Lord Howe	2	0.22
Auckland	1	0.11
TOTAL	915	100.00

Table 2.4: Absolute number and proportion of records in the Marine Soft Sediment Biodiversity Bibliographic Database referencing New Zealand's Fisheries Management Areas (FMA).

FMA	Number of records cited	Proportion of records cited (%)
FMA 1	297	29.48
FMA 2	53	5.24
FMA 3	127	12.56
FMA 4	9	0.89
FMA 5	55	5.44
FMA 6	6	0.59
FMA 7	233	23.05
FMA 8	72	7.12
FMA 9	154	15.23
FMA 10	4	0.40
TOTAL	1010	100

Table 2.5: Number and proportion of records in the Marine Soft Sediment Biodiversity Bibliographic Database for macroinvertebrates and macrophytes by coastal area.

Coastal Area	Number of records for macroinvertebrates	% of records for macroinvertebrates	Number of records for macrophytes	% of records for macrophytes
Banks	2	0.19	0	0.00
Bay of Plenty	50	4.63	64	10.96
Campbell	28	2.59	11	1.88
Cook Strait	192	17.76	17	2.91
Cuvier	5	0.46	1	0.17
Dusky	3	0.28	0	0.00
East Cape	19	1.76	10	1.71
Egmont	2	0.19	0	0.00
Ellesmere	42	3.89	9	1.54
Foulwind	17	1.57	10	1.71
Foveaux	16	1.48	5	0.86
Hauraki	183	16.93	107	18.32
Hokianga	25	2.31	47	8.05
Hokitika	22	2.04	11	1.88
Jackson	18	1.67	8	1.37
Kaipara	22	2.04	50	8.56
Karamea	17	1.57	10	1.71
Mahia	30	2.78	12	2.05
Mernoo	1	0.09	0	0.00
Milford	7	0.65	1	0.17
Mokau	31	2.87	10	1.71
North Cape	13	1.20	2	0.34
Nuggets	17	1.57	9	1.54
Oamaru	23	2.13	12	2.05
Otago	36	3.33	18	3.08
Palliser	48	4.44	13	2.23
Patea	31	2.87	10	1.71
Pegasus	59	5.46	24	4.11
Poor Knights	14	1.39	35	5.99
Puysegur	1	0.09	0	0.00
Raglan	30	2.78	50	8.56
Snares	1	0.09	0	0.00
Tasman	37	3.42	19	3.25
Three Kings	11	1.02	0	0.00
Turnagain	27	2.50	9	1.54
TOTAL	1080	100.00	584	100.00

Table 2.6: Number and proportion of records in the Marine Soft Sediment Biodiversity Bibliographic Database for the intertidal and subtidal depths for each coastal area.

Coastal Area	Intertidal	% Intertidal	Subtidal	% Subtidal
Banks	0	0	4	0.32
Bay of Plenty	30	6.26	49	3.97
Campbell	12	2.51	36	2.91
Cook Strait	20	4.18	224	18.14
Cuvier	0	0.00	13	1.05
Dusky	1	0.21	7	0.57
East Cape	11	2.30	29	2.35
Egmont	0	0.00	6	0.49
Ellesmere	16	3.34	44	3.56
Foulwind	11	2.30	23	1.86
Foveaux	2	0.42	22	1.78
Hauraki	130	27.14	106	8.58
Hokianga	16	3.34	33	2.67
Hokitika	11	2.30	28	2.27
Jackson	11	2.30	24	1.94
Kaipara	14	2.92	29	2.35
Karamea	11	2.30	23	1.86
Mahia	14	2.92	37	3.00
Mernoo	0	0.00	3	0.24
Milford	2	0.42	13	1.05
Mokau	14	2.92	43	3.48
North Cape	1	0.21	24	1.94
Nuggets	11	2.30	23	1.86
Oamaru	14	2.92	27	2.19
Otago	15	3.13	39	3.16
Palliser	20	4.18	53	4.29
Patea	14	2.92	45	3.64
Pegasus	21	4.38	61	4.94
Poor Knights	7	1.46	20	1.70
Puysegur	0	0.00	3	0.24
Raglan	18	3.76	36	2.91
Snares	0	0.00	3	0.24
Tasman	18	3.76	43	3.48
Three Kings	0	0.00	23	1.86
Turnagain	14	2.92	38	3.08
TOTAL	479	100	1234	100

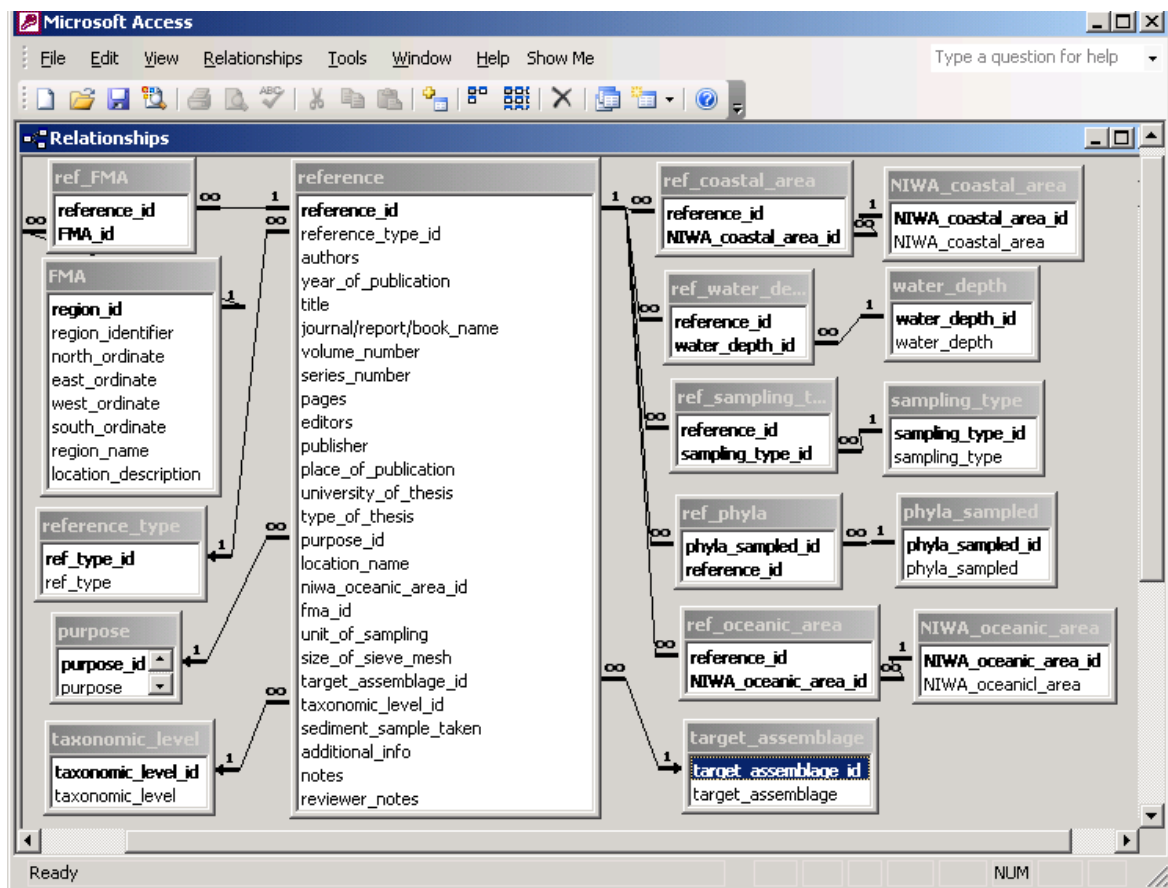


Figure 2.1: Entity Relationship Diagram (ERD) of the Marine Soft Sediment Biodiversity Bibliographic Database.

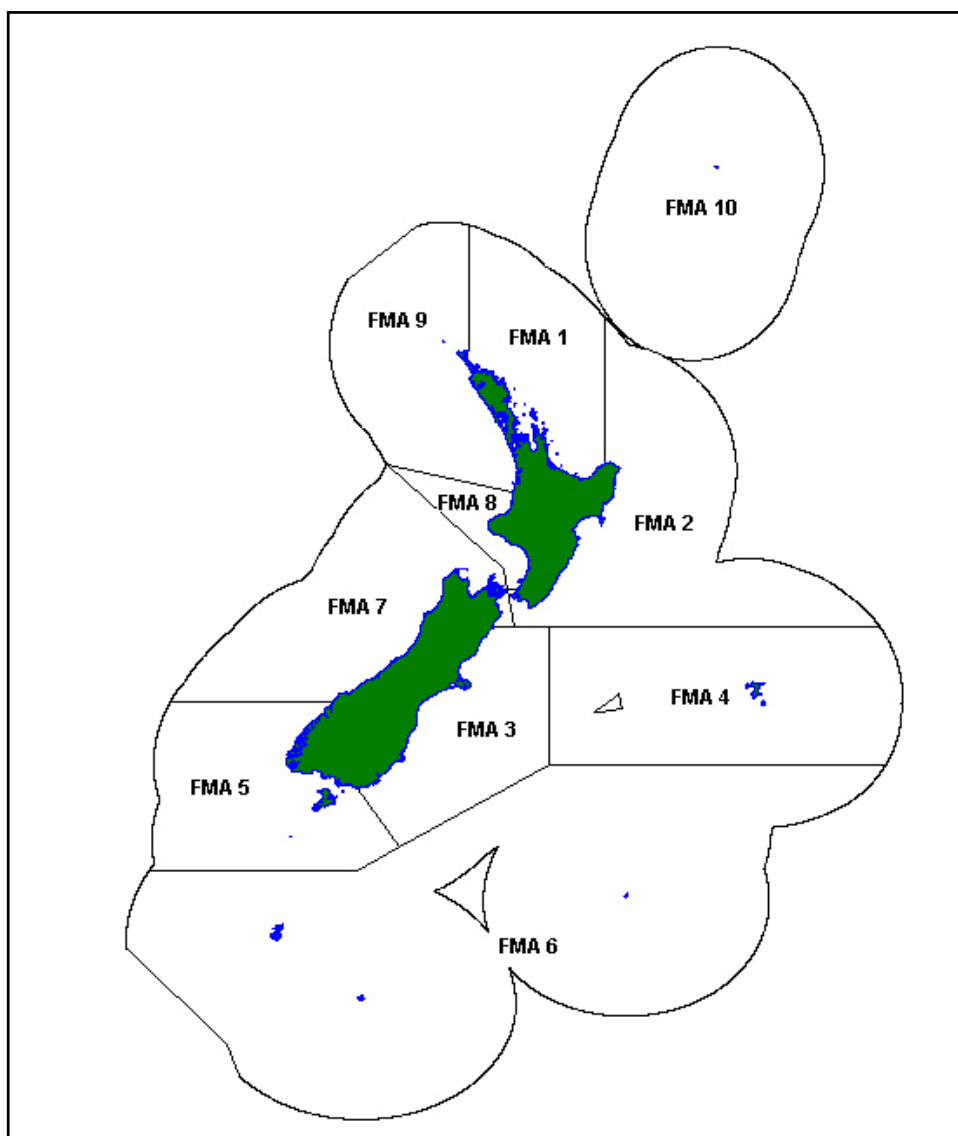


Figure 2.2: Map showing the Fishery Management Areas (FMAs) of the New Zealand region.

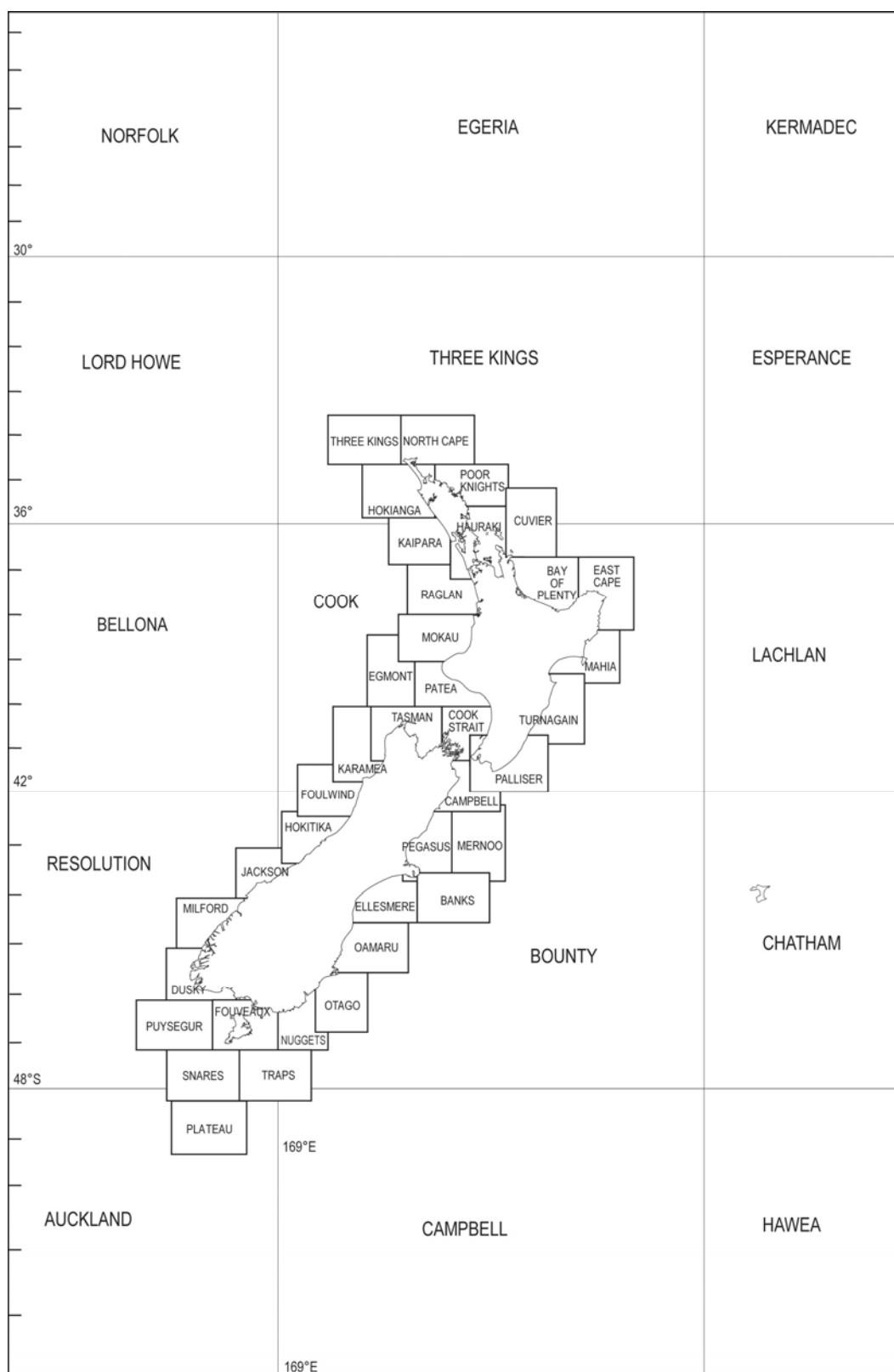


Figure 2.3: Map showing NIWA Coastal and Oceanic Areas of the New Zealand region.

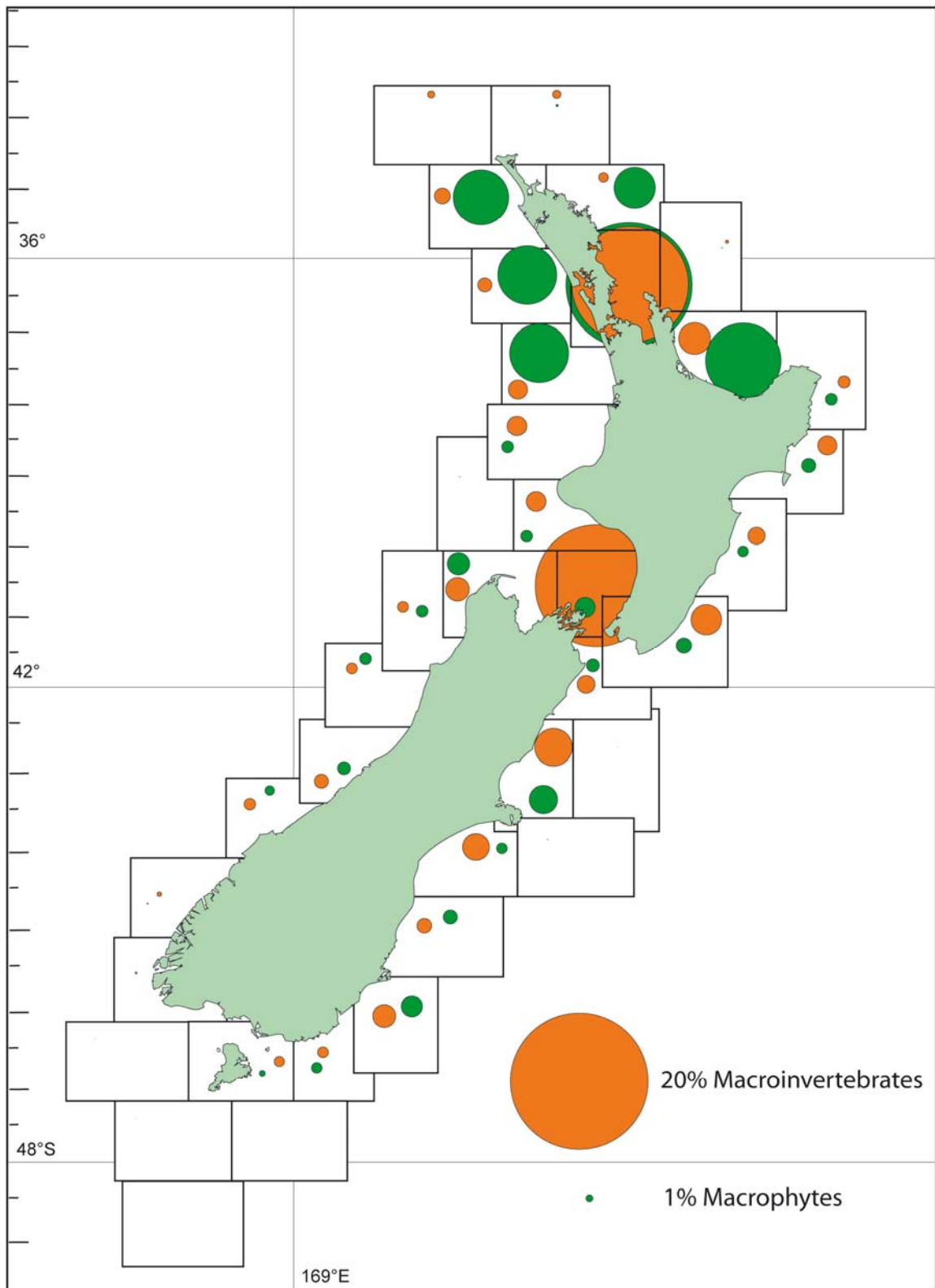


Figure 2.4: Distribution of macroinvertebrate and macrophyte records (as a percentage of the total for each) in the Marine Soft Sediment Biodiversity Bibliographic Database by coastal area.

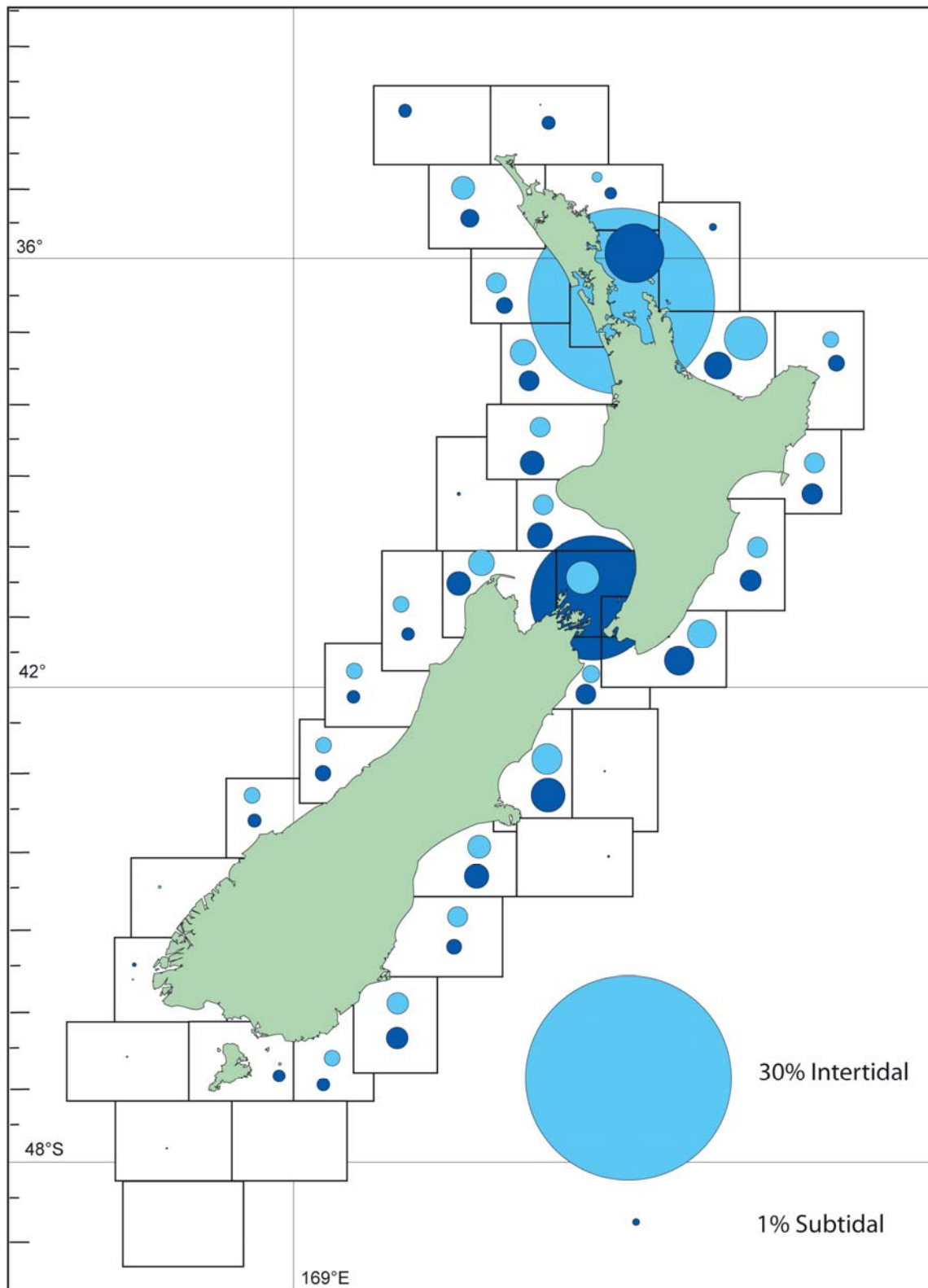


Figure 2.5: Distribution of intertidal and subtidal records (as a percentage of the total for each) in the Marine Soft Sediment Biodiversity Bibliographic Database by coastal area.

3. SEAGRASSES AND MANGROVES

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3.1 Introduction

Seagrasses (*rimurehia*) and mangroves (*manawa*) are conspicuous vegetation types in New Zealand's estuaries as well as occurring occasionally on other parts of the coastline. In the former, they constitute the boundary between terrestrial and saltmarsh fringing vegetation and the estuary proper. Features that distinguish these communities from lower latitude counterparts are that the southern latitudinal limit for mangroves occurs in the mid-north island of New Zealand and that in New Zealand, both seagrasses and mangroves are represented by only one species (see discussion below for seagrass).

Globally, seagrass meadows have been described as being one of the most valuable coastal ecosystems in terms of the value-added benefits of the services they provide (Costanza et al. 1997). Both seagrasses and mangroves are important primary producers, stabilise the substrata and serve as nursery habitat for juvenile fish. They provide structure and act as direct and indirect sources of food for a diverse fauna thereby locally enhancing diversity (Jackson et al. 2001, Kathiresan & Bingham 2001). Seagrasses play a significant role in the global oceanic carbon budget and are estimated to contribute 12% of net ecosystem production in the ocean (Duarte & Chiscano 1999). Both seagrass and mangrove ecosystems have been markedly reduced in area on a global scale and remain under threat through coastal development and anthropogenic impacts on water clarity and quality (Duarte 1999, ITTO 2002).

This review summarises the state of knowledge with respect to taxonomy, growth requirements, distribution, and habitat characteristics of seagrasses and mangroves in New Zealand. As far as is possible from the information available, we identify hotspots of biodiversity and areas of particular vulnerability. However, to a great extent, the incomplete knowledge of the mangrove and seagrass ecosystems in many parts of the country means that this is likely to be a biased assessment. Hence we emphasise the importance of highlighting gaps in knowledge and identifying possible future research directions.

3.1.1 Scope

Information on New Zealand seagrass and mangrove ecosystems is contained in a wide range of publication types. In total 177 mangrove references and 110 seagrass references have been included in the associated database, with fewer than 20 of these being common to both topics. Thirty percent of the references in the database refer to studies or observations from the Hauraki area, 10 % from Bay of Plenty, 6 % from areas north of Auckland, 6% from Pegasus coastal area and 4% from the remainder of the South Island. A relatively large proportion (55%) are non site specific references. This statistic is reflected in the number of non-specific popular articles, or “grey literature”, as opposed to targeted scientific studies.

Only a quarter of the New Zealand mangrove references sourced during this review constitute scientific publications and books although this proportion is somewhat higher, around 40%, for seagrasses. For mangroves the remaining 75% of publications are made up of client or government department commissioned reports and popular articles. Many of the reports of mangrove and seagrass ecosystems have been recorded as part of broader surveys, for example the coastal resource inventories, first order surveys published by DOC for Northland, Auckland, Waikato and Bay of Plenty Conservancies in 1990. Such surveys provide a useful assessment of the potential significance of mangrove forests (an alternative term commonly used throughout the world to describe mangrove ecosystems is ‘mangal’ (Kathiresan & Bingham 2001)), when viewed as an ecosystem component with other vegetation types

and associated fauna. Around a quarter of the seagrass literature is contained in reports commissioned or prepared by government departments, i.e. regional councils and universities. These largely started to appear in the 1970s and have continued regularly since. Mangroves have received considerably greater attention in the popular press compared to seagrasses, reflecting fluctuations over time in human perceptions of the value of mangrove ecosystems (i.e. as mangroves have been variously perceived as a 'nuisance' and 'benefit'). The majority of popular style articles have been written since the 1980s.

Historically, seagrass and mangrove ecosystems were prized by Maori for their role as habitat for shellfish and fish (e.g. Crisp et al.1990) and seagrass leaves were also occasionally used to adorn items of clothing (Hamilton 1901). Mangrove forests and mudflats continue to provide habitat for customary fisheries of pupu (cats eye), titiko (mud snail), and tuna (shortfinned eel) in the Hauraki Region (MfE 1999).

The earliest publications listed in our database date back to the late nineteenth century when seagrasses were described as very plentiful and occurring from the top of the North Island to Stewart Island (Colenso 1869). However, Captain Cook had earlier referred to mangroves in his journals of 1769, describing their presence at Whitianga which he called "the River of Mangroves" because of their abundance (Crisp et al.1990).

European settlers described what they considered to be the "unlimited commercial potential" for exporting seagrass, found on the coast of the North Island, for purposes such as mattress stuffing in England (Smith 1878). By the early part of last century, reclamation of mangrove swamps to increase areas of productive land in North Auckland was being encouraged (e.g. Rowan 1917).

The earliest university studies of mangroves and seagrasses were conducted in the Auckland (Baylis 1935) and Christchurch (Thompson 1930) areas respectively. After a hiatus during the 1940s the remaining studies have been completed during each decade since the 1950s. Around thirty unpublished theses (dominated by MSc theses) have been focused on aspects of New Zealand mangroves and seagrasses. These range from biology and physiology of the plants themselves to the utilisation of mangrove forests by a range of fauna.

New Zealand mangroves were described in general terms in a book dealing with mangrove forests throughout the world (Chapman 1977) and since then there is only one dedicated book that has been published on mangroves in New Zealand (Crisp et al.1990). Although included in a largely taxonomic research on seagrasses of the world (den Hartog 1970), New Zealand seagrasses were not included in global assessment of seagrass ecosystems in any comprehensive manner until a recent review by Inglis (2003).

Throughout this review we have aimed to reference pertinent and targeted publications as much as possible to illustrate salient points rather than those that make only incidental reference to mangroves or seagrasses as parts of other studies. In addition, where thesis research has subsequently been published, we have preferentially referred to the published paper.

3.2 Review of scientific literature

3.2.1 Seagrasses

The main topics of research for New Zealand seagrasses, in approximate decreasing order of frequency, are seagrass demography, ecology and physiology (Ramage & Schiel 1997, 1999, Turner et al. 1999, Turner & Schwarz 2006a) fauna associated with seagrasses (Henriques 1980, Woods & Schiel 1997, van Houte-Howes et al. in press) and seagrass distribution (Findlay & Kirk 1988, Ismail & Israel 1997, Stanton et al. 1977). The impact of anthropogenic activities on seagrass beds has been addressed to a limited degree through some university studies e.g. Miller (1998).

Seagrass research has until recently been largely concentrated around Auckland, Christchurch and Otago in association with proximity to universities.

3.2.2 Mangroves

The key topics related to mangroves that have been the subject of scientific research and are documented in peer reviewed scientific papers are, in approximate decreasing order of frequency, mangrove demography, ecology, physiology and production (e.g. Woodroffe 1982 a,b, May 1999, Burns & Ogden 1985, Osunkoya & Creese 1997, Burns et al. in press), historical and contemporary assessments of environmental links to mangrove growth (e.g. latitude (de Lange & de Lange 1984), sedimentation (Young & Harvey 1996), and relationships between mangrove forest characteristics and invertebrates (Morrissey et al. 2003, Ellis et al. 2004). Utilisation by other fauna is a topic that has been favoured by MSc theses (e.g. birds (Cox 1977), zooplankton and fish (Davenport 1979, May 1999, Saunders 1999). Historical distribution (Pocknall et al. 1989) and mapping techniques have received lesser attention (Gao 1998, 1999 a, b).

3.3 Current state of seagrass knowledge

3.3.1 Taxonomy

The seagrass flora of New Zealand is represented by only one genus, *Zostera*, in the family *Zosteraceae*. Species of the genus *Ruppia* and *Potamogeton* that are able to grow in brackish as well as fresh water are found in New Zealand including the Chatham Islands (Champion & Clayton 2004) but are not considered here. This is in accordance with den Hartog (1970) who noted that despite some of these taxa being extremely tolerant of relatively high salinity, they nevertheless do not penetrate permanently into the purely marine environment.

The earliest reports of *Zostera* in New Zealand have variously referred to *Z. nana*, *Z. marina*, *Z. meulleri* and *Z. tasmanica* and *Zostera novazelandica* (Kirk 1878, Smith 1878, Oliver 1923, Cheeseman 1925, Setchell 1933, Armiger 1964). Considerable morphological variability occurs within natural seagrass populations in New Zealand and until recently it has been generally accepted that there were two species, *Z. capricorni* Aschers, which also occurs in eastern Australia and *Z. novazelandica* Setchell, described as endemic to New Zealand (Setchell 1933). Various reports have determined that *Zostera capricorni* could be considered confined to the North Island, while *Z. novazelandica* could be considered an endemic species reportedly found throughout coastal New Zealand (den Hartog 1970, Moore & Edgar 1976 Johnson & Brooke 1989, Webb et al. 1990).

This division remained until Les et al. (2002) identified the lack of molecular divergence among Australian and New Zealand *Zostera*. Through phylogenetic analyses of morphological characters and DNA sequences of samples from a limited number of locations throughout New Zealand Les et al. (2002) recommend the taxonomic merger of Australian and New Zealand *Zostera* within a single species, *Zostera capricorni*. More comprehensive surveys and phylogenetic analyses will be required to categorically confirm the existence of a single species nation-wide. Furthermore at the time of writing, no samples of permanently submerged beds on offshore islands have been investigated using molecular techniques although initial investigations are underway (author's unpublished information). Regardless of these uncertainties, certainly the temperate seagrass flora of New Zealand is impoverished in comparison to more tropical locations.

3.3.2 Distribution and extent

Two comprehensive reviews have recently described the current state of knowledge of New Zealand seagrass ecosystems. The first (Inglis 2003) provides a particularly useful summary of the state of knowledge of distribution at the time of writing. The very process of publishing this information has enabled other sites that were not included at that time to be highlighted (Figure 3.1). The second review was conducted by Turner & Schwarz (2006b) and was focused toward management of seagrass ecosystems in New Zealand. These reviews provide a strong basis for assessing the current knowledge of biodiversity, and where they have adequately reviewed the literature for a certain topic we refer to those reviews, rather than repeat their full text.

Seagrass occurs throughout New Zealand in different types of estuaries, as well as on some open coast rocky intertidal platforms (e.g. Bradstock 1989, Ramage & Schiel 1997, 1999). They occur throughout the mainland coast of New Zealand (data compiled in Inglis 2003) from Parengarenga Harbour in the north to Stewart Island in the south (Cromarty & Scott 1996). Scientific studies published in journal articles or from university theses are available from as far south as Otago Harbour, where the effect of seagrass beds on water movement (Heiss et al. 2000) and techniques for seagrass mapping have been addressed (Ismail & Israel 1997), to the eastern Bay of Islands in the north where a study of macrofaunal communities associated with seagrasses was undertaken (Hayward 1981).

In New Zealand, seagrass is generally considered to be intertidal on soft sediments and it is found predominantly between mid and – low tidal levels (Webb et al. 1990) forming extensive beds (meadows), or mosaics of discrete patches surrounded by unvegetated sediments in estuarine environments (Turner 1995). However the beds may extend as subtidal fringes into the shallow areas of sheltered estuaries (Schwarz 2004) and permanently submerged beds have been recorded in the Bay of Islands, and on offshore islands such as Slipper Island, the Cavallis and Great Mercury (Hayward et al. 1981, Grace & Whitten 1974, Grace & Hayward 1980, Grace & Grace 1976) and at least some of these are still present in 2004 (NIWA unpublished data).

Internationally, there is considerable research and historical evidence to show that the equilibrium between growth and loss processes in seagrass beds can be upset, leading to a regression of meadows and potentially total loss over a number of years (Hemminga & Duarte 2002). Seagrass decline is now considered to be a common phenomenon throughout the world (Short & Wyllie-Echeverria 1996). On the basis of historical reports (e.g. Cokayne 1967, Ogilvie 1978, Oliver 1923), Inglis (2003) concluded that New Zealand was no exception and that there is evidence to suggest extensive declines in the area of seagrasses since the late nineteenth and early twentieth centuries. Documented examples include the Avon-Heathcote estuary (Deely 1992), Tauranga Harbour (Park 1999 a, b, 2001), Whangarei Harbour (Morrison 2003) with the greatest losses considered to have occurred since the 1920s and 1930s (MfE 1997).

3.3.3 Growth requirements

Spatial and temporal dynamics of intertidal *Zostera* have been documented in Manukau Harbour, Whangapoua Harbour (Turner et al. 1996) and at Kaikoura (Ramage & Schiel 1999). There is evidence to suggest a seasonal pattern with a winter minimum in above-ground biomass recorded at sites from both the Coromandel Peninsula (Turner & Schwarz 2006a) and Otago Harbour (Ismail 2001). In Otago Harbour changes in cover and spatial extent have been shown to occur over periods as short as one year (Ismail 2001). The need to understand changes over relevant time-scales was highlighted by Turner et al. (1996) who also stressed the need to study seagrasses at several different spatial scales concurrently (e.g. rhizome demography, patch expansion and contraction, landscape patterns). A good local understanding of spatial and temporal dynamics is essential to ensure that snapshots of areal coverage from techniques such as remote sensing are meaningful (Fyfe et al. 1999).

There is little known about the reproductive ecology of seagrasses in New Zealand, in particular the role of sexual reproduction in establishment and maintenance of seagrass beds. *Zostera* is perennial in

New Zealand, and from the limited number of studies that have been reported, appears to reproduce primarily from vegetative reproduction (Inglis 2003). Site specific information on the timing of flowering is available only for a limited number of South Island locations. Den Hartog (1970) reported that *Z. novaezelandica* (with a nation-wide distribution) flowered between the months of November and March with fruits being found only in March. Ismail (2001) found the same pattern for seagrasses in Otago Harbour, however a longer flowering season that lasts from October to June was reported from a comprehensive study of *Zostera* on intertidal platforms at Kaikoura (Ramage & Schiel 1997, 1999).

Recent research has begun to highlight some of the environmental constraints imposed on seagrass growth in New Zealand estuaries e.g. water clarity (Schwarz 2004) suitability of sediments (Schwarz et al. 2004) and nutrients (Ismail 2001, Turner & Schwarz 2006a). Nitrogen fixation has been shown to occur in seagrass sediments (Hicks & Silvester 1990) although the degree of subsequent assimilation by seagrasses has not been quantified. In contrast to mudflats, which act mainly as nutrient regeneration areas, *Zostera* beds have been shown to be characterised by intensive internal nutrient cycling (Kasper 1983).

3.3.4 Role in the ecosystem

A study from Ohiwa Harbour noted that seagrasses baffle water motion and stabilise and trap sediment (Daniel 1984). Accordingly Heiss et al. (2000) showed that in Otago Harbour current velocities were significantly reduced inside a seagrass patch resulting in suspended mud settling in this low-energy environment and being protected from re-suspension by seagrass cover. This is in common with seagrass beds of similar morphology elsewhere in the world (Fomesca 1996).

A widely cited function of seagrass beds throughout the world is to provide habitat and sources of food for fish, crabs and shrimps, including species that are commercially important in other ecosystems. Until recently there have been very few scientific studies of this role for New Zealand seagrasses. However a growing number of findings are suggesting that these roles may be too important to ignore.

Seagrasses in New Zealand have been shown to have an effect on macrofauna communities in that they differ from surrounding unvegetated sediments (van Houte-Howes et al. in press) and Henriques (1980) showed that seagrass habitats in the Manukau Harbour had a higher species diversity and abundance of macrofauna than comparable non-vegetated habitat. Studies of the animal communities associated with seagrasses include meiofauna (e.g. Hicks 1986, 1989; Bell & Hicks, 1991), macrofauna (e.g. Henriques 1980, Alderson 1997, Woods & Schiel 1997, Turner et al. 1999) and include reports of the small endemic limpet *Notoacmea helmsi* (*scapha*) found on the leaves of *Zostera* (summarised by Inglis 2003). Berkenbusch and Rowden (2003) in a study of ghost shrimps as 'ecosystem engineers' showed that seasonal variation in the number of species and individuals of macrofauna in Otago Harbour were associated with changes in seagrass biomass. This was consistent with an expectation that seagrass plants provide living space for other fauna via their own physical structure. Berkenbusch and Rowden (2003) suggested that likely interactions between ghost shrimp and seagrass may be important in determining other components of habitat structure, such as macrofaunal species composition.

It is only recently that detailed scientific studies have been undertaken on the fish communities associated with seagrass beds. Two studies by Morrison & Francis (2001 a,b) have now shown that seagrass beds, particularly those that remain submerged at low tide, provide important nursery functions for a range of juvenile fish species, snapper (*Pagrus auratus*) being especially notable. This is a significant finding in light of anecdotal evidence that a dramatic decline in seagrass area between 1921 and 1931 in Hobson Bay and Stanley Bay in Auckland was associated with marked reductions in catches of snapper and other carnivorous fishes (Powell 1937). In addition, apart from the descriptions of their existence, there is a complete absence of research on the composition, structure and function of subtidal beds on offshore islands although this is currently being addressed by DOC (Waikato Conservancy) and NIWA (authors unpublished data).

Intertidal seagrasses have also been reported as providing an important food source for the introduced Black Swan (*Cygnus atratus*) (Sagar et al. 1995).

3.3.5 Threats and vulnerability

There have been no recent assessments of the overall condition of New Zealand's seagrass beds and therefore none of the threats to seagrass habitats. However, changes in sediment regimes that affect turbidity, sedimentation rates or sediment texture, have been identified as a serious threat to New Zealand's estuarine systems in general (Norkko et al. 2002). Hence it is reasonable to identify this as a potential ongoing threat to seagrass beds, although the historical effects may already be evident (Inglis 2003). Effects on seagrasses may be direct through smothering or indirect through a reduction in water clarity. Suggested techniques and approaches to monitoring change as a result of anthropogenic effects are summarised in Turner and Schwarz (2006b).

The availability of reliable photography and good historical field data limits seagrass change analysis to the last 40–50 years. An example of how the situation can fluctuate is illustrated by Whangamata Harbour (Cawthron Institute 2000) where there is an indication that seagrass beds increased in extent between 1944 and 1965 and subsequently declined again between 1965 and 1998. The reasons behind this change have not been elucidated.

3.4 Current state of mangrove knowledge

3.4.1 Taxonomy

Variously called *Avicennia marina* or *Avicennia resinifera* or *Avicennia marina* var. *resinifera* (Chapman & Ronaldson 1958, Lynch 1973) there is one currently recognised mangrove taxa in New Zealand *A. marina* subsp. *australasica* (Walp.) J. Everett. Although it is not known exactly when the mangrove arrived in New Zealand, fossil wood evidence suggests that mangroves were present in the Miocene 10 to 15 m.y.a. (Sutherland 1985, Fleming 1979). Crisp et al. (1990) suggested that the eastern and western limits of mangrove distribution may host genetically distinct populations owing to the geographic isolation from each other but we are not aware of research investigating this distinction.

3.4.2 Distribution and extent

Useful summaries of the understanding at the time, of the extent, function and role of New Zealand mangroves are provided by Hackwell (1989) and by Crisp et al. (1990). *Avicennia marina* is the most widespread mangrove species in the world, extending from East Africa to Fiji and to the North Island of New Zealand. The southern extent of its distribution is in New Zealand and southeastern Australia (Victoria, at 38° 27' S). The New Zealand population is therefore of interest from the perspective of the genetic variability within this morphologically plastic species.

In New Zealand, mangroves occur naturally, as far south as Ohiwa Harbour (38° 00' S) on the east coast of the North Island and at Raglan Harbour (37° 48' S) on the west coast (Figure 3.2). Naturally occurring communities have historically been reported from further south in Kawhia Harbour and a planted specimen forms the southern-most, west coast record at the Awakino River 38° 39' S near Kawhia (Daniel 1984). Mangroves planted in 1980 at Tolaga Bay (38° 22' S) near Gisborne, have been able to become established (Crisp et al. 1990) and early to mid Holocene pollen samples suggest the occurrence of historical mangrove forests in the Poverty Bay, East Cape Region for about 4000 years from c. 9800 – 6000 years BP (Mildenhall & Brown 1987).

In the 1970s the Department of Lands and Survey conducted Coastal Reserves Surveys which included an appraisal of coastal areas (north of Auckland), some of which contained mangrove swamps, that

might be considered suitable for reserve purposes (Chapman 1976, 1978 a,b,c). In 1984 the Nature Conservation Council attempted to develop a national strategy for the management of mangrove forests and undertook the first comprehensive inventory of mangrove distribution (Hackwell 1989) estimating the area at 19 300 ha.

The most recent estimate of the extent of area occupied by mangroves in New Zealand is from the Land Cover database which used satellite imagery from 1996/97 (Terralink, NZ Ministry of Agriculture and Forestry). The total area was estimated at 22,500 hectares for 1996/97 but there is acknowledgment that these estimates are likely to be somewhat inaccurate and efforts are underway to update these estimates.

Mangroves form the boundary between the land and estuarine soft sediments in many North Island estuaries. As such, they have undergone decreases and increases in the area they occupy, for a range of reasons. Mangrove forests have been subject to land reclamation (Nature Conservation Council 1984) since the late 19th century, resulting in reductions in area in some locations. A Nature Conservation Council leaflet (1975) states that of the original 20.5 square miles of mangrove and salt marsh in Hokianga prior to the 1920s, only 10.64 square miles remained due to 48% of the original mangrove area being reclaimed. Daniel (1984) notes that while 1945 aerial photographs show three areas of mangroves in Opotiki Harbour they had disappeared by 1966. Localised die-off events have been recorded in Whangarei Harbour attributed variously to one-off pollution events, unknown causes and to natural succession of mangrove to salt marsh as sediments accrete resulting higher ground (Clunie 1993).

In contrast, expansion in area over recent decades illustrates the plant's response to catchment changes and other anthropogenic impacts at this interface (Burns et al. in press). In some locations mangrove areas have been mapped in detail e.g. the Auckland region (Morrissey 1994) and Tauranga (S. Park Environment Bay of Plenty, unpublished data). Spread of mangroves has been documented in Ohiwa Harbour (Daniel 1984, Burns & Ogden 1985), the Firth of Thames (Young & Harvey 1996, Brownell & Brejaart, 2001), Whangape Harbour (Nichol et al. 2000), Whangamata (Environment Waikato 1998), Rangaunu (Shaw & Maingay 1990) and Whangarei (Morrison 2003). In the period since New Zealand has been colonised by humans and particularly since European colonisation, the habitat for mangroves has vastly increased due to estuarine sedimentation (Nichol et al. 2000), linked to increased sediment runoff from catchment activities. Under a deluge of silt, sandflat habitats become smothered and mangroves spread rapidly, expanding from the headwaters and sides of the estuary out into areas that were previously floored with clean sand (Green et al. 2003). Craggs et al. (2001) found that in the Whitford embayment in Auckland, where the area of mangroves has increased by over 50% over the last 50 years, distribution of mangroves appeared to be associated with areas of high sedimentation rates, and a high mud content of the sediments. This meant that the greatest coverage of mangroves was seen in the upper estuary. Further anthropogenic effects related to the alteration of the physical environment for mangrove growth include the construction of causeways. Causeways have the potential to alter estuarine hydrodynamics and may act alone or in concert with increased catchment urbanisation to increase the deposition of fine sediments and so increase available habitat for mangroves (Hume & Bell 1986).

3.4.3 Growth requirements

In northern New Zealand, mangroves grow as tall trees up to 12 m in height with a 70 cm basal trunk diameter (Burns 1982) but they become smaller and more shrub-like (less than 1 m) with increasing latitude. De Lange and de Lange (1994) disputed the traditional view that climatic stress, particularly air temperature, controlled the southern limit of mangroves in New Zealand and suggested that coastal processes affecting propagule dispersal were more important controls. Thus, if it were able to disperse to suitable sites *Avicennia marina* would be capable of colonising further areas wherever environmental conditions were within its physiological tolerance. However, Burns et al. (in press) suggest that its

realised niche in New Zealand is already likely to be close to, if not equivalent to, its potential niche. This is supported by recent research showing that frost tolerance levels were less than reported values for other subtropical plants, suggesting that New Zealand mangroves exhibit frost tolerance levels sufficient only to protect from the normal frost temperatures encountered (Beard et al. 2003).

Superimposed on the latitudinal gradient defining mangrove distribution and forest structure in New Zealand, are variations within estuaries. Differences in tree form are often spatially distributed, with tall trees of several metres height occurring at the seaward edge of a forest or around tidal channels and with stunted trees less than 1 m tall at the landward side of the forest. This pattern lead Burns et al. (in press) to emphasise that mangrove forests within an estuary should be viewed as a diverse patch mosaic of stands differing in age and environmental stress, rather than a single homogenous unit.

On a global scale, the development and productivity of mangrove forests depends on temperature, rainfall and sediment conditions, although their highly developed morphological, biological, ecological and physiological adaptations means that they are able to exist under a wide range of extreme environmental conditions (Kathiresan & Bingham 2001). Where conditions are suitable then, primary production, tree stature and growth rates are correlated with many variables including latitude, salinity, nutrient availability, flooding frequency, chemical status of the soil and tidal force. There is not yet sufficient information available on New Zealand mangroves to state definitively whether mangroves at a given site are nutrient limited although there is emerging evidence that additional nutrients may enhance mangrove growth (Burns et al. in press, author's unpublished data). Unravelling growth limiting factors requires multi-factorial experiments to deal with complications involved in separating supply and availability of nutrients as well as the effect of the ways that nutrients are utilised within the plant (e.g. Feller et al. 2003a).

3.4.4 Role in the ecosystem

In New Zealand, mangroves are often highlighted as important and characteristic features of the vegetation, partly because of their integral connection with landward (e.g. saltmarsh, freshwater wetlands) and seaward vegetation communities (Cromarty & Scott 1996). Noted examples are the mangroves from Whangateau Harbour to Mangatawhiri Spit (Mitchell et al. 1992) and those within Parengarenga Harbour (Shaw et al. 1990).

Knox (1983) outlined a series of models for the role of mangroves in the estuarine ecosystem while working toward a model for the Upper Waitemata. It is notable that, with the exception of referring to New Zealand macroinvertebrate taxa, data on nutrient cycling, assumptions of the relevant importance of detrital pathways and transfer of organic matter to higher trophic levels (i.e. fish) were almost exclusively based on international literature. This illustrates a major gap in understanding that has only recently begun to be addressed. Since that time, in New Zealand, mangroves have been found to be as productive, with respect to litter production, as their tropical counterparts (Woodroffe 1985 May 1984), although growth has been shown to differ between old and young stands within a single forest (Burns et al. in press) and in relation to position in an estuary (Hofstra et al. submitted.).

In New Zealand few large organisms feed directly on mangroves, although some insects do, including scale insects, the leaf-tying caterpillar, mealy bugs etc. (Hackwell 1989) and all these insects are likely to be fed upon by other consumers including spiders and insectivorous birds (Daniel 1984, Woodroffe 1983, Cox 1977). A number of native birds (e.g. heron, bittern, Pukeko, kingfisher, Banded Rail and Spotless Crake) inhabit mangrove swamps or utilise them as feeding grounds (Hackwell 1989). Mangroves also fringe important areas for wading birds at places such as Miranda on the Firth of Thames. At Miranda, expansion of the area occupied by mangroves at the expense of intertidal flats has been implicated in reduced use of parts of the coastline for wading birds (Woodley 2004).

As for seagrasses, mangroves are considered internationally to be important nurseries for coastal and inshore fisheries. Although there are a number of useful observations recorded in publications such as

Bradstock (1989), and in May's (1979) thesis, there is little hard scientific data on how fish use mangroves in New Zealand. The research that has been done led to Hackwell (1989) to describe the mangrove ecosystems of New Zealand as being relatively simple with low associated species diversity in contrast to their tropical counterparts. However, in the Manukau Harbour, the mangrove forest has been shown to have a greater total number of benthic faunal species and twice the number of individuals per unit area than comparable non-vegetated habitat (Henriques 1980). In mangrove forests elsewhere in New Zealand numerous macroalgae and macro-invertebrates are found among the pneumatophores, and a range of fish species have been recorded as visiting the mangroves to feed (Ritchie 1976, May 1979, Bradstock 1989). Chapman (1977) listed a number of organisms including the crab *Helice crassa*, the oyster *Saccostrea cucullate*, the barnacle *Elminius modestus* and mussels that could be found on New Zealand mangrove pneumatophores. He also noted the molluscs *Amphibola crenata* and *Zeacumantus lutulentus* that crawl over the mud, and also highlighted the ubiquitous algal turf (*Caloglossa* and *Catanella*, Morton 1976) that clothes the lower pneumatophores.

More recent research has described the results of detailed scientific studies which have investigated benthic macrofaunal relationships with different ages and types of mangrove forests. Numbers of macrofaunal taxa were found to be larger at younger sites and differences in faunas were coincident with differences in the nature of the sediment (Morrissey et al. 2003, Ellis et al. 2004).

3.4.5 Threats and vulnerability

Contemporary threats to New Zealand mangrove ecosystems include local effects such as development e.g. causeways (Roper et al. 1993), and the potential for ad hoc management as pressure from community groups increases to remove mangroves from areas where they have spread in response to accelerated sedimentation. In the longer term, global effects also need to be considered, for example sea level rise which is widely acknowledged to be a factor that is likely to create change in these plant communities at the interface between land and sea (e.g. Schaeffer-Novelli et al. 2002). Recent debate on the role of mangroves in the New Zealand coastal environment, stimulated by a need to balance conservation and management, has prompted a number of community directed articles (e.g. Graeme 2002, Woodley 2004). Green et al. (2003) published information that aimed to inform the debate on the values and management attached to mangroves in New Zealand. These articles serve to highlight that there is insufficient hard scientific research at a range of scales to make confident decisions on the effects of various alternative management regimes.

3.5 Biodiversity 'hotspots'

There are a number of gaps in knowledge from a biodiversity perspective, with respect to both seagrass and mangrove ecosystems. These gaps in information make identification of hotspots of biodiversity premature. It is possible to progress toward delineating areas of high plant abundance or biomass but the dearth of information on the relative ecological and physical values of different seagrass and mangrove communities precludes ranking sites as to value, without strong bias to the few sites that have been studied in detail. Nevertheless, some areas that include seagrass and mangrove ecosystems have already been singled out as having a degree of significance, e.g. extensive seagrass beds are somewhat incidentally included in Farewell Spits' RAMSAR site designation.

3.6 Gaps in knowledge

Dromgoole & Foster (1983) made a statement with respect to the marine biota of the Auckland Harbour, which can equally be applied to mangroves and seagrasses throughout New Zealand that: "*despite numerous publications and reports (on marine biology) that can be identified, replicable quantitative data are rare*". This review has shown that there are many photographic and general observations, of aspects such as utilisation of mangrove forests by fish that have been made by community groups,

conservation groups and residents. While this is invaluable information it is easily refuted when it comes to legal decisions regarding management options and cannot adequately substitute for the absence of rigorous scientific studies.

There are some major scientific gaps for both seagrasses and mangroves identified in this review that are related to biodiversity.

For seagrasses which have a New Zealand-wide distribution there are potentially important geographic areas that have been largely unstudied according to the scientific literature. Notable gaps are areas north of the Poor Knights and south of Otago. Subtidal seagrass beds have been almost completely ignored and with the exception of records from some islands off the North Island coast other possible sites are known only anecdotally (author's unpublished information). The scant attention paid to historical distribution (over decadal scales) and the development of mapping techniques is somewhat surprising given the commonplace usage of such techniques elsewhere in the world (e.g. McKenzie et al. 2001).

Accurate updated measures of the area of coastline colonised by mangroves are also required, as is a historical interpretation of any changes in distribution.

There is a lack of knowledge of the existence, or significance, of genetic diversity of populations of both seagrass and mangroves.

The role of seagrass and mangrove habitat as nursery grounds or adult habitat for fishery species is relatively unknown for New Zealand. Utilisation by different life stages of macrofauna in general, is a notable gap in the published scientific literature.

There is very little information for either plant group on production of organic matter from a range of types of sites, its subsequent ecosystem transfer and hence its role in ecosystem functioning.

The impact of anthropogenic activities on seagrass beds has received extremely limited attention. A lack of understanding about the relative importance of vegetative and sexual reproduction in re-establishment following declines in seagrass abundance, places severe limitations on our ability to manage or assist re-establishment efforts. A further barrier to such efforts is the paucity of studies that have been undertaken in New Zealand of the dynamics of seagrass colonisation, expansion, recession and mortality processes at the scale of a patch or a seagrass bed. An important gap for the biodiversity of the estuaries, as a whole in the North Island, is an understanding of the flow on effects of active management of mangroves for other components of the estuarine ecosystem.

Our knowledge of the potential for seagrass and mangrove growth to be affected by altered nutrient concentrations in the New Zealand environment is almost non-existent. Similarly, the effects of possible future environmental change such as climate change/sea level rise for seagrass beds and mangroves, is poorly understood.

3.7 Recommendations for future research

- Undertake surveys that will establish the current (and as far as possible, the past) distribution of mangrove and seagrass (including subtidal) habitat around New Zealand. Such surveys can be based upon a variety of already available information, but they are likely to also require the acquisition of new data derived using direct (e.g. diver-surveys) and indirect mapping methods (e.g. using aerial photographs).
- Carry out studies of the genetic diversity of seagrass and mangrove populations, as a first step to appreciating the possible ecological significance of any such diversity.
- Determine the spatial and temporal use of seagrass and mangrove habitat by different life stages of fish and ‘shellfish’ (with an emphasis on commercial species), paying particular attention to understanding any relationship between fish/shellfish utilisation of macrophyte habitat and the presence of their food items (e.g. ephyphitic algae, macrofauna).
- Quantify the production of organic matter by seagrass and mangroves and the subsequent transfer of such matter to other systems, in order to begin an understanding of their role in marine ecosystem function of these habitats in New Zealand.
- Examine the dynamics of seagrass recession, mortality, colonisation and expansion processes at the scale of a patch and a seagrass bed as part of studies that attempt to understand the impact of specific anthropogenic activities on seagrass and improve the ability to manage this habitat. Studies that consider the effect of anthropogenic impacts on mangrove habitat should also be conducted.
- Determine the influence of differing nutrient concentrations on seagrass and mangrove growth in order to understand how regional changes in nutrient inputs to coastal waters will impact these habitats at the ‘landscape’ scale. An assessment of the influence of likely climate change on the large-scale distribution of these macrophyte habitats could be usefully conducted.

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Table 3.1: List of locations in Figure 3.1 where seagrasses have been recorded in New Zealand. Details of site description and original references are listed in Inglis (2003). Additional seagrass beds are included (49 to 53) and locations 17 and 18 probably no longer have extant *Zostera* beds (Duffy 1994).

No.	Location	No.	Location
1	Parengarenga Harbour	25	Moutere Inlet
2 & 3	Muriwhenua wetlands	26	Waikawa Bay (Queen Charlotte)
4	Whangarei Harbour	27	Wairau Lagoons
5	Whangapoua Wetlands	28	Kaikoura Peninsula
6	Waitemata Harbour	29	Karamea Estuary
7	Tairua Estuary	30	Saltwater Lagoon
8	Whangamata estuary	31	Okarito Lagoon
9	Wharekawa estuary	32	Avon-Heathcote Estuary
10	Kaipara Harbour	33	Akaroa Harbour
11	Manukau Harbour	34	Purau Bay, Lyttleton Harbour
12	Firth of Thames	35	Brooklands Lagoon
13	Kawhia Harbour	36	Otago Harbour
14	Tauranga Harbour	37	New River Estuary
15	Maketu-Waihi estuaries	38	Awarua Bay
16	Ohiwa Harbour	39	Toetoes Harbour
17	Ahuriri Estuary and wetlands	40	Freshwater
18	Te Angiangi Marine Reserve -East	41	Paterson Inlet - Stewart Island
19	Te Tapuwae O Rongokako	42	Moeraki Beach
20	Pauatahanui Inlet	43	Mahurangi Harbour
21	Farewell Spit	44	Whangateau Harbour
22	Whanganui Inlet	45	Whitianga Harbour
23	Waimea Inlet	46	Manaia Harbour
24	Parapara Inlet	47	Te Kouma Harbour
		48	Otago estuary
No.	Location	Description	Source
49	Slipper Island	Subtidal bed in South Bay	Grace & Whitten 1974
50	Great Mercury Island		Grace & Grace 1976
51	Urupukapuka Island	Subtidal beds to 2 m deep in Urupukapuka Bay	Hayward et al. 1981
52	Cavalli Islands		Grace & Hayward 1980
53	Blackhead point to Kairakau	Intertidal siltstone and mudstone platforms	Duffy 1994

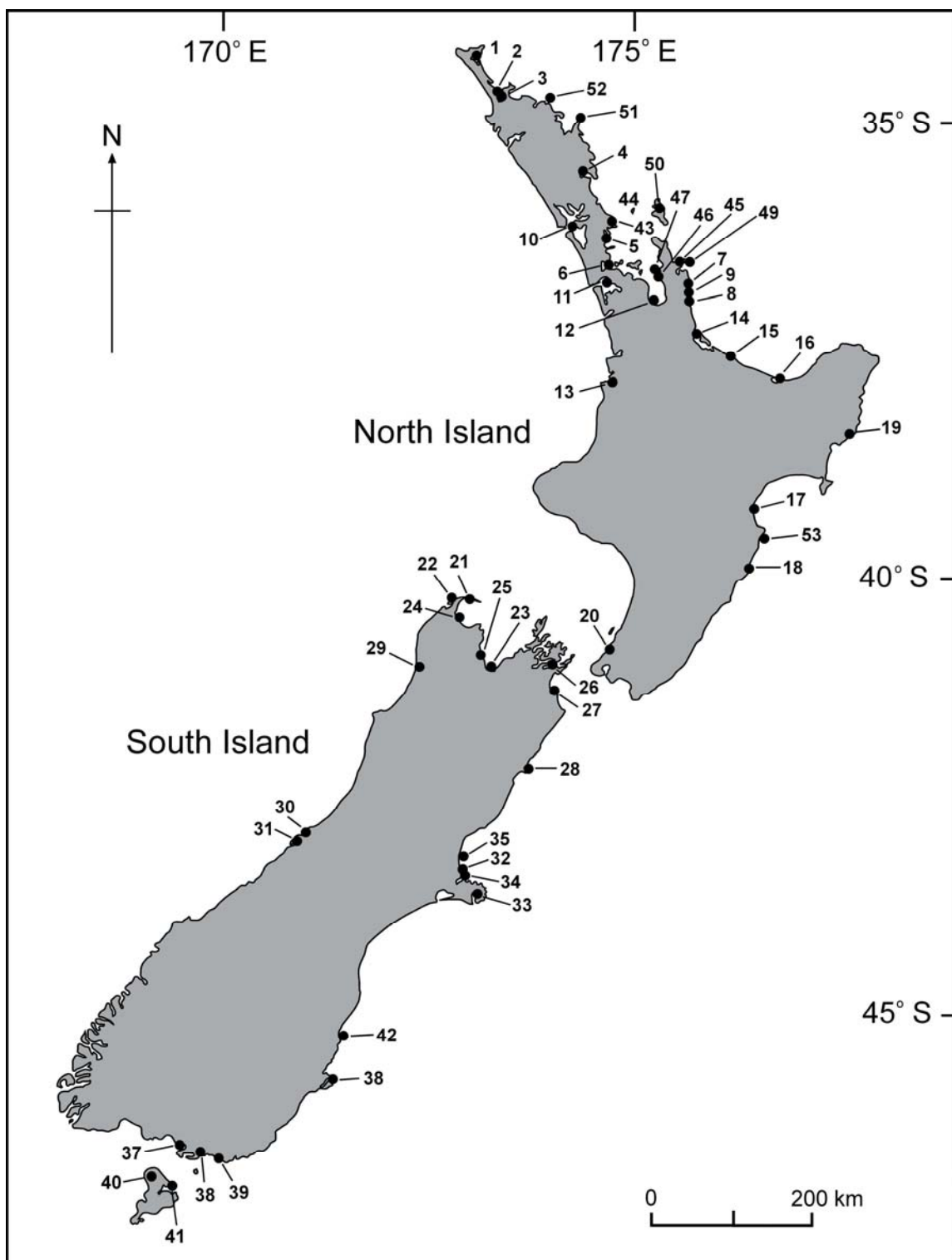


Figure 3.1: Locations from which *Zostera* has been recorded in New Zealand. Details for locations are provided in Table 3.1. Reproduced courtesy of G. Inglis (NIWA).

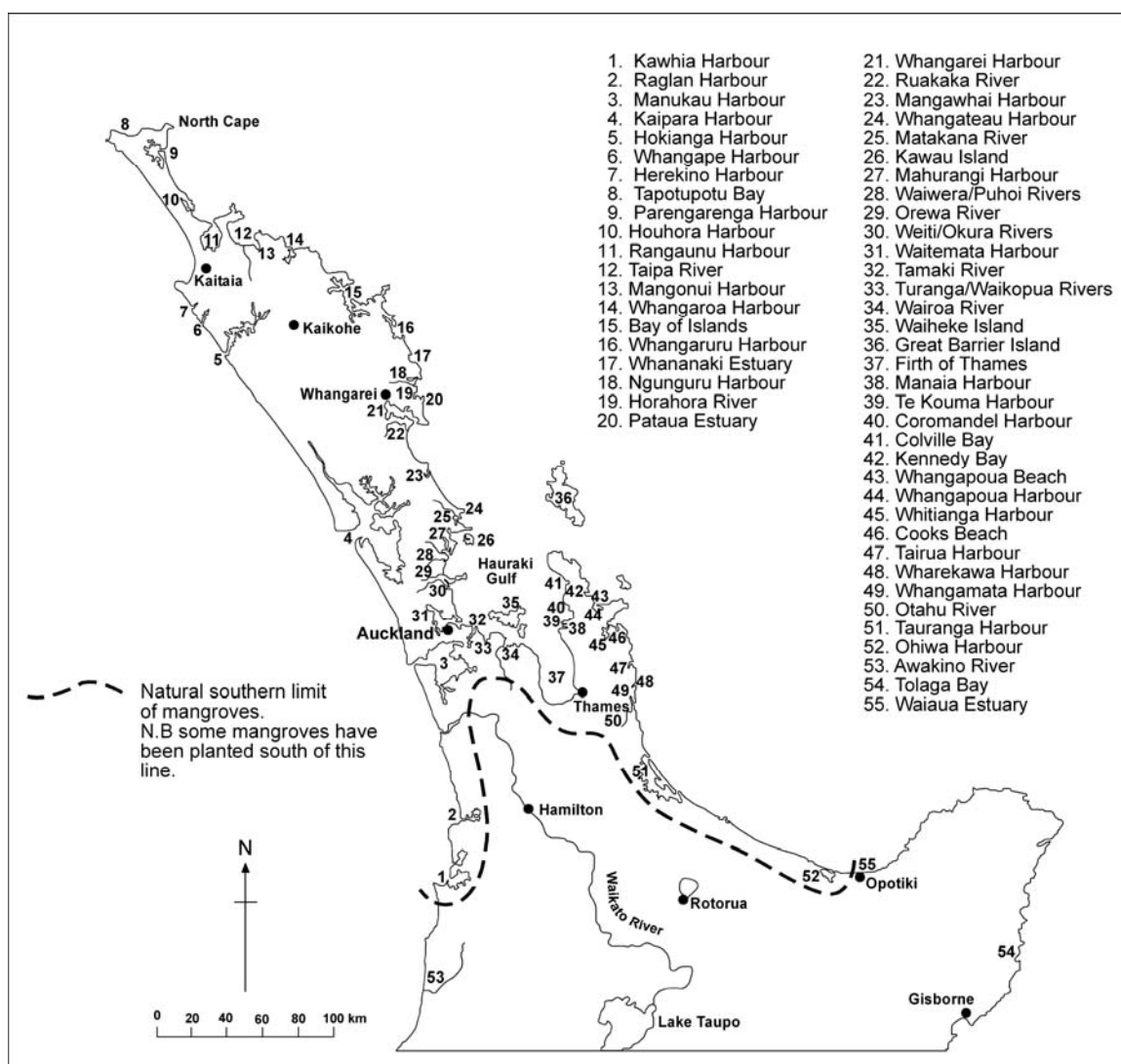


Figure 3.2: Distribution and range of mangroves in the late 1980s in New Zealand. Reproduced from Crisp et al. 1990.

4. MACROALGAE

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4.1 Introduction

This review presents existing information on soft-sediment marine assemblages around New Zealand based on both published and unpublished sources. The purpose of the review is to identify gaps in the current knowledge of macroalgae in these environments, the location of hotspots of biodiversity as well as areas of particular vulnerability, and to make recommendations on areas or assemblages that could be the subject of directed research in future years. Publications included in the accompanying database are restricted to those that refer to macroalgae in the context of marine species assemblages.

Macroalgae occur much less frequently in soft-sediment environments than on rocky reefs, normally requiring hard substrata for attachment. Diversity is increased in areas where there are settlement surfaces available such as stable cobbles, shell beds, bivalves, and mangroves. In some parts of the world seagrass leaves provide important substrata for algal growth and the interactions between seagrasses and their epiphytic load, for example in relation to shading, photosynthesis, nutrient relationships, has been the focus on a number of studies (e.g. Harlin 1994, Cummins et al. 2004). In New Zealand *Zostera* beds are not reported as supplying significant habitat for macroalgal growth. Macroalgal diversity in estuarine environments is impoverished when compared with that found in coastal waters: relatively few species of macroalgae are tolerant of varying salinity although the contribution these species make to estuarine and harbour biomass and productivity may be very significant in certain locations and/or at particular times of the year (Nienhuis 1994; Raffaelli et al. 1998).

There is a substantial international literature about the phenomenon of “green tides” which occur when species of *Ulva* and *Enteromorpha* grow very abundantly, apparently in response to human modification of the environment (organic enrichment and eutrophication) (e.g., Valiela et al. 1997, Taylor 1999). Unattached macroalgae may accumulate intertidally and subtidally over soft sediments and in some areas they continue to grow and to photosynthesise. The presence of such “algal mats” in some situations provide refuge for invertebrates (Raffaelli et al. 1998) although accumulation of large drifts can modify silt deposition and create an hostile chemical environment, preventing recruitment of infauna larvae (Taylor 1999).

“Rhodolith”, or “maerl”, beds (made up of free living non-geniculate coralline red algae) are widely distributed in polar, temperate and tropical oceans. Rhodolith beds are habitats of high biodiversity and serve as important refuge sites and nursery areas for many fish and invertebrate species (including commercially valuable species) (Foster 2001). Owing to their range in depth and their geographic extension around the world, rhodolith beds are key habitats for management and preservation of coastal resources. Rhodolith beds are being disturbed by dredging for fertilisers and trawling on a worldwide scale, (e.g., Hall-Spencer & Moore 2000) which has led them to be included in a European Union Directive for environment protection (BIOMAERL team 1998).

4.1.1. Scope

The database prepared for this review consists of research published in journal papers (27), conference proceedings (3), and books (1) as well as information recorded in unpublished technical reports (32) and theses (7). Not included in the database but cited in the text are a series of papers that describe the regional macroalgal flora of New Zealand (cited in Adams 1994, also Neale & Nelson 1998, Nelson et al. 2002). Although these papers include species occurring in soft-sediment habitats they do not discuss species assemblages. Many other reports and papers were reviewed and subsequently excluded from the database, as the information they contained on macroalgae was too scanty to justify inclusion.

4.2 Current state of knowledge

4.2.1. Taxonomy

The New Zealand region has a macroalgal flora of approximately 770 species, of which only a small proportion is reported to live in association with soft sediment environments (Adams 1994; Hurd et al. 2004). There have been, however, very few targeted collecting programmes for macroalgae in these environments and little consideration given to the role of macroalgae in the assemblages and communities associated with soft sediments. Hence the underlying knowledge of the flora found in soft sediment habitats in New Zealand waters is poor. The species lists presented in published accounts of soft sediment communities suggest that little regard has been paid to correct identification of macroalgae, and rarely have specimens been lodged in registered herbaria. Few papers refer to permanent voucher specimens thus preventing the development of knowledge based on improved understanding of species concepts, distribution and biology.

Some taxonomic papers have focused on taxa commonly occurring in soft sediment environments and harbours/estuaries in New Zealand e.g. *Gracilaria* (Nelson 1987), or Australasia e.g. *Bostrychia*, *Stictosiphonia* (King & Puttock 1989); these have not been included in the database as their focus is predominantly taxonomic and they do not relate to assemblages or communities.

The combination of few targeted collections, a paucity of permanent material for further examination and study, and an apparent lack of interest in the contribution of macroalgae in soft sediment habitats, constitute major impediments to an improved understanding of these environments in the New Zealand context.

4.2.2. Distribution and extent

It is not possible to arrive at a consistent view of the distribution of macroalgae in soft sediments around New Zealand based on the literature published to date. The data available are geographically patchy, the studies of soft sediment environments have largely overlooked the macroalgae and the sampling regimes employed make it difficult to compare results between studies. The majority of the publications reviewed here deal with separate localities (reviewed from north to south), or focus on single species.

Very little detail is available about macroalgal assemblages, with most accounts either simply making reference to the presence of macroalgae encountered in the course of research focused on other organisms, or, examining specific aspects of the biology or population dynamics of single species. Although the focus of this review was intended to be solely on macroalgal associations, papers with a focus on two genera (*Ulva* and *Gracilaria*) have been included. Papers or reports written about beds or mats of *Ulva* are likely to comprise a complex of more than one *Ulva* species, and could also include members of the genera *Enteromorpha*, *Cladophora* and *Rhizoclonium*. The cryptic morphology and uncertain taxonomy of members of these genera makes it difficult for field workers to identify them correctly.

In the northern North Island on the east coast there have been a series of studies based on dredge sampling, examining subtidal associations in soft sediments in near-shore waters ranging from the Cavalli Islands (Grace & Hayward 1980), Urupukapuka I. (Bay of Islands) (Hayward et al. 1981), Tutukaka (Brook et al. 1981), and on both the west and east coasts of Great Barrier Island (Hayward et al. 1982, 1986 a,b, Jeffs & Irving 1993; Francis & Grace 1986), with one study to the east of Coromandel Peninsula at Great Mercury I. (Grace & Grace 1976). A number of these refer to the presence of rhodoliths, red algae that are associated with high biodiversity when documented in other parts of the world (discussed in detail below).

Francis & Grace (1986) published the results of a study of macroalgae of northeastern Great Barrier Island including macroalgae present in areas of soft sediment. They refer to the *Hummbrella hydra* zone found at the interface of rock and sand beyond the lower edge of the kelp forest -“in areas with high sediment loads, or shifting sand, a zone of red algae was found” - with *Caulerpa flexilis* occupying hollows and the edges of sand basins. They referred to a cluster of other red algal taxa occurring in association with *Hummbrella hydra* - *Delisea compressa*, *Acrosymphyton firmum* dominating and with *Ptilonia mooreana*, *Callophyllis* sp., *Pseudoscinaia* sp. also present. This zone had not previously been recorded in ecological studies of northern New Zealand, although the seasonal distribution of ephemeral red algae had been recorded by Hawkes when discussing the red algae *Schmitzia evanescens* and *Hummbrella hydra* (Hawkes 1982, 1983). Hawkes suggested that the life history alternation and gametophyte stages of both *Schmitzia* and *Hummbrella* with small abrasion resistant alternative phases were adapted for survival in habitats subject to substrate movement during winter storms. *Hummbrella* was found to be the spring/summer dominant species in areas of unstable substrates subject to wave surge and/or currents. Jeffs & Irving (1993) summarised information available on the northeastern coast of Great Barrier Island and presented some new data including manta board profiles that revealed a range of sediment types distributed as an extensive matrix of substrata/habitat patches. They suggested that previous sampling based on dredge sampling may have under-represented the diversity and pattern of sediments and the associated flora and fauna.

Chapman & Ronaldson (1958) examined the mangrove and saltmarsh flats of the Auckland isthmus and provided a very brief description of the algae found on mud flats and associated with mangroves (*Avicennia marina* subsp. *australasica*). In the Waitemata Harbour at Hobson Bay, Chapman & Larcombe (1974) carried out an ecological investigation of soft sediment and rocky intertidal habitats and their report included data on the surrounding vegetation, macroalgae, macroinvertebrates, fish and waterbirds, including records of macroalgae associated with and/or growing on mangroves. Orakei Basin in the Waitemata Harbour has been the focus of several studies (Turnbull 1954; Stevens et al. 1993; Hayward & Hayward 1999) primarily in relation to excessive macroalgal growth resulting from anthropogenic physical and biotic changes, particularly eutrophication.

In the Manukau Harbour the growth of *Gracilaria* and human modifications of the harbour led to a number of investigations. Larcombe (1975) discussed the distribution of *Gracilaria* (as *G. secundata*) in the upper Manukau Harbour in Onehunga Bay, particularly in relation to nutrients. At this time *Gracilaria* was considered to be affecting the ecology of the intertidal soft sediment areas by “promoting the settlement of fine sediments in areas where it has attained high densities”. Larcombe noted that faunal composition was changing with an increase in finer sediments. Henriques (1976, 1977) reported on the historical distribution and fluctuations in the extent and position of the *Gracilaria* meadows, as well as presenting data on hydrology, geology and water chemistry, sedimentology and coliforms in the Manukau Harbour. He carried out a survey of macroalgae occurring on the soft sediments, documented extensive *Gracilaria* meadows including measuring *Gracilaria* biomass, and reported on regeneration experiments for *Gracilaria*. Grange (1979) carried out a shallow subtidal survey of the macroflora and fauna of the sand-flats of Manukau Harbour. *Gracilaria* was recorded at 31 of the 42 stations, the most commonly recorded species of the 126 documented. Only 3 other macroalgae were recorded and these appeared as only 5 records. Despite the abundance and widespread distribution of the *Gracilaria* the paper discusses macrofaunal communities with only passing reference to the occurrence of *Gracilaria*. Henriques (1980) reported on the results of a survey of a narrow

segment of Manukau Harbour intertidal soft sediment faunal community, considering the effect of nutrient enrichment and presence of macrovegetation on faunal density and diversity.

Research in the Bay of Plenty, particularly in Tauranga Harbour, has focused on the nuisance growth of the green alga *Ulva*, and these papers are reviewed in section 3.2.2.

The Pauatahanui Inlet north west of Wellington was the site of integrated studies of the physical and biological environment. Healy (1980) summarised research at Pauatahanui and made reference to the importance of microalgae in formation of salt marshes, stating that macroscopic algae are “not important colonising species in estuarine areas around Cook Strait. However, a number of algal species grow in the Inlet”. In the intertidal mud flats *Hormosira banksii*, *Codium dichotomum*, species of *Myriogramme*, *Ceramium* and *Chondria* were referred to, and the association of *Gracilaria chilensis* (as *G. secundata*), *Gelidium crinale*, *Enteromorpha* and *Ulva* spp. commonly occurring with *Zostera* beds was recorded as well as the occurrence of the articulated coralline *Corallina officinalis*. In addition a range of filamentous green algae and several species of reds including the bladed *Gigartina circumcincta*, finely branched *Centroceros* and the tufted *Caulacanthus ustulatus* were recorded, subtidal patches of *Ulva* mapped, and macroalgae associated with salt marsh vegetation such as *Catenella nipae* and *Bostrychia scorpioides* recorded.

The Whanganui Inlet (NW Nelson) is the second largest estuary in the South Island and Davidson (1990) reported on an ecological investigation that included data on terrestrial vegetation, macro-invertebrates, fish, and waterbirds. Although macroalgae were not referred to in the abstract, *Gracilaria* was characterised as one of the 17 main habitat types. In addition although “numerous species of algae were noted from the Whanganui Inlet” and “the greatest diversity was observed subtidally from the entrance while the largest quantities of algae were recorded from intertidal Whanganui Inlet” there is little detail provided and no indication that specimens were retained. Some approximations of primary productivity in the inlet were produced with contributions of macroalgae included although it was acknowledged as being “difficult to accurately estimate due to large fluctuations throughout the year”.

In a report of the ecology of the Waimea Inlet (Davidson & Moffat 1990) macroalgae were not mentioned in the abstract although *Ulva* and *Enteromorpha* were mentioned in the habitat description for the “fine sand flats” and *Gracilaria* for the “mudflats”. Detailed maps of the inlet were provided as well as the percentage area and number of hectares of different habitat types. The size of *Gracilaria* beds was estimated to be 11.1 hectares or 0.32% of the area surveyed.

Davidson (1992) reported on the intertidal and shallow subtidal ecology of the Abel Tasman National Park Nelson providing maps of the distribution of substrate and vegetation in the park, including an *Ulva/Gracilaria* association recorded from Wainui Inlet estimated to be 2.7 hectares. Rhodolith beds of unknown extent recorded from the Totaranui area in areas of strong tidal currents were also mapped and stated to be the “only significant beds recorded in the Nelson/Marlborough region”.

Although there is little mention of macroalgae in a preliminary intertidal and subtidal investigation of Croisilles Harbour, Davidson & Duffy (1992) recorded red algae in a muddy sand habitat dominated by a bed of *Chaetopterus* sp. The red algae were attached to the worm tubes with algal cover exceeding 15%.

Davies (1931) published the results of an ecological investigation of Nelson Haven soft sediment (mudflat) habitats including data on the surrounding vegetation, macroalgae and macro-invertebrates, and published a number of photographs of views across the mud flats as well as views of *Zostera* and cockles, although referring only to *Ulva* and “various filamentous species which thrive along the foreshore”. Davies notes that “algal vegetation is poorly represented”. An ecological survey of the tidal flats of Riwaka-Tapu Bay conducted for the purpose of assessing potential impacts of nutrient enrichment from a proposed sewage treatment scheme reported on fauna, sediment, *Zostera* and recorded *Gracilaria*, *Ulva* and *Enteromorpha* (Knox & Fenwick 1978). In places *Gracilaria* covered 40% of the substrate in areas of the river channel where there was well sorted sand bottom at depths of

approximately 0.5 m. Also in the Nelson area Stanton *et al.* (1977) surveyed the texture, flora and fauna of Delaware Inlet as baseline data for future studies including assays of salinity and nitrogen levels of the intertidal flats. They recorded the presence of *Ulva* and *Enteromorpha* close to *Zostera* beds on sandy sides of channels occurring on buried living cockleshells. Coppard (1981) documents the marine flora of Oruawairua Island, Marlborough Sounds, predominantly from the rocky intertidal (sandstone) but also includes algal observations from soft sediment (i.e. fine gravel) habitat from which two species were recorded (*Ulva*, *Scytothamnus*). This record of *Scytothamnus* appears somewhat anomalous and may represent the red alga *Gracilaria chilensis*, a much more likely component of a soft sediment habitat.

Knox and co-workers prepared a series of reports on various estuarine and soft sediment environments where human modifications were either anticipated or had occurred and where baseline data were being gathered. Knox (1974) reported on preliminary investigations into changes in Blaketown Lagoon Greymouth (i.e. water quality, hydrology, sediment, vegetation, macroinvertebrates) particularly those contributing to macroalgal growth associated with construction of a new outlet for the lagoon and sealing off of the old outlet. Knox *et al.* (1978) carried out a survey of macrophytic vegetation in the Brooklands lagoon, Waimakariri, as a baseline for assessing any future changes and recorded *Enteromorpha* spp., *Gracilaria secundata* and *Monostroma* sp. in the soft sediment habitat of the lagoon. Knox *et al.* (1976) reported on the Okarito Lagoon Westland at a time when there were plans to log the surrounding forest for rimu and concern was being expressed at the potential impacts on the lagoon, in particular whether increased sedimentation would influence the food chains in the lagoon and threaten bird life. There was virtually no reference to macroalgae in the report although there were records of *Enteromorpha* sp. and *Gelidium longipes*, the latter clearly a misidentification, based on current understanding of this taxon (Nelson & Farr 2003).

The papers of a number of authors investigating the Avon-Heathcote estuary are primarily focused on single species of macroalgae and are reviewed in section 3.2.2.

A number of studies have examined the communities and assemblages occurring on the soft sediments of the Otago Harbour. At Aramoana, Hamel & Barr (1974) examined zonation of invertebrates, macroalgae and *Zostera* in the intertidal flats. This report refers to 13 macroalgal taxa (7 identified to species, 6 records to genus level only). Macroalgae were not a significant component of the overall analyses carried out with *Ulva* recorded as an important element in Zone I (closest to mean low tide) and *Enteromorpha* in Zone III (near the high tide line including salt-marsh turf). Rainer (1981) examined soft-bottom benthic communities in Otago Harbour and Blueskin Bay and noted that the presence of shell or macroscopic algae was usually associated with elevated species diversity. Rainer concluded that the presence of macroscopic algae, principally *Adamsiella* (as *Lenormandia*) had affected sediment composition in some areas by favouring the deposition of silt and organic detritus, with resulting differences in the fauna. Although Rainer applied a number of measures of diversity to the communities/assemblages macroalgae were not included in the calculation of the diversity indices. The weight of algal material collected from the surface of each sample was recorded, but macroalgae were not identified by genus or species (although *Ulva* was mentioned). In a study of sediment macrobenthos in the upper Otago Harbour Grove & Probert (1999) concluded that a combination of percent sand, macroalgal content, water depth and chromium concentration correlated best with the observed community structure. They also recorded the weight of algal material collected from surface of each sample, but did not identify the species present although both *Ulva* and *Adamsiella* (as *Lenormandia*) *chauvinii* are mentioned. Specific associations between fauna and algae are referred to, in particular the occurrence of two herbivorous gastropods with *Ulva*, an ascidian found attached to *Adamsiella*, as well as an association of this red alga with a crab and an ophiuroid.

Grange (1985) conducted a soft sediment community survey on the shores of Freshwater Basin in Milford Sound for the purpose of assessing possible impacts of a proposed development, and four taxa of macroalgae were recorded.

Stewart Island soft sediment assemblages involving macroalgae are probably the best documented of any in the country. Batham (1969) gave a descriptive account of the ecology of Glory Cove based on samples obtained from intensive bottom trawling, and referred to the dominant cover of *Adamsiella* (as *Lenormandia*) *chauvinii* over much of the bottom, recording only three other seaweed species. This paper concentrated on the identification of the macrofauna, commenting particularly on the “unusual wealth of echinoderms”. Soft-bottom assemblages of Paterson Inlet, Stewart Island were studied by Willan (1981) who characterised the muddy areas as having extensive algal growth, particularly of the species *Adamsiella chauvinii*, and *Rhodymenia* spp. which can attain 100% cover. These algae were found to occur in areas of negligible current scour with muddy substrate and higher numbers of epi- and infaunal taxa than in the sand assemblages of higher current flow. Roper et al. (1988) concluded that the *Adamsiella* meadows in Big Glory Bay “probably play an important role in stabilising the muddy bottom and provide a refuge for animals”.

Hare (1992) reviewed data compiled over 22 years from Paterson Inlet on marine benthic assemblages. She reported on the algal communities dominated by *Adamsiella* (as *Lenormandia*) and *Rhodymenia* spp. on the muddy seafloor of the central inlet, and proposed a relationship between these algal communities and free-lying brachiopods occurring in the area. It was suggested that the red algae may sufficiently stabilise the finer fractions of sediment by trapping them and thus enable the brachiopods to live on these muds without being smothered or buried by sediment. Hare recorded that only dredge stations with red algae contained brachiopods.

There were different assemblages on the mud of central Paterson Inlet, distinguished primarily by different red algae rather than by faunal species, and this was considered to be related, in part, to depth. *Adamsiella* dominated in beds found at 6–20 metres along the shores and in the bays of the mid-inlet, whereas in deeper areas at around 20–25 metres an assemblage characterised by two species of *Rhodymenia* occurred. An extensive inshore sand/shell association dominated by *Asparagopsis/Delisea/Brongniartella* was found in 6–13 metres: all these species are also known to occur on rocky substrata. It was considered that the currents in areas around the base of rocky reefs in mid-Paterson Inlet are not strong enough to prevent settlement and growth of algae and thus permit the colonisation of macroalgae and their growth on shell fragments. Hare (1992) also made reference to algal associations in Port Pegasus and Port Adventure, Stewart Island, and to *Adamsiella* beds in Ranui Cove at the Auckland Islands.

Gracilaria spp. occur throughout New Zealand in estuaries and harbours in areas of soft sediment from the low intertidal to the upper subtidal zone. Interest in the uses of this agarophyte genus, ranging from harvest of wild stocks, enhancement and cultivation, has resulted in a number of research studies, theses and publications. These studies are primarily focused solely on *Gracilaria*, examining aspects of the physiology, population biology, and reproduction of *Gracilaria* spp. (primarily *G. chilensis*, although *G. truncata* has also been studied) from Auckland, Wellington, Dunedin, Invercargill (Beever 1965; Luxton 1977, 1981; Terzaghi et al. 1987; Lignell 1988; Nelson 1989; Intasuwan 1990; Pickering 1990; Pickering et al. 1990; Pillai 1992; Stevens 1992).

Names applied to the species of *Gracilaria* that predominates in estuarine and harbour environments in New Zealand have changed over the past 15 years. It was earlier considered to be a form of *G. secundata* but it was realised (Nelson 1987) that this name is only correctly applied to a species found on open, wave exposed coasts and that the estuarine/harbour species was undescribed. At the same time as *G. sordida* was being described, based on New Zealand material, the name *G. chilensis* was published (Bird et al. 1986; Nelson 1987). These two species were found to be identical and synonymised, with *G. chilensis* having priority (Bird et al. 1990). Subsequently it has become clear that there is another species of *Gracilaria* present in the Auckland area. Although the second species is morphologically similar to *G. chilensis*, recognition that this species is distinct has been established using both molecular sequencing data and the presence of gigartinine (Candia et al. 1999; Wilcox et al. 2001). At present this additional species is known solely from the Manukau Harbour and from the Orakei Basin in the Waitemata Harbour (voucher material in WELT, Te Papa) (Holmgren et al. 1990) and appears to be

related to a species that is widespread worldwide, almost certainly being spread by human-mediated means.

The green algae *Ulva* and *Enteromorpha* have been the focus of a number of studies internationally owing to their involvement in “green tide” phenomena. Recent systematic studies employing molecular sequencing data have established that these genera are paraphyletic with respect to each other: generic separation based on thallus form (placement in *Ulva* for sheet-like thalli and *Enteromorpha* for tubular thalli) does not reflect the phylogenetic relationships of species placed in these taxa. As a consequence they have been synonymised and all species previously placed in *Enteromorpha* are now members of the genus *Ulva* (Hayden et al. 2003). In the only full account of the green algal flora published to date Chapman (1956) described many new entities, and within the genus *Enteromorpha* distinguished 46 separate taxa, including subspecific rankings, many of which subsequent authors have had difficulty recognising. Taxonomic investigation of *Ulva sensu lato* in New Zealand is required: preliminary molecular sequencing data of samples from New Zealand (including material from the Avon-Heathcote estuary) indicate that species concepts previously applied in New Zealand are likely to be incorrect (McIvor and Maggs, unpublished data, pers. comm.).

In New Zealand studies on *Ulva* have been centred in the Bay of Plenty and in the Avon Heathcote estuary, Christchurch. In the Bay of Plenty a number of reports have been prepared on the presence of *Ulva* spp. in nuisance quantities in coastal waters during the 1980s and 1990s (Hawes et al. 1992; Bay of Plenty Regional Council 1992; Hawes 1994; Park 1994, 1996; de Winton et al. 1998). Hawes et al. (1992) reviewed management strategies for sea lettuce growth in the Bay of Plenty considering the international literature on sea lettuce and identifying several directions (nutrient limitation, temperature, sporulation, desiccation, grazing, light) for future research that would be important for understanding the problems occurring in the Bay of Plenty. The Bay of Plenty Regional Council produced a popular brochure/leaflet on sea lettuce (Bay of Plenty Regional Council 1992) detailing its life history, distribution and impact on the Bay of Plenty harbours as well as explaining the actions of the Council to monitor and investigate the causes of nuisance blooms as well as the removal of beach cast deposits and in-harbour accumulations. Hawes (1994) summarised research underway in the Bay of Plenty that was attempting to identify the causes of nuisance blooms including student studies at Auckland University. Park (1994, 1996) reviewed the baseline monitoring of sea lettuce blooms in Tauranga Harbour and Ohiwa Harbours reporting on sea lettuce biomass, nutrient status, environmental influences and sediment water interactions in relation to growth and the development of nuisance blooms. De Winton et al. (1998) presented a description of the temporal and spatial variations in sea lettuce abundance within intertidal and subtidal habitats between 1994 and 1998 and the probable role of the physical harbour environment in influencing these patterns, the results of physiological investigations into growth response to conditions of light, nutrient availability and temperature, as well as determinations of the genetic and morphological variation within the sea lettuce population of Tauranga Harbour.

The Avon Heathcote estuary has been the site of a number of biological studies, some of which have included research on the proliferation of *Ulva* and *Enteromorpha* species on the tidal flats. Considerable attention has been focused on the variations in algal abundance and possible relationships with various environmental parameters. The effluent from the Christchurch Drainage Board sewage treatment works has been implicated as having a causal role. Bruce (1953) discussed pollution in the estuary relevant to the distribution and density of *Ulva* spp. She recorded the disappearance of *Zostera* and the increase in abundance of *Ulva* from the early 1930s, in relation to currents, sediment, slope of the beach, salinity, organic matter in the mud, nitrogen and sulphur content. Bruce also discussed the abundance of *Scytothamnus* in the estuary and analysed nitrogen content in two samples. This record appears somewhat anomalous and may represent the red alga *Gracilaria chilensis*, a much more likely component of the estuarine habitat. Williams (1959) referred to three common “species” although referring to them only by generic names (*Enteromorpha*, *Ulva* and *Gracilaria*) in research that repeated Bruce’s study conducted 7 years previously. Some measurements of wet weight were reported and compared with the earlier study.

Steffensen (1974, 1976a, b) carried out ecological studies to assess the effect of sewage discharge on *Ulva* and other macroalgae. This research produced data on the distribution, percentage cover and density of algae within the estuary, the standing crop of *Ulva lactuca* in the Avon-Heathcote estuary plus experiments assessing effects of nutrients and temperature on growth of *Ulva lactuca* in culture. Although the focus of the study was the Avon-Heathcote estuary, the research included periodic collections from other South Island estuaries. Knox & Kilner (1973) documented algal growth, hydrology, sediments, nutrients, and distribution of the estuarine biota, including seasonal distributions of green algae between 1969 and 1970, and experiments involving nutrients and growth rates. The disappearance of *Zostera* was also documented as well as data summaries for several physical characteristics of the estuary: hydrology, salinity, effluent discharge, surface sediments, and water quality. In 1992 Owen presented a general review of the history and biology of the Avon-Heathcote Estuary, including a section on “sea lettuce” and also mentioned *Gracilaria* “blooms” (Owen 1992). Knox (1992) reviewed the research on *Ulva* in the Avon-Heathcote review in a report prepared to assess the physical and biological changes in the Avon-Heathcote estuary since 1973. This report provides reference and data summaries for several physical characteristics of the estuary: salinity, effluent discharge, surface sediments, and nutrient status.

Laboratory and field experiments were conducted to determine empirical relationships among thallus size, water velocity, drag and plant detachment of *Ulva lactuca* in sheltered habitats in the Avon-Heathcote estuary (Hawes & Smith 1995). A model was constructed to predict/describe growth of sea lettuce based on a variety of “scenarios” (e.g. temperature, irradiance and nutrient concentrations) in order to assess the potential impact of effluent on nuisance growth of the *Ulva* in the estuary (Hawes & O’Brien 2000). Hawes (2001) reported on sea lettuce (*Ulva* spp.) and *Gracilaria* in the Avon-Heathcote estuary, discussing factors affecting growth, the impacts of these two species on other estuary components, control options, and suggested trials of further controls and monitoring methods.

A particular growth form of the giant kelp *Macrocystis pyrifera* has been reported from soft sediment habitats in sheltered bays in Paterson Inlet as well as in Port Pegasus, Stewart Island (Moore 1943; Gerard & Kirkman 1984). This growth form of *Macrocystis* consists of branched fronds with no basal meristems or holdfasts and has been found in clumps on the soft mud bottom.

4.3 Rhodoliths

Rhodoliths are morphologically diverse, free-living forms of non-geniculate coralline red algae that form extensive beds on soft sediments. They occur worldwide over wide latitudinal and depth ranges (Foster 2001, Steller et al. 2003) and form structurally and functionally complex habitats “made up of branching or rounded thalli that collectively create a fragile, structured biogenic matrix over coarse or fine carbonate sediment” (Steller et al. 2003). These beds are known to support a rich diversity of associated species including rare, unusual and endemic species. Recent studies in the northern hemisphere have revealed that these benthic communities are not resilient and easily impacted by a number of different anthropogenic activities such as harvesting, trawling, anchoring, or activities that reduce water quality through siltation and eutrophication, effluent discharges, offshore dumping, coastal structures that influence currents (e.g. breakwaters, quays, sea-walls, marinas), as well as the impact of aquaculture (shellfish rafts and fish cages) (Barbera et al. 2003; Steller et al. 2003). Taxonomy of rhodoliths is often difficult as fertility is infrequently found, and the identification of non-geniculate coralline algae relies heavily on reproductive characteristics. Systematic studies of the non-geniculate coralline algae of the central New Zealand region are currently underway (MFish contract ZBD2001/05).

In a global review of rhodolith beds one area in New Zealand was recorded (near Kapiti Island) (Foster 2001). A study of the Kapiti area reported rhodoliths from one locality off the east coast of the island. The rhodolith bed was 25 cm deep in places, but the full extent of the bed was not defined (Battershill et al. 1993). Rhodoliths have also been reported from a number of northern North Island sites and from

sites in the northern South Island (Figure 4.1), although these publications have not been cited in published accounts summarising rhodolith associations.

In a study of the macrobenthos of the Cavalli Islands in northeastern North Island, rhodoliths were recorded as “an important component of the sediments” of the Cavalli Passage (Grace & Hayward 1980). The rhodoliths were in depths of 5–10 m and associated with *Tawera spissa*. Grace & Hayward (1980) observed that the rhodoliths provided attachment surfaces for bryozoa, serpulid polychaetes and small algae, as well as grazers such as chitons, limpets and a variety of epifauna such as amphipods, crabs, isopods, ophiuroids and gastropods. The position of the rhodolith beds coincided with the highest diversity recorded in the survey area. Although both living and dead rhodoliths were recorded from an area of coarse sediment in the Bay of Islands south of Urupukapuka Island (Hayward *et al.* 1981) no data were provided about any associated organisms.

Brook & Grace (1981), in a study of sub-tidal associations at Tutukaka, reported on the occurrence of non-geniculate coralline algae encrusting dead cockle shells in areas of fine muddy sand and also the “*Corallina*-*Maoricolpus*-*Notomithrax*” association, with both corallina turf, encrusting non-geniculate corallines and the presence of poorly developed rhodoliths in some areas at depths of 1–7 m in gravelly muddy sand, associated with a diverse epi- and infauna. A “gravelly substrate” association recorded by Hayward *et al.* (1982) at Rakitu Island (east of Great Barrier Island) included various algae (*Caulerpa*, *Codium*, “*Lithothamnion*”, *Zonaria*), chitons, polychaetes and bryozoa associated with pebbles and large shells, in pebbly to coarse sandy pebble gravel at 12–18 m. They also recorded rhodoliths from the “gravelly substrate” association and a “*Selenaria squamosa*” association although made no specific comment on their association with other taxa. Hayward *et al.* (1986b) in a study west of Great Barrier reported an association in depths of 10–15 m in areas of strong currents or wave exposure (high energy situations in coarse sediment) where the sandy shelly gravel substrate was characterised by a rhodolith-holothurian (“*Cucumaria*”- *Glycymeris laticostata*) association and a rich subsidiary epifauna. This was one of two very distinctive associations in terms of overall biotic composition of the six associations recorded by Hayward *et al.* Pink finely branched live rhodoliths were present in all stations and dead white specimens comprised a large proportion of the sediment. They reported that a rich and diverse fauna indicated that the rhodoliths provided a favourable habitat for epifauna within the coarse substrate as well as for infauna. Rhodoliths were also found in smaller numbers associated with a *Corbula zelandica* and *Venericardia purpurata* sub-association. Grace & Grace (1976) reported that beds of rhodoliths were found to be associated with the abundant *Tawera spissa* and *Venericardia purpurata* community around Great Mercury Island, and they mapped the presence of rhodoliths occurring in coarse sand to shell gravel at 4–15 m depth, in a channel where there were strong currents. They commented on the problems of dredge sampling this kind of habitat and the likelihood of recording a higher proportion of epifauna to infauna than actually occurs on the sea bed.

Davidson (1992) recorded rhodolith beds from the Totaranui area in areas of strong tidal currents although was not able to document the extent of these algae. He considered that these rhodoliths were the “only significant beds recorded in the Nelson/Marlborough region”.

4.4 Role in the ecosystem

Macroalgae are known to be important structural and functional components of marine ecosystems. However, their function in soft sediment ecosystems has received little attention in New Zealand. Healy (1980) referred to the contribution of *Ulva* to the organic detritus in the Pauatahanui Inlet, providing some limited data on the extent of the beds (approximately 23 ha. in 1977) and biomass (0.15 kg of dry matter per square metre), calculating a contribution of 35 tonnes of organic detritus annually. Healy referred to a seasonal cycle in which the whole thalli of *Ulva* die off in winter. In the Delaware Inlet, Nelson, Gillespie & MacKenzie (1981) examined the relative contributions of macro- and microalgae to primary production in the estuary. Juniper (1983) discussed the deposition and decomposition of macroalgal detritus in this inlet, whilst Mackenzie (1983), in the same conference volume, discussed primary production, making reference to the seasonality of macroalgal beds in terms of abundance and distribution. Mackenzie reported that macroalgal beds occupied at maximum about 10–15% of the total area and contributed about 0.8% biomass, although stating that the high photosynthetic rates may mean the macroalgae account for about 60% of net total daily production.

There is not a great deal of literature in a New Zealand context concerning the specific interactions of particular macroalgae with invertebrates. In Paterson Inlet rafts of free-lying *Hormosira banksii* were found to provide a refuge for numerous epifaunal species, crustacea and mollusca on sheltered mudflats (Hare 1992). Hare recommended that further investigation of these areas be undertaken given their potential as nursery areas for species such as flatfish and scallops. Iwasaki (1993) recorded *Enteromorpha* spp. in the soft sediment habitat of Pauatahanui Inlet when carrying out a survey of the meiobenthic copepod assemblages associated with different substrata.

Drift macroalgae can become beach-cast or form subtidal deposits and/or accumulations. Research on nearshore systems suggests that accumulations of beach-cast macroalgae are a source of dissolved and particulate carbon and nutrients - “The carbon supports detrital based nearshore foodwebs that include benthic suspension feeders, nearshore fishes, seabirds and beach waders. Detrital biomass in the surf-zone can exceed the offshore production by a factor of four” (Lavery 1999). Kirkman & Kendrick (1997) have identified that harvesting of beachcast macroalgae presents a number of threats to the coastal environment such as the disturbance associated with harvesting activity (e.g. impacts on vulnerable dune vegetation, shorebirds and nesting areas), and the long term effect of exporting nutrients and detrital carbon from nearshore coastal regions. They also raise the issue of the environmental and economic sustainability of commercial enterprises depending on beachcast material given the substantial inter-seasonal and inter-annual variations in biomass and retention times, and the ecosystem and food chain linkages of drift algal material. Beachcast material apparently also plays a role in coastal geomorphological processes and the formation and stability of dunes (Kirkman & Kendrick 1997).

The retention time of drift macroalgae on beaches is not well understood – and the relationship between deposition of newly beach-cast material, and the re-suspension and deposition of material which has been detached for some period, will differ with location, season and inter-annually. In some habitats drift algae once deposited reside on the shoreline until they have been dispersed through consumption, decomposition and fragmentation, whereas in other situations drift algae have a short residence time on the shore and then are carried offshore or dispersed subtidally. Some data exist on the distribution of *Macrocystis pyrifera* and *Durvillaea antarctica* on a beach near Christchurch (Inglis 1989; Marsden 1991 a, b). Distribution patterns of stranded *D. antarctica* and *M. pyrifera* differed through the year with *D. antarctica* consistently distributed at higher tidal levels than *M. pyrifera*. For *D. antarctica*, biomass decreased significantly downshore and varied seasonally with a maximum of approximately 3–4 kg.m⁻¹ of beach transect in winter decreasing to 0.4 kg. m⁻¹ during spring and summer. Although the standing crop of beachcast *M. pyrifera* fluctuated greatly during the annual cycle without any apparent seasonal pattern, thalli were distributed uniformly up the beach suggesting regular input characteristics.

In an experimental study the role of buried algal mats on the colonisation of macrofauna was examined in an intertidal sand-flat (Ford et al. 1999) and it was found that the effect of the macroalgal mats differed both between and within seasons.

Brown et al. (1999) examined spatial and temporal variations in the copper and zinc concentrations of two green seaweeds from Otago Harbour, highlighting the value of these algal species as biomonitors for trace metals. This research concluded that Otago Harbour was uncontaminated with respect to Cu and Zn, and illustrated interspecific variation in accumulation capacity of these elements.

The Orakei Basin, in Waitemata Harbour, Auckland, is an artificially enclosed pond with sluice gates controlling flow in and out. Since 1933 there have been complaints associated with nuisance plant growths and odours. A series of studies have focused on the Orakei Basin (Turnbull 1954; Stevens et al. 1993; Hayward & Hayward 1999) primarily in relation to problems resulting from anthropogenic physical and biotic changes particularly eutrophication. In the early 1990s it was realised that the predominant species, a red alga present in very large quantities, was not native to New Zealand, but because of the absence of fertile material it could only be placed to family level (Solieriaceae) (Nelson 1994). Stevens et al. (1993) conducted a study commissioned by the Auckland City Council, to determine the importance of nutrients on the growth of algae in the Orakei Basin. The biomass of macroalgae was monitored at 14 sites, and although a variety of algae were recorded, the species of Solieriaceae predominated throughout the year, with other taxa appearing seasonally. Hayward & Hayward (1999) noted the abundance of introduced exotic taxa in the Basin and the fact that the dominant marine animals were recent introductions to New Zealand (e.g. Asian mussels, Pacific oysters, introduced barnacles) as were the dominant macroalgae (“Solieriaceae sp. indet.” and *Codium fragile* ssp. *tomentosoides*). Prior to the early 1990s no voucher material had been retained from the Orakei Basin so it cannot be established when either the species of Solieriaceae or the apparently introduced species of *Gracilaria* first appeared in this locality. Subsequently “Solieriaceae sp. indet.” has been found in large quantities growing unattached above soft sediments in the Manukau Harbour but this has not been investigated, although reference specimens have been lodged in the herbarium at Te Papa.

4.5 Threats and vulnerability

Of the 22 species of macroalgae considered to be human mediated introductions to New Zealand, 20 species have been collected from harbour environments (Nelson 1999; Nelson et al. 2004). Some of these records are of macroalgae that grow unattached over soft sediments (e.g. *Chnoospora*, Nelson & Duffy 1991), sometimes in large quantities (e.g. Solieriaceae sp.indet., Nelson 1999). There have not been studies to examine the impact of these taxa on the surrounding flora and fauna, or the ways in which they modify their receiving environments.

Rhodolith beds are considered to be particularly vulnerable to anthropogenic modifications. However, rhodolith associations are as yet poorly documented in New Zealand and no research has been performed here on responses to such stressors as trawling, siltation, or eutrophication.

4.6 Hotspots and gaps in knowledge

The majority of publications provide very little information on macroalgal assemblages. Of the documents reviewed, 21 are on aspects of the biology of *Gracilaria* spp. (8) and *Ulva* spp. (13), and the majority (39) are geographically or regionally focused. The majority of the regional accounts have an animal-macrobenthic focus and only make passing reference to macroalgae.

4.6.1. Taxonomy

The underlying knowledge of the macroalgal flora found in soft sediment habitats is poor, and there are few examples of targeted collecting programmes for macroalgal assemblages. There is a critical need to build up collections from these habitats in order to develop a basis for future taxonomic and ecological studies. The understanding of the taxonomy of the *Ulva/Enteromorpha* complex in New Zealand is poor and the taxonomy of rhodoliths of Northland, the region where they have been most frequently recorded, remains unknown. (Northland lies outside the area currently studied through MFish Biodiversity research on non-geniculate corallines.)

4.6.2. Distribution: geographic and environmental

Certain areas have received a greater level of attention than others and this is reflected in the number of papers focused on specific harbours/estuaries e.g. Auckland - Manukau Harbour (8) and Waitemata Harbour (5), Bay of Plenty (in relation to *Ulva* - 6), Nelson (8), Avon-Heathcote (10), Otago (5), Stewart Island (4) (Figure 4.2). For many parts of the New Zealand region there is no information available on the macroalgal component of soft sediment associations/communities (e.g. west coast of the North Island other than the Pauatahanui Inlet and Manukau Harbour; west coast of the South Island, soft sediment shores of the inner fiords apart from Milford Sound; the Marlborough Sounds; the east coast of the South Island other than the Avon-Heathcote estuary and Otago Harbour; Chatham Islands; sites on Stewart Island other than Paterson Inlet; offshore islands including the Kermadec Islands, subantarctic islands).

Macroalgae characteristically growing associated with mangroves have been little studied in New Zealand and the reports of these are located primarily in the taxonomic literature. The occurrence of diverse macroalgae in association with subtidal beds of horse mussels is known anecdotally but there have been no published accounts of these assemblages. The macroalgal components of biogenic reefs in New Zealand have not been studied.

4.6.3. Role in ecosystem

In the international literature macroalgae are recognised to contribute to diversity in soft sediment environments, for example, through the provision of structural complexity, modification of flow and sediment regimes, and through their contributions to productivity. In the New Zealand context the roles of macroalgae in these aspects of soft sediment assemblages have not been explored.

Considerable volumes of beach-cast seaweed are harvested annually in various parts of New Zealand and there is commercial interest in the potential for increased harvest volumes and new harvest regions. There is little research available, however, on the impact of these activities. A critical feature of the harvest of beachcast seaweed is the potential for negative impacts on other organisms either directly or indirectly through the effects of physical removal and harvesting processes on nutrient cycling and carbon flows within nearshore food chains, on coastal stability and geomorphology, and through the impacts of vehicles and equipment on the beach.

4.6.4. Diversity

No papers have been published that specifically address the nature of the relationships between macroalgae associated with soft sediments and high biodiversity, although higher macrofaunal diversity has been noted in the presence of macroalgae in Otago Harbour (Rainer 1981) and at Stewart Island (Hare 1992). The studies in the northeastern North Island that located rhodolith beds also recorded increased diversity within these assemblages. Based on international experience it is highly likely that rhodolith beds and other biogenic sediments in which macroalgae are present will be found to be local biodiversity hotspots.

4.7 Recommendations for future research

The following areas of research are suggested as addressing significant gaps in the knowledge available about the New Zealand marine region. The priorities are influenced by international experience, and the established links to high biodiversity and vulnerable systems:-

- Research on rhodolith beds in New Zealand should include the mapping of their geographical distribution and extent, and distribution in relation to environmental parameters (currents/water movement, sediment loads, nutrients) in order to provide missing baseline data, but also to investigate the diversity of associated assemblages, and assess the relative vulnerability of rhodolith beds to perturbation. This research will result in improved taxonomic understanding of the rhodoliths and associated fauna through the establishment of permanent reference collections for systematic research, and enhanced understanding of the structural and functional components of biogenic reefs.
- Targeted collections of macroalgae in soft sediment environments in New Zealand – these collections should result in an improved basis for taxonomic studies, permanent reference collections, improved understanding of diversity both geographically and associated with specific environments,
- Ecological studies to examine relationships between macroalgae and associated fauna e.g. the contribution of macroalgae to productivity in New Zealand nearshore and soft sediment habitats, nutrient relationships, the role of macroalgae in habitat structuring, provision of nursery areas and influence on faunal settlement, resilience to disturbance and to modified sediment regimes, impacts of fishing methods, etc. Temporal (seasonal and inter-annual) variations in assemblages need to be considered, and would be of particular relevance in the case of studies addressing the origins and dynamics of populations of nuisance species.

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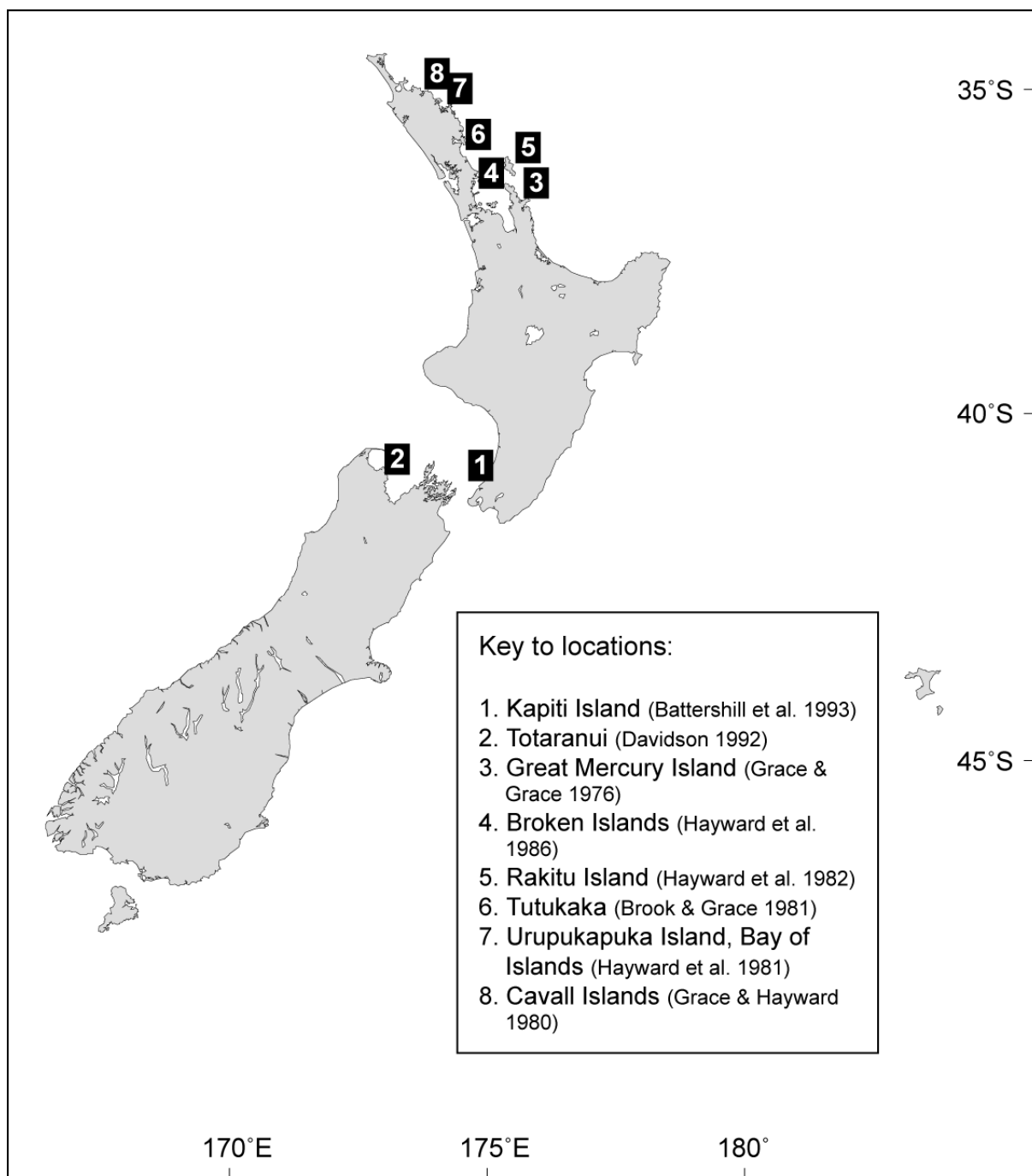


Figure 4.1: Map showing published locations of rhodolith beds around New Zealand.

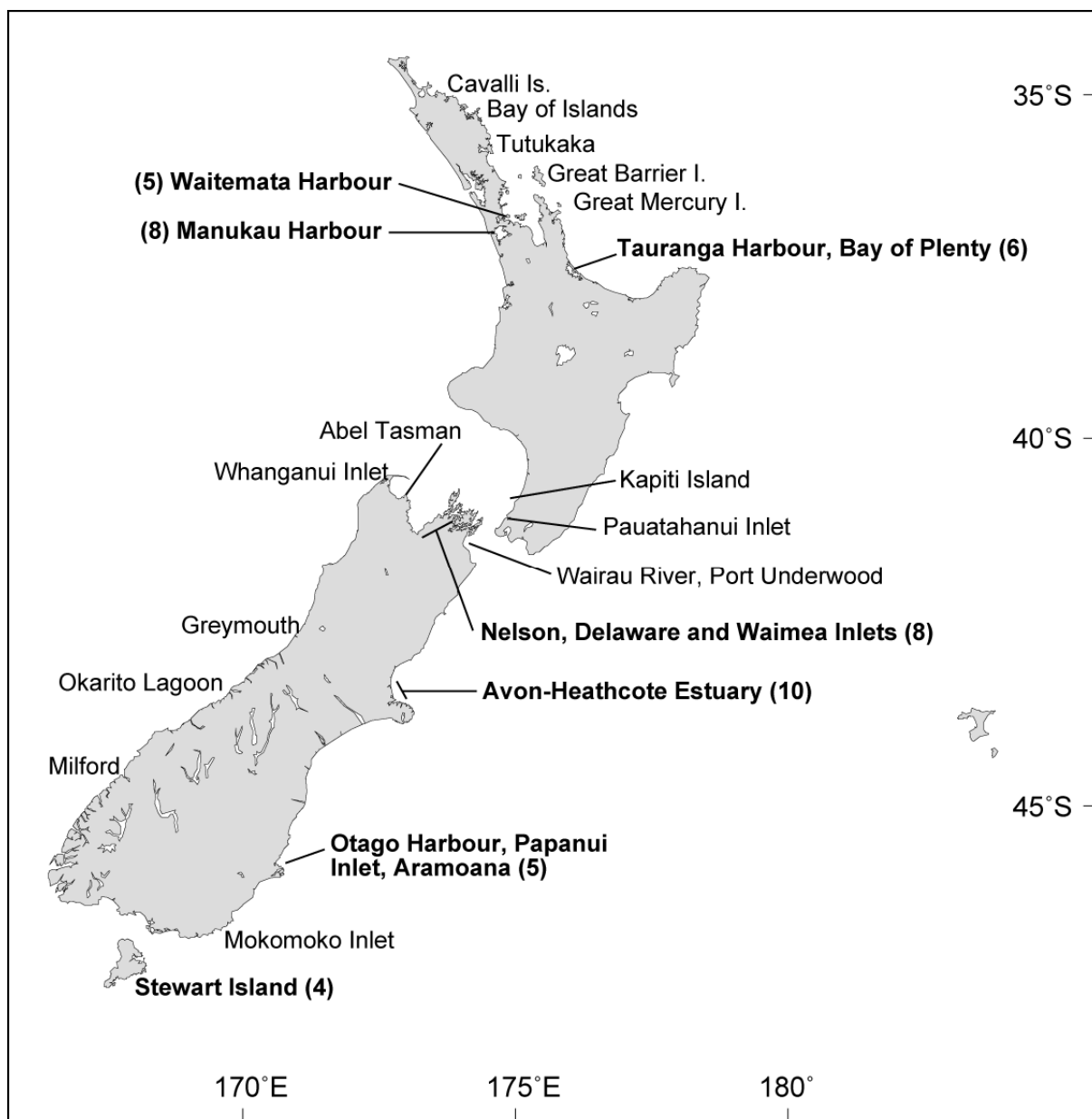


Figure 4.2: The geographic distribution of the majority of the studies included in the database. Forty-six of the seventy studies included were carried out at the seven locations shown in bold. The number of publications for each of these locations is given in brackets.

5. INTERTIDAL MACROINVERTEBRATES

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5.1 Introduction

Soft sediment environments are dominant coastal features and associated macrobenthic assemblages play an important ecological role through a variety of functions, such as the provision of food to higher trophic levels (Hines et al. 1990), influence on nutrient and organic matter fluxes (Raffaelli et al. 2003), and linking of benthic and pelagic processes (Lohrer et al. 2004a). In addition, coastal sedimentary habitats support benthic species that are important for commercial and recreational harvest, such as bivalves (Beentjes et al. 2006), and provide nursery habitats for commercial fish species, such as flatfish (Jackson et al. 2001). Intertidal soft sediments are generally distinguished by their physical environment, with exposed beaches located on open coasts characterised by a very dynamic physical setting, with tidal inlets, estuaries and bays found in sheltered locations.

New Zealand's coastline is extensive and covers a diverse range of coastal environments, from exposed and sheltered beaches to estuaries, lagoons and sheltered bays (Hume et al. 1992). Most research effort on New Zealand's sedimentary benthic assemblages has been focused on estuarine environments, predominantly in relation to land-derived impacts such as inputs of sediments, pollutants, nutrients and organic matter (e.g., Pridmore et al. 1991, Nipper et al. 1998, Ellis et al. 2000, Norkko et al. 2002). Considerably fewer studies have assessed exposed beach macrofauna and there has been no study to date that presents a comprehensive assessment of exposed beach macrofaunal assemblages in New Zealand.

In recognition of the importance and vulnerability of New Zealand's estuaries, the New Zealand Ecological Society held an Estuarine Symposium at their 1975 annual conference and one of the outcomes was the collation of available information by McLay (1976). In his review, McLay (1976) included data from topographic maps, population censuses and from a questionnaire that had been sent to authorities and individuals. He acknowledged that the classification of estuarine environments was deliberately broad; it resulted in a total of 301 estuaries, a total estimated estuarine area of 100 000 ha, and one estuary per 32 km of coastline on average. Questionnaire results indicated that a large number of estuaries were considered slightly polluted with significantly more North than South Island estuaries seriously polluted and an increase in the degradation over the past 10 years, which was more pronounced in the South Island. McLay (1976) concluded that the majority of estuaries have not been studied, whilst demands on estuarine ecosystems were continuously increasing.

Since McLay's (1976) preliminary inventory of estuarine knowledge, there has been no review of New Zealand's coastal sedimentary ecosystems other than one on coastal oceanography and sedimentology and geomorphic classifications of estuaries (Hume & Herdendorf 1988, Hume et al. 1992, 2007). Comprehensive classifications of intertidal soft sediment habitats based on ecological data and demographic characteristics are available for other countries such as Australia (Edgar et al. 2000), but are conspicuously absent in New Zealand. Yet, classifications based on reliable baseline data are considered pertinent for the management and conservation of coastal ecosystems (Edgar et al. 2000).

The current review compiles existing information on macroinvertebrate assemblages in New Zealand intertidal soft sediment habitats, including those where seagrass, mangroves, and macroalgae occur (see also Chapters 3 and 4). In general, literature is reviewed in a north to south direction, with the exception of studies that incorporate information from different locations. Data on sheltered environments is reviewed separately to that of exposed beaches, owing to the profound differences in the characteristics

of these habitats.

5.1.1 Scope

This review is predominantly based on peer-reviewed papers published in scientific journals. Although soft-sediment data are also reported in “grey” literature documents (e.g., monitoring reports and students’ theses), these studies have not been peer-reviewed and are frequently difficult to access. Included publications are those that focus on intertidal macroinvertebrates in the framework of benthic assemblages.

In addition to the literature search conducted for the literature database (Chapter 2), a systematic search of published literature (including cross-references) was subsequently conducted, covering the earliest publication date (dependent on the journal) to 2007, using the following databases: Aquatic Sciences and Fisheries Abstracts (including Biological Sciences, Biology Digest, BioOne.1, Conference Papers Index, Ocean Abstracts, Scopus Natural Sciences), Science Direct.

Keywords were searched individually or in combination and included the following search terms: “macrobenth*”, “benth*”, “marine”, “sediment*”, “communit*”, “assemblage”, “composition”, “macroinverte*”, “New Zealand”, “coast*”, “estuar*”, “beach”, “inlet”, “bay”, “embayment”, “sand*”, “intertidal”, “tidal”, “mudflat/mud flat”, “sandflat/sand flat”, “seagrass”, “mangrove”, “infauna*”, “impact*”, “disturb*”, “pollut”, “contam*”, “impact”, “decline”, “eutrophic*”, “land-use/land use”, “non-native”, “non-indigenous”, “exotic”, “introduced”.

Additionally, author searches were conducted using names of prominent soft sediment ecologists in different New Zealand research organisations, e.g., S.F. Thrush, J.E. Hewitt – NIWA; C.A. Pilditch – University of Waikato; P.K. Probert – University of Otago.

5.2 Current state of knowledge

5.2.1 Assemblage diversity and distribution

There have been a considerable number of New Zealand studies of intertidal soft sediment macroinvertebrates, ranging from general descriptions of dominant species to quantitative assessments of assemblage compositions in relation to environmental variables (Oliver 1923, Ellis et al. 2006). Early studies (to approximately the early 1980s) were based on general observations of conspicuous animals and/or on transects along a particular gradient (Oliver 1923, Fincham 1977); they provide some information about macroinvertebrate assemblages, but are not necessarily representative of a location. More recent studies have applied more rigorous sampling designs and analytical statistical methods, which have allowed comprehensive evaluations of benthic assemblages (e.g., Turner et al. 1995, Thrush et al. 2003a, Ellis et al. 2006). The vast majority of studies have been geographically focused in the Auckland region, with research efforts predominantly centred in Manukau Harbour (e.g., Cassie & Michael 1968, Grange 1977, Pridmore et al. 1990.). At the same time, soft sediment research has been biased in favour of sheltered bays and inlets with macroinvertebrate assemblages of exposed beach environments remaining largely unstudied. Even for sheltered sedimentary habitats, available descriptive data are limited, as research efforts have been predominantly focused on particular forces that influence assemblages (e.g., pollution and human-caused disturbances, structuring organisms) or on specific groups of species (e.g., deposit- and suspension-feeders), and have frequently involved manipulative field experiments instead of mensurative studies (e.g., Roper et al. 1988, Norkko et al. 2002, Thrush et al. 2006). Descriptive (and at times comprehensive) data sets are included in past and current monitoring programmes, usually funded by regional authorities, however, these data have not been peer-reviewed and are often difficult to access (e.g., Estuarine Research Reports by Knox & Kilner 1973, Knox et al. 1977, 1978). As a consequence, descriptive data concerning the diversity and distribution of macrofaunal assemblages from intertidal sediments throughout New Zealand are limited to few locations. In addition, few studies have analysed benthic assemblages in a broader context to

elucidate generalities in assemblage patterns over different spatial or temporal scales (but see Turner et al. 1995, Thrush et al. 2000, Ellis et al. 2006, Berkenbusch & Rowden 2007). Recent ecological studies have applied survey data to the development of models to predict the probability of occurrence and densities of macrobenthic species in relation to habitat change (Thrush et al. 2003b, 2005). Whilst research efforts have predominantly focused on habitat degradation, New Zealand studies have largely overlooked ecological aspects concerning the significance and functioning of intertidal soft sediment assemblages. For example, there is little information available regarding trophic interactions (e.g., food web studies) and the productivity of intertidal soft shore macroinvertebrates in an ecosystem context.

5.2.1.1 Sheltered bays and inlets

5.2.1.1.1 An early New Zealand-wide study

An early account of benthic animals associated with different marine habitats was provided by Oliver (1923), who described littoral plant and animal communities from intertidal areas throughout New Zealand. His observations span a range of locations, including Parenga-renga Harbour (Northland), Cheltenham Beach/Rangiototo Channel (Auckland), Tauranga Harbour and Maunganui Beach (Tauranga), Avon-Heathcote Estuary (Canterbury), and Golden Bay (Stewart Island). Sedimentary habitats were broadly divided into exposed and sheltered environments, encompassing beaches, sand- and mudflats, and observed fauna were classified according to the most dominant species, resulting in broad classifications of different macroinvertebrates assemblages (termed “associations”) (Oliver 1923). In addition to unvegetated sedimentary habitats, Oliver (1923) also provided some information on dominant fauna associated with seagrass beds (“grass-wrack formation”), saltmarsh (“salt-reed swamp formation”) and mangroves (“mangrove formation”). Although his study was based on observations and not on detailed quantitative data, it provides a general overview of large macroinvertebrates that dominate biotic assemblages in different intertidal sedimentary habitats. The description of dominant-species associations from different locations showed that diversity and abundance of conspicuous species vary between some locations, but a number of species commonly occur in sedimentary habitats throughout New Zealand.

In the Auckland region, the large intertidal bay at Cheltenham Beach in Rangiototo Channel was characterised by a diverse assemblage of bivalves, burrowing polychaetes, brittle stars, crabs and gastropods, termed the “*Dosinia-Tellina* association” (Oliver 1923). The bivalves *Dosinia subrosea*, *Tellina* [*Macomona*] *liliana*, *Myodora* [*Myadora*] *striata*, *Antigona* [*Austrovenus*] *stutchburyi*, and *Amphidesma novae-zealandiae* [*Paphies* sp.] occurred commonly across the intertidal sandflat with *Callanaitis* [*Bassina*] *yatei*, *Mactra* [*Cyclomactra*] *ovata*, *Soletellina nitida* at lower abundance. Burrowing polychaetes included *Nephtys macrura* [*Algaophamus macroura*] and other unspecified species. The gastropods *Alcithoe arabica* and *Struthiolaria papulosa* were common at the low tide mark, whereas *Ancilla* [*Amalda*] *australis* was present across the intertidal area, with *Calliostoma pellucidum* and *Cominella adspersa* occasionally present. The hermit crab *Eupagurus novae-zealandiae* [*Pagurus novizealandiae*] was also common, with seastars *Patiriella regularis* and *Asterias* [*Coscinasterias*] *calamaria* restricted to the low-tide zone. Brittle stars such as *Amphiura aster* were rare and the burrowing ghost shrimp *Callinassa filholi* occurred at low abundances. An area vegetated by small mangroves at Shoal Bay was characterised by the burrowing mud crab *Helice crassa*, with the snail *Amphibola crenata* present on the sediment surface, and abundant freshwater snails, *Potamopyrgus antipodum* [*antipodarum*], *Phytia ornata* [*Ophicardelus*?] and small amphipods at the upper edge of the area.

Oliver (1923) reported the “*Antigona* association” from sheltered sedimentary environments in North and South islands, including the mudflats in Parengarenga Harbour, extensive sandy areas of Tauranga Harbour, and the (Avon-)Heathcote Estuary. This association was dominated by the New Zealand cockle *Austrovenus stutchburyi*, different species of burrowing crabs, and a number of different gastropods on the sediment surface. In Parengarenga Harbour, *Austrovenus stutchburyi* occurred at low abundances with *Helice crassa* in unvegetated areas, while the gastropods *Amphibola crenata*,

Cerithidea bicarinata [*Zeacumantus lutulentus*] and *Cominella lurida* [*glandiformis*] were common on the sediment surface. *Austrovenus* was also present on the extensive mud flats covered by seagrass (*Zostera*), but *Helice crassa* was replaced by the highly abundant stalk-eyed mud crab *Hemiplax* [*Macrophthalmus*] *hirtipes*; the small bivalve *Nucula hartvigiana* and the gastropods *Lepsiella scobina*, *Turbo smaragdus*, *Cominella glandiformis*, *Monodonta* [*Diloma*] *subrostrata*, and *Zeacumantus lutulentus* were also present. Gastropod shells were frequently colonised by the polychaete *Vermilia carinifera* [Serpulidae], the chiton *Acanthochiton zealandicus* [*Acanthochitona zelandica*], and the limpet *Crepidula crepidula* [*Maoricrypta monoxyla*].

In Tauranga Harbour, burrowing crabs included *Heterograpsus* [*Hemigrapsus*] *crenulatus* and *Macrophthalmus hirtipes*, which co-occurred with highly abundant *Austrovenus stutchburyi*, the wedge shell *Macomona liliana* (at low densities) and also large numbers of the gastropods *Zeacumantus lutulentus*, *Cominella glandiformis*, *Diloma subrostrata*, *Cominella adspersa*, *C. maculosa* and *Turbo smaragdus*. *Amphibola crenata* was abundant near the high-tide area. Associated fauna attached to mollusc shells included an unidentified sea anemone species, limpets *Crepidula crepidula* [*Maoricrypta monoxyla*] and *Notoacmea parviconoidea*, chitons *Amaurochiton glaucus*, and barnacles *Elminius modestus*. Extensive intertidal areas vegetated by *Zostera nana* [*muelleri*] supported a similar assemblage which also included *Helice crassa*, the small bivalve *Nucula hartvigiana*, and the gastropod *Neothais succinta* [*Thais orbita*] at the sediment surface. Feeding on seagrass leaves were the gastropods *Turbo smaragdus*, *Diloma subrostrata*, *Cantharidus tenebrosus huttoni* [*Micrelenchus tenebrosus*] and *Haminea zealandica* [*Haminoea zelandiae*]. Also attached to *Zostera* leaves were two unidentified species of sea anemone and the limpet *Notoacmea scapha*.

In unvegetated Avon-Heathcote Estuary mud flats, *Austrovenus stutchburyi* co-occurred with high numbers of *Helice crassa* and *Hemigrapsus crenulatus*, the less common bivalve *Cyclomactra ovata*, and at lower tidal levels the polychaetes *Scoloplos cylindrica* [*cylindrifer*] and *Aricia* [*Orbinia*] *papillosa*. The two crab species were also abundant on high-tide banks, with the amphipod crustacean *Melita inaequis* and the polychaetes *Nereis* [*Neanthes*] *kerquelenensis*, *Nephtys macrura* [*Algaophamus macroura*] and *Scolecoplepides benhami*. On the sediment surface, *Amphibola crenata*, *Monodonta corrosa* [*Diloma subrostrata*], and *Cominella glandiformis* were highly abundant with the limpet *Notoacmea pileopsis* occurring on larger shells; Oliver (1923) commented that the gastropod *Zeacumantus lutulentus*, which is part of this association at North Island locations is absent in this South Island estuary.

Sandflat areas covered by *Zostera* in Golden Bay, Stewart Island supported a relatively rich association which contained large-sized molluscs, namely *Austrovenus stutchburyi*, *Paphia intermedia* [current name unknown], *Amphidesma novae-zealandiae* [*Paphies* sp.], and *Macomona liliana*. The crab *Macrophthalmus hirtipes* was also present with the gastropods *Alcithoe arabica elongata* [*Alcithoe arabica*], *Trophon* [*Xymene*] *ambiguus*, *Monodonta atrovirens* [*Diloma zelandica*], and *Micrelenchus tenebrosus* on the sediment surface and on *Zostera* leaves (Oliver 1923).

Oliver's (1923) early description of characteristic macrofauna in different intertidal habitats was followed by a number of studies, mostly confined to single locations, that were based on quantitative data of benthic assemblages in a variety of soft sediment habitats. Quantitative data from ecological surveys and monitoring programmes have provided assessments of macroinvertebrate assemblage structure over different spatial and temporal scales, with the vast majority of studies located in Manukau Harbour.

5.2.1.1.2 Manukau Harbour, North Island

Early benthic studies in Manukau Harbour considered macroinvertebrate distribution in relation to sediment properties (Cassie & Michael 1968; Grange 1977; Pridmore et al. 1990). The first systematic study of the macroinvertebrate assemblage composition of Manukau Harbour was conducted by Cassie & Michael (1968), who examined benthic fauna across Karore Bank mud flats. Their study was the first of its kind in New Zealand, applying multivariate analysis techniques to elucidate the relationship

between benthic fauna and sediment properties; however, as the application of multivariate techniques was the main focus of their study, macrofaunal assemblages are not described in detail. Furthermore, the relatively large sieve size used (2.5 mm mesh) means that smaller-sized benthic fauna (i.e., polychaetes) were not included in their study. Nevertheless, the authors present data about dominant macrofaunal species and about sediment preferences of species associations. Twelve species were sufficiently abundant to allow numerical analysis across all stations, with a subset of eight species allowing correlations with sediment grain size. Abundant species were dominated by bivalves, *Chione* [*Austrovenus*] *stutchburyi*, *Macomona liliana*, *Amphidesma australe* [*Paphies australis*], *Nucula hartvigiana*, *Cyclomactra ovata*, *Solemya parkinsoni* [*parkinsonii*], *Soletellina siliqua* [*siliquens*], *Leptomya retiaria*, with the remainder composed of two crab (*Hemiplax* [*Macrophthalmus*] *hirtipes*, *Halicarcinus cookii*) and two tubiculous polychaete species (*Owenia fusiformis*, *Pectinaria australis*). Multivariate analysis identified two distinct assemblages, one characterised by *Austrovenus stutchburyi* and *Macomona liliana* (*Chione-Macomona*), including *Paphies australis* and *Nucula hartvigiana*, and the second assemblage defined by *Owenia fusiformis* and *Halicarcinus cookii* (*Owenia-Halicarcinus*), including *Leptomya retiaria*. Data were insufficient to assign the remainder species to existing or new assemblages. The *Chione-Macomona* assemblage appeared to favour coarse sediment whereas the latter assemblage was positively correlated with fine sediment, so that the authors concluded that the two assemblages are mutually exclusive. To support their conclusion, Cassie & Michael (1968) referred to two (unpublished) mud flat surveys in the Auckland region, at Hobson Bay and Whangateau (north of Auckland), that showed similar results: at Hobson Bay, one assemblage defined by *Austrovenus stutchburyi*, *Macomona liliana*, and *Nucula hartvigiana* was correlated with coarse sediments, whereas *Halicarcinus cookii* constituted a separate assemblage correlated with fine sediments; at Whangateau, sediments were uniformly coarse and only one assemblage was present, which was dominated by *Austrovenus stutchburyi* and *Macomona liliana*, and also contained *Paphies australis* and *Nucula hartvigiana* (Cassie & Michael 1968).

A subsequent study of intertidal macroinvertebrates and sediment properties in Manukau Harbour examined species composition and trophic structure in relation to sediment grain size to provide a baseline ecological survey across the harbour's extensive sand flats (Grange 1977). Sampling stations were spread across 17 different sandflat areas, covering different habitats but avoiding areas of potential industrial pollution. A total of 63 macroinvertebrate species (greater than 1 mm mesh) were identified and bivalves, gastropods, and polychaetes were the most diverse taxa (more than 12 species each). The bivalves *Macomona liliana*, *Chione* [*Austrovenus*] *stutchburyi*, *Soletellina siliqua* [*siliquens*], *Nucula hartvigiana*, the sea anemone *Anthopleura aureoradiata* (usually attached to hard substrates such as cockle shells) and the polychaete *Owenia fusiformis* were the most common species across stations (present at at least 20 out of 57 stations). Abundance data were not specified, but species were categorised into feeding guilds (deposit-, suspension-feeders, carnivores/scavengers or herbivores) to ascertain the optimum mean sediment grain size for each guild. Accordingly, deposit feeders appeared to favour finer sediment (fine sand), whereas suspension feeders favoured medium sand, with carnivores and scavengers preferring intermediate grades. There was a clear inverse relationship between the proportion of deposit feeders and sediment grain size, with most stations conforming to the trend of increasing deposit feeders abundance with decreasing sediment grain size (Grange 1977).

The sheltered habitats of six upper Manukau Harbour mud flats were studied as part of an examination of benthic macrofaunal assemblages in relation to runoff from different sub-catchments (Roper et al. 1988). There were a total of 39 taxa and significant differences in the number of taxa and of individuals between mudflat locations. The 11 most common taxa (based on their overall frequency of occurrence or their abundance at a particular location) were nemerteans, tubificid oligochaetes (principally two species, *Tubificoides fraseri* and *Limnodriloides* sp.), the polychaetes *Heteromastus filiformis*, *Paraonia* sp., *Prionospio* ?*aucklandica*, *Neanthes* ?*uniseriata*, the amphipods *Paracorophium excavatum*, *Proharpinia hurleyi*, the crabs *Helice crassa* and *Macrophthalmus hirtipes*, and the snail *Amphibola crenata*. Except for *Helice crassa*, all common taxa showed significant differences in abundance between locations, and the most abundant taxa (median abundance at least 25 individuals/core) were oligochaetes, *Heteromastus filiformis*, and *Proharpinia hurleyi*. One notable pattern was the within-site homogeneity and between-site heterogeneity of macrofauna assemblage

compositions. The authors noted that species richness of these mudflat assemblages was relatively low in comparison with Manukau Harbour sand flats, but considered the values comparable to those reported from intertidal mudflats in Australia and the United States (Roper et al. 1988). In their evaluation of intertidal benthic assemblages in relation to sediment toxicity, Nipper et al. (1998) included some general information about resident mudflat macrofauna in Manukau, Aotea and Raglan harbours, and also Okura and Tamaki estuaries. They reported a total of 59 taxa across all estuaries and sites were numerically dominated by nematodes, polychaetes (unidentified sabellid and capitellid species, *Scolecopides benhami*, *Nicon aestuarinensis*), the amphipod *Corophium* [*Paracorophium*] *lucasi*, the crab *Helice crassa*, the small bivalve *Arthritica bifurca* and the snail *Potamopyrgus estuarinus*. Analysis of benthic assemblage structure revealed distinct assemblages at each site, including those that were within the same estuary. The authors noted that assemblages were very similar to those reported by Roper et al. (1988), with similar within-site homogeneity and between-site heterogeneity as mudflat assemblages (Nipper et al. 1998).

Pridmore et al. (1990) also considered trophic group and sediment grain size in their comprehensive survey of intertidal macroinvertebrate assemblage composition and feeding guilds in Manukau Harbour. These authors conducted an intensive sampling programme to describe the variability of assemblage structure and densities of common taxa across different sand flats around the harbour. Sampling sites were selected remote from obvious pollution sources and were established as part of a regular, long-term monitoring programme in the harbour (Turner et al. 1995). In the initial 1987 survey, a total of 95 taxa (> 500 micron sieve) were identified, with 39–63 taxa present at each site and 29 taxa reported from Manukau Harbour for the first time (Pridmore et al. 1990). The distribution of individual taxa was similar across sites, but total number of individuals differed significantly between sites. Overall, the majority (69%) of individuals belonged to one of 8 species, the polychaetes *Heteromastus filiformis*, *Magelona ?dakini*, *Macroclymenella stewartensis* and *Goniada emerita* (27.0, 8.4, 5.1 and 2.8%, respectively), the bivalves *Tellina* [*Macomona*] *liliana*, *Nucula hartvigiana* and *Soletellina* [*siliquens*] (11.6, 7.4% and 4.0%, respectively), and the amphipod *Proharpinia hurleyi* (2.7%). These species were present at all sites, and *Heteromastus filiformis* was the most abundant species at all but one site, representing up to 50% of the total number of individuals; at other sites the distribution of individuals amongst taxa was more equitable. At the same time, rare species appeared to be present at all sites. Each site showed some variation in the 10 most abundant taxa, and relative abundance of dominant taxa differed significantly between sites, with polychaetes consistently more abundant than bivalves or amphipods. Multivariate assessment revealed that although sites shared a number of taxa, assemblage compositions differed markedly between sites. A distinct pattern noted by the authors was the presence of either polychaete- or bivalve-dominated assemblages, which was particularly evident at two sites where this pattern persisted over a period of at least one year. When distinguishing between feeding guilds, deposit feeders accounted for more than 70% of individuals at each site, and the relatively high proportion of suspension feeders at one site was solely attributed to the high abundance of *Austrovenus stutchburyi*. As all sites were mid-tidal sand flats with similar grain size, the authors suggested that other environmental factors than grain size or biological interactions may be reflected in the differences in assemblage composition (Pridmore et al. 1990). Subsequent studies conducted in Manukau Harbour suggested that wind-generated waves were the main factor controlling macrobenthic assemblages (Commito et al. 1995, Thrush et al. 1996)

Following the establishment and the initial sampling of sites in Manukau Harbour in 1987 (Pridmore et al. 1990), Turner et al. (1995) presented a comprehensive assessment of the stability of macrobenthic assemblages over the first 5.5 years (1987–1993) of the bi-monthly, long-term monitoring programme. As such it is the only published study that presents long-term data of New Zealand soft sediment assemblages. As data were based on the same locations, sampling methods, and frequent sampling occasions, the authors were able to evaluate the absolute and relative structural stability of infaunal assemblages in the harbour, while also incorporating environmental factors (e.g., wind-wave disturbance, water temperature). Their assessment shows that assemblages exhibited some short-term, seasonal and inter-annual variability, but overall assemblage structures were persistent over the study period. Sites supported distinctly different species compositions and abundances and these differences

remained evident over time. For example, the respective polychaete- and bivalve-dominated sites detected by Pridmore et al. (1990) retained the prevalence of either taxonomic group over time. Part of the differences in assemblage compositions appeared to be related to mean wind condition, reflecting physical disturbance through wind-generated waves. The authors concluded that five of the six sites were highly stable with the remaining site at an intermediate level of stability, owing to large population fluctuations (predominantly owing to short-lived polychaete species). They also considered that the stability exhibited by Manukau Harbour assemblages signifies some degree of resilience, as macrofauna assemblages retained their original compositions over time in spite of different types and magnitudes of physical disturbance and major recruitment events (Turner et al. 1995).

5.2.1.1.3 Auckland region, North Island

Another study of urban runoff in the Auckland region examined macrobenthic assemblages in similar habitat in four different estuaries (or sub-estuaries of larger system), for which little information concerning intertidal macrofauna is otherwise available (Morrissey et al. 2003a). The study included two urbanised and two non-urbanised estuaries: Hellyers Creek/Upper Waitemata Harbour and Pakuranga/Tamaki Estuary in urbanised locations, and Te Matuku Creek/Waiheke Island and Paremoremo Creek/Upper Waitemata Harbour in predominantly rural/native forest catchments. Macrofauna were sampled twice, in 1995/1996 followed by a less comprehensive sampling regime in 1997. The total number of macrofauna taxa (>500 micron sieve) in each estuary was similar with highest values recorded at Te Matuku and Paremoremo creeks (3.0–12.8 taxa/core). Highest average densities were documented at Paremoremo Creek (46–240.7 individuals/core) with lowest values at Pakuranga (8.3–44.5 individuals/core), but there was no statistical difference in this community parameter overall, most likely owing to the large within-site variability of abundance data. On both sampling occasions, the composition of faunal assemblages at Te Matuku Creek was significantly different to that at the other three estuaries, and in 1995/1996 macrofauna assemblages at Paremoremo Creek were also distinctly different to the other locations. Dissimilarities between sites varied between 66.1% and 88.9% and the greatest differences were evident between Te Matuku Creek and the other sites. The same taxa contributed to differences in assemblage composition between estuaries and the five taxa that contributed the most to dissimilarities in each estuary included the bivalves *Arthritica bifurca*, *Austrovenus stutchburyi*, non-native *Theora lubrica*, oligochaetes, the polychaetes *Cossura* sp. 1, *Paraonid* sp. 1, polydorid spionids, capitellids, nereids, and *Prionospio aucklandica*, the corophiid amphipod sp. 1, and *Helice crassa*. These taxa were generally present in all estuaries, but relative abundances varied between estuaries, and the only discernible pattern was the relatively higher abundance of several taxa in Paremoremo Creek. In addition to differences between estuaries, benthic assemblages also showed a high degree of variability within each estuary over different spatial scales (metres to 100s of metres). Within-site differences were largest in Pakuranga and Paremoremo Creek and differences were mostly determined by the relative abundances of the majority of taxa that also largely influenced between-site differences (Morrissey et al. 2003a).

Okura Estuary, a marine reserve north of Auckland, was the location of two studies (one mensurative, one experimental) that determined benthic infaunal assemblages (greater than 500 micron) in relation to sediment deposition (Norkko et al. 2002, Anderson et al. 2004). Anderson et al. (2004) describe mid-intertidal assemblage compositions from three different depositional regimes within the estuary, including a number of environmental variables that may influence assemblage patterns. Macrofauna assemblages were represented by a total of 73 taxa and showed a clear separation between areas of different depositional environments, with the largest separation between macrofauna at high depositional sites, compared with low and medium ones. Taxa that showed higher abundances at the latter environments were the bivalves *Austrovenus stutchburyi*, *Nucula hartvigiana*, *Paphies australis*, the gastropod *Cominella glandiformis*, the chiton *Sypharochiton pelliserpentis*, the limpet *Notoacmea helmsii* [helmsi], the barnacle *Elminius modestus* and the sea anemone *Anthopleura* sp. Assemblages at these sites were also characterised by the presence or greater abundance of several crustaceans, including the amphipods *Waitangi* sp., *Paracallioppe* sp., Phoxocephalid sp., the cumacean *Coloristylis lemurum*, the crab *Halicarcinus* sp., and several polychaetes including *Prionospio* spp., *Macroclomenella stewartensis*, *Aonides* sp., and other syllids. In comparison, assemblages in areas

considered to experience high sediment deposition were primarily characterised by greater relative abundances of oligochaetes, polychaetes, including nereids, *Cossura coasta*, *Notomastus* sp., *Glycera lamellipoda* and other glycerids, *Boccardia* spp., *Scoloplos cylindifer* [*cylindrifer*] and other orbinids, *Polydora* spp., pectinarids, and crabs, *Helice* sp. and *Macrophthalmus* sp. A significant proportion of the variation in assemblage composition was explained by the total amount and grain size characteristics of trapped sediment (as a measure of sedimentation) and the authors concluded that the deposition of small amounts of sediment have an important influence on intertidal estuarine macrobenthic assemblages (Anderson et al. 2004). Also in Okura estuary, Norkko et al. (2002) monitored the response of intertidal benthos to the experimental deposition of thick (3–9 cm) layers of fine terrigenous sediment at a sheltered muddy sand habitat and an exposed sand flat. Data from un-manipulated control sites provide general information about macrofaunal assemblages (>500 micron mesh) and reveal that both types of habitat shared some of the 10 most dominant taxa, namely *Nucula hartvigiana*, *Macomona liliana*, *Austrovenus stutchburyi*, *Aquilaspio aucklandica*, *Scoloplos cylindrifer*, Orbinidae, Paracalliopiidae. Dominant taxa at the sheltered site also included Nereidae, Oligochaeta, and *Anthopleura aureoradiata*, and this habitat was numerically dominated by polychaetes (42% of total macrofauna abundance) with *Aquilaspio aucklandica* the most common species. Taxa exclusive to the exposed site included *Paphies australis*, *Scolecopsis* sp., and *Aonides oxycephala*, and bivalves were the most abundant macrofaunal group (49%). The mud crab *Helice crassa* occurred at both sites throughout the estuary. The authors noted that there were fewer taxa at the sheltered than at the exposed site and highest abundances of taxa and individuals were recorded in the top 2 cm of the core compared with 2–15 cm sediment depth.

Related studies also assessed sedimentation effects in North Island estuaries, but as these studies were specifically aimed at assessing the response of macrofauna to terrestrial sediment deposits, general information on macrofaunal assemblages is limited to the reporting of dominant taxa only (Cummings et al. 2003, Hewitt et al. 2003, Thrush et al. 2003a, Lohrer et al. 2004b). In Whangapoua Harbour (Coromandel Peninsula), the five most dominant taxa at different intertidal sites along a wave gradient on the intertidal sand flat included oligochaetes, different species of polychaetes, bivalves and crustaceans (cumaceans and amphipods). There was variation between sites and sampling times, but dominant species consistently included oligochaetes, the polychaetes *Aquilaspio aucklandica*, *Lumbrineris brevicirris* [*Scoletoma brevicirra*], Nereidae, the bivalve *Nucula hartvigiana*, and Lysianassidae amphipods (Hewitt et al. 2003). Similarly, Cummings et al. (2003) reported the following dominant species from mid-tidal sand flats in the same estuary: the polychaetes *Aquilaspio aucklandica*, *Aonides oxycephala*, *Prionospio* sp., *Aglaophamus* sp. and nereids, and bivalves were also common, including *Nucula hartvigiana*, *Austrovenus stutchburyi*, and *Macomona liliana*. Thrush et al. (2003a) conducted their study in Whitianga Harbour (also Coromandel Peninsula) and common species at this location also included oligochaetes and *Aquilaspio aucklandica*, but also the polychaetes *Aonides oxycephala*, *Heteromastus filiformis* and *Scoloplos cylindrifer*, the bivalves *Austrovenus stutchburyi* and *Arthritica bifurca*, and the amphipod *Paracorophium* sp. In the Whitford embayment/Auckland, two study sites at mid-tidal level were distinguished by the presence or absence of live *Austrovenus stutchburyi*, empty shells and shell fragments (Lohrer et al. 2004). At the site without *Austrovenus stutchburyi*, common taxa (more than 10 individuals/core) included *Aonides oxycephala*, *Macomona liliana*, *Orbinia papillosa*, *Aquilaspio aucklandica*, and Paracalliopidae amphipods. The same taxa, except for the first two species, also occurred commonly at the site that contained abundant *Austrovenus stutchburyi*, in addition to *Scoloplos cylindrifer*, *Heteromastus filiformis*, *Nucula hartvigiana*, and the limpet *Notoacmea helmsi* (Lohrer et al. 2004b).

5.2.1.1.4 Other North Island locations

Wood (1963) conducted a qualitative survey of intertidal macrofauna on the sand flats of Marakopa Estuary, on the west coast of North Island for an estuarine-open beach comparison. Macrofaunal species (greater than 1.25 mm) were identified from a number of sites within the estuary including rocky areas, but individuals were not counted, so that no quantitative data were presented. Soft sediment macrofauna included *Amphidesma* [*Paphies*] *australis*, the mud snail *Amphibola crenata*, the freshwater snail

Potamopyrgus zelandica [antipodarum], the polychaetes *Aglaophamus macrura* [macroura], *Glycera* ?*tessalata*, *Nicon* sp., a large number of crustaceans, including *Helice crassa*, *Callianassa filholi*, a mysid shrimp, a calliopiid and an unidentified amphipod, the isopods *Pseudaega punctata* and *Scyphax ornatus*, and the beach hopper *Talorchestia* sp. In conclusion, Wood (1963) commented on the occurrence of different species throughout the estuary and suggested that the species distribution was determined by differences in salinity.

An experimental study of the effect of deposit feeding by *Macomona liliana* on sediment stability on Tuapiro sandflat in Tauranga Harbour briefly mentions a number of taxa (retained on a 0.92-mm mesh sieve) that were present in the study plots (Lelieveld et al. 2004). Apart from *Macomona liliana*, macrofaunal species included *Austrovenus stutchburyi*, the polychaete *Aglaophamus macroura*, *Aquilaspio* sp., and *Orbinia papillosa*. The remaining taxa were indicated as families only and included the polychaete families Maldanidae, Nereidae, Pisionidae, Polynoidae, and the gastropod families Cominellidae, Cerithiidae, and Trochidae.

In the south of North Island, Pauatahanui Inlet was part of the most comprehensive, multidisciplinary study conducted in a New Zealand estuary to date (Healy 1980). As part of the biological component, intertidal macrofauna (greater than 1 mm) were sampled at 37 sites in the inlet and assemblage types were broadly categorised in relation to sediment grain size. Although no quantitative data were presented, macrofaunal assemblages were described in relation to different sedimentary habitats within the inlet. Overall, 37 different species were identified, of which 13 occurred at at least 40% of sites. The most abundant species was *Chione* [*Austrovenus*] *stutchburyi*, which was present at all sites, reaching densities of up to 2500 individuals/m² across the intertidal zone. Other common species were *Tellina* [*Macomona*] *liliana*, *Nucula hartvigiana*, gastropods *Amphibola crenata*, *Zeacumantus lutulentus*, *Diloma subrostrata subrostrata*, *Cominella glandiformis*, polychaetes *Axiiothella* sp. and *Scolecopides benhami*, and crabs, *Helice crassa*, *Macrophthalmus hirtipes*, and *Halicarcinus varius*. Pairwise analysis of similarity identified three distinct assemblage types which shared a number of common species but were distinctly different and characterised by different sediment types and the presence of seagrass, *Zostera capricornii* [muelleri]. Fine sediments at the head of the inlet and adjacent to major streams were dominated by *Nucula hartvigiana*, *Macomona liliana*, the polychaetes *Capitellethus* sp., *Axiiothella* sp., and *Austrovenus stutchburyi*. The latter species occurred at very low densities whereas *Axiiothella* sp. reached densities of almost 500 individuals/m². Assemblages associated with coarse sand were defined by *Austrovenus stutchburyi*, *Amphibola crenata* and *Diloma subrostrata*, with *Cominella glandiformis* frequently occurring in large groups. The mud crabs *Macrophthalmus hirtipes* and *Helice crassa* were present in the lower and upper intertidal zone, respectively, whereas the occurrence of other crab species, *Hemigrapsus crenulatus*, *H. edwardsi*, and *Cyclograpsus lavauxi* was dependent on the presence of rocks. In coarse and gravel sediments, *Paphies australis* replaced *Austrovenus*, but was mostly restricted to one area within the inlet. The sea anemone *Anthopleura aureoradiata* was present on cockle shells in high salinity areas close to the estuary mouth, whereas the small polychaete *Boccardia* (*Paraboccardia*) *syrtis* [*Boccardia syrtis*] inhabited cockle shells throughout the inlet. The third assemblage type was associated with extensive seagrass (eel grass) beds, which were predominantly on the eastern end of the inlet, with scattered beds in most areas and on the offshore sandbank. *Austrovenus stutchburyi* and *Macomona liliana* were also common in this assemblage, which was characterised by high densities of the topshell *Microlenchnus* [*Micrelenchnus*] *tenebrosus*, the limpet *Notoacmea helmsi*, *Zeacumantus lutulentus*, bubble shell *Haminoea zelandica* [zelandiae], and the commonly occurring polychaete *Aglaophamus macroura*. When distinguishing by trophic group, the majority of species were either deposit- or filter-feeders with the former group favouring fine sand and mud and the latter preferring coarse sediments. Assemblages at most sites agreed with this general trend and three sites that did not conform were considered unstable or under stress. For the remainder of sites in the inlet, it was concluded that assemblages compared favourably with similar ones in harbours throughout New Zealand (Healy 1980). Read (1984) conducted a quantitative survey of intertidal polychaetes on the sheltered sand flat of upper parts of Pauatahanui Inlet and reported 47 species of macrofauna (greater than 500 micron), which included 22 polychaete species. The 14 most common species (present in more than 10% of cores) included *Austrovenus stutchburyi*, *Macomona liliana*, Oligochaete sp., 2, a nemertean species, and nine polychaetes, *Microspio maori*, *Capitella* sp.,

Heteromastus filiformis, *Axiothella serrata*, *Boccardia acus*, *Boccardia syrtis*, *Scolecopides benhami*, *Nicon aestuariensis*, *Paradoneis* sp. *Microspio maori* was the most frequent and abundant species, with a 20% higher occurrence than the next ranked *Capitella* sp. The author noted that the macrofauna assemblage was dominated by deposit-feeders, representing 95% of individuals and 32 species, including 8 of the most common species (Read 1984).

5.2.1.1.5 South Island

Davies (1931) describing the distinct characteristics of tidal mud flats in Nelson Haven only commented that molluscan and other animal life was poor, i.e., in areas exposed at low tide. Another inlet in the same area, Delaware Inlet near Nelson, was subject of a general survey by Stanton et al. (1977). The authors surveyed substrate type, flora and fauna of the intertidal sand flat and also collected data on water salinity and nitrogen content. The general description of dominant intertidal macrofauna was limited to four different mollusc species, which included *Amphibola crenata*, *Chione* [*Austrovenus*] *stutchburyi*, *Paphies australe* [*australis*] and the mussel *Mytilus edulis* (on hard substrate, i.e., cobbles). The distribution of molluscs was related to distinct habitats broadly defined by the substrate type. Accordingly, *Amphibola crenata* was dominant at the sediment surface across large high intertidal areas of the inlet, where sediment was muddy and appeared to contain a high amount of fine detritus. In contrast, *Austrovenus stutchburyi* reached high densities in low intertidal areas, adjacent to main channels, in mud, sand and fine gravel; densities decreased with an increase in surface exposure. *Paphies australis* was less widespread than the previous two species and only occurred in two small areas which were briefly exposed at low tide and characterised by coarse sand and fine gravel; at one site this species co-occurred with high densities of *Austrovenus* (Stanton et al. 1977).

Also in the north of the South Island, Stephenson (1978) studied intertidal macrofauna and heavy metals in four mollusc species at Waikawa Bay/Marlborough Sounds. The distribution of benthic macrofauna was assessed quantitatively across the entire intertidal area, covering different habitats in regards to sediment type, vegetation cover and tidal zone. A total of 41 macrofaunal species were recorded with the greatest number of species present in areas vegetated by seagrass (*Zostera* sp.) with a sand/silt substrate. The common species of this habitat type included the bivalves *Nucula hartvigiana* and *Solemya parkinsonii*, the gastropods *Notoacmea helmsi*, *Turbo smaragdus* and *Diloma subrostrata* [*Diloma subrostrata*], the crabs *Halicarcinus whitei* and *Hemigrapsus crenulatus*, and the polychaetes *Glycera americana* and *Platynereis australis*. *Austrovenus stutchburyi* was the most prominent species and present at most sampling sites (24 of 29), reaching a maximum density of up to 2800 individuals/m². *Amphibola crenata* was the characteristic species at mid-tide level and although tidal position and substrate type appeared to influence the species distribution, Stephenson (1978) noted that assemblage structure across the bay varied relatively little.

A survey of benthic fauna of sheltered intertidal areas at Farewell Spit, northwest South Island provides a general description of common species (Anderson et al. 1978). A total of 29 taxa were distinguished and abundances of different macrofaunal taxa (unspecified mesh size) and the presence of seagrass (*Zostera*) were described in general terms according to shore height. With the exception of the lugworm *Abarenicola affinis*, polychaete species were listed but only reported in generic terms without distinguishing between species; they encompassed *Aglaophanius macroura*, *Axiothella quadrimaculata*, *Glycera* sp., *Hemipodus* sp., *Lepidasthenia* sp., *Magelona papillicornis*, *Orbinia papillosa*, *Perenereis nuntia*, *Platynereis australis*, *Scolecopsis* sp., and *Travisia olens*. Other taxa included the sea cucumbers *Trochodota dendyi*, nemertines, *Amaurochiton glaucus*, *Chione* [*Austrovenus*] *stutchburyi*, *Cominella adpersa* and *C. glandiformis*, *Macomona liliana*, *Paphies australe* [*australis*], *Zeacumantus lutulentus*, *Zediloma atrovirens* [*Diloma zelandica*], an unidentified amphipod, unidentified shrimps, *Talorchestia quoyana*, *Eliminus modestus*, an unidentified spider crab, *Hemiplax* [*Macrophthalmus*] *hirtipes*, and *Edwardsia tricolor* [N.B. The latter species was reported as a sea anemone and therefore likely to be *Anthopleura aureoradiata*.] The burrowing sandhopper *Talorchestia quoyana* only occurred in the upper beach zone of the inlet (including above high water). The sheltered intertidal sand flat was characterised by scarce seagrass on the upper shore, with dense

patches turning into dense seagrass mats c. 800–900m from the shore, extending into the lower intertidal zone. Taxa common in the intertidal area were *Abarenicola affinis* (mostly close to shore) and other polychaetes, nemertines, an unidentified amphipod, unidentified shrimps, *Paphies australis*, *Austrovenus*, *Diloma zelandica* and both *Cominella* species. *Trochodonta dendyi* and *Macomona liliana* were present in the lower intertidal zone and as seagrass cover increased, an unidentified spider crab and the mud crab *Macrophthalmus hirtipes* became common, together with both *Cominella* species. *Diloma zelandica*, *Macomona liliana*, and *Austrovenus* were the dominant species where seagrass cover was dense and *Zeacumantus lutulentus* was also present at low densities. The authors also noted that gastropod and bivalve shells in the lower intertidal area were colonised by barnacles, *Elminius modestus*, chitons *Amaurochiton glaucus*, with the sea anemone *Edwardsia tricolor* [see above note] commonly occurring on cockle shells (Anderson et al. 1978).

In the Canterbury region, the Avon-Heathcote Estuary has been recognised as being substantially affected by urban and industrial development, however, published data on intertidal macroinvertebrates are restricted to a single, early account of assemblages in different habitat types of the estuary (Morgans 1969, Stephenson 1980). Morgans (1969) provides a brief summary of intertidal macrofauna in Avon-Heathcote Estuary in regards to different substrate types and tidal level. Although a number of species were shared amongst habitats, the author noted that different macrofaunal assemblages were characteristic for each habitat type. Assemblages were defined by differences in abundance of common species and the presence or absence of others. At the entrance of the estuary (mouth and channel), the substrate consisted of clean sand and supported *Amphidesma australe* [*Paphies australis*] and *Chione* [*Austrovenus*] *stutchburyi* (both in the low intertidal and including *Elminius modestus* on their shells), the polychaetes *Glycera americana*, *Lumbrineris sphaerocephala*, *Scolecopides benhami*, *Perinereis nuntia*, *Algaophamus macroura*, *Orbinia papillosa*, nemertines and low densities of the burrowing ghost shrimp *Callinassa filholi*. The crabs *Hemigrapsus crenulatus* and *Helice crassa* were also present; the latter species and the gastropods *Zediloma* [*Diloma*] *subrostrata*, *Amphibola crenata*, and *Cominella glandiformis*, were recorded at highest densities in this type of habitat. The muddy sands of the lower estuary contained a characteristic assemblage of abundant *Paphies australis*, *Austrovenus stutchburyi*, and *Macomona liliana*. Polychaetes included *Abarenicola affinis*, with *Haploscoloplos* [*Scoloplos*] *cylindrifer*, *Scolecopides benhami*, *Perinereis nuntia*, *Glycera americana*, and *Aonides* sp. occurring at high densities. *Hemigrapsus crenulatus*, *Helice crassa* and *Hemiplax* [*Macrophthalmus*] *hirtipes* were common, with *Diloma subrostrata* and *Cominella glandiformis* prominent at the sediment surface and *Anthopleura aureradiata* attached to shells and pebbles. In comparison with the aforementioned substrate types, Morgans (1969) considered the sandy mud and muddy habitat of the middle estuary extremely fauna-rich and noted that the low tide area was dominated by polychaetes, in particular high densities of *Boccardia polybranchia* and *Nicon aestuariensis*, and different species of nemertines. *Amphibola crenata* was also common and extremely abundant in the mid-intertidal zone, whereas *Boccardia polybranchia* was replaced by *Scolecopides benhami* at this tidal level. *Helice crassa* and *Macrophthalmus hirtipes* were also present, as was *Austrovenus stutchburyi*. The muddy sand of the upper intertidal areas was inhabited by *Cyclomactra ovata*, sipunculid worms, *Macrophthalmus hirtipes*, *Helice crassa*, and nemertines. One area in this habitat which consisted of anoxic mud supported an abundant fauna of *Amphibola crenata*, *Diloma subrostrata*, *Cominella glandiformis*, *Macrophthalmus hirtipes*, *Helice crassa*, *Austrovenus stutchburyi*, *Macomona liliana* and several of the aforementioned species of polychaete. The upper estuary mud flats were characterised by a similar assemblage to that present at muddy sand sites, with low numbers of *Austrovenus stutchburyi* and *Amphibola crenata*, nemertines, several polychaete species, crabs (*Hemigrapsus crenulatus*), and *Cyclomactra ovata* in the high shore sandy areas (Morgans 1969).

General data of macroinvertebrates in estuaries and inlets in the Otago region are available through quantitative studies that examined benthic assemblages in relation to particular structuring forces, such as sediment enrichment and organisms that influence associated macrofauna (Ford et al. 1999, Berkenbusch et al. 2000). Ford et al. (1999) studied macrofaunal recolonisation of sediments in Papanui Inlet following defaunation and sediment enrichment by alga (*Ulva* spp.). Macroinvertebrates (larger than 500 micron) at the intertidal sand flat site encompassed 37 taxa with two numerically dominant

species, the small bivalve *Perrierina turneri* and the amphipod *Paracorophium excavatum*, representing at least 88% of all individuals. Adult and juvenile *Paracorophium excavatum* largely influenced the recolonisation of defaunated plots and taxa that were consistently important in distinguishing between treatments were *Perrierina turneri*, juvenile *Austrovenus stutchburyi*, *Edwardsia* sp. and *Torridoharpinia hurleyi*, all of which were more abundant in control plots than in experimental ones. Rare species (fewer than 1 individual per core), the spionid polychaetes *Scololepides* [*Scolecopides*] *benhami* and *Boccardia syrtis*, and the amphipod *Torridoharpinia hurleyi* showed seasonal differences in abundance, with significantly higher densities in winter than summer (Ford et al. 1999). Berkenbusch et al. (2000) conducted a mensurative study to assess macroinvertebrate assemblages in relation to burrowing ghost shrimp. Assessing the impact of ghost shrimp bioturbation over a small spatial scale (tens of metres) and seasons showed that macrofaunal assemblages (larger than 500 micron) at an intertidal Otago Harbour sand flat differed significantly in relation to ghost shrimp density, with differences persisting throughout the year. The total number of species and of individuals was significantly lower at high-density than low-density ghost shrimp sites, and macrofaunal assemblages differed significantly between different ghost shrimp density sites. Six taxa (of a total of 56) contributed the most (50%) to observed dissimilarities throughout seasons and included *Perrierina turneri*, *Paracorophium excavatum*, Tanaidae 1, Syllidae 1, Enchytraeidae, Tanaidae 2, and *Paracallioppe novizealandiae*. The former two species appeared to have the greatest influence on dissimilarities throughout the year and both species showed higher densities at low-density ghost shrimp sites, which the authors attributed to the lower level of sediment disturbance at these sites.

5.2.1.1.6 Assemblages of vegetated habitats

An early study of macroinvertebrates in the Auckland region examined intertidal fauna at eight sites in Manukau Harbour in relation to nutrient enrichment and the presence of macroalgae, seagrass and mangroves (Henriques 1980). Quantitative sampling was conducted at different habitats and included bare sites, dense algal mats (*Gracilaria secundata* var. *pseudoflagellifera*) [possibly *Gracilaria chilensis*, see Chapter 4], dense seagrass (*Zostera muelleri*), and mangroves (*Avicennia resinifera* [*marina* subsp. *australasica*]), and some of the sites also differed in their proximity to pollution sources (sewage oxidation ponds, industrial discharge). Macrofaunal samples were sieved on a relatively large mesh size (6.25 mm) so that only large-sized macrofaunal species were considered and polychaetes were notably absent as sites were characterised by different bivalves, gastropods and crustaceans. A number of species commonly occurred at all sites, including *Chione* [*Austrovenus*] *stutchburyi*, *Macomona liliana*, *Helice crassa*, *Cominella glandiformis*, *Zeacumantus lutulentus* and *Zediloma* [*Diloma*] *subrostrata* and there was no difference in assemblage structure between bare sites and those containing *Gracilaria* meadows. Mangrove and seagrass habitats revealed a higher total number of species and a more even distribution of individuals among species than comparable unvegetated areas, and mangrove habitat also supported a higher total number of individuals (Henriques 1980).

Two recent investigations in Auckland estuaries examined differences in benthic fauna in relation to the age of mangrove stands and to different levels of sedimentation, respectively (Morrissey et al. 2003b, Ellis et al. 2004). These studies do not provide a comparison between mangrove and unvegetated habitats, but present some general information on mangrove macrofauna in New Zealand. At Puhinui Creek, a sub-estuary of Manukau Harbour, mangrove stands of two different age classes showed clear differences in sediment characteristics and associated benthic macrofauna (Morrissey et al. 2003b). Common taxa included *Helice crassa*, the copepod *Hemicyclops* sp., oligochaetes, *Nicon aesturinus* [*aestuarensis*], *Capitella capitata*, *Scolecopides benhami*, and *Potamopyrgurus antipodarum*, and infaunal assemblage compositions were distinctly different between mangrove age classes. The total number of individuals did not differ significantly, but the total number of taxa and densities of several of the common taxa showed significant differences between young and old mangrove stands, generally with higher numbers at less established mangrove sites. The authors related these differences to the maturing of mangroves and the concomitant compaction of sediments causing a decrease in species abundance and diversity and a possible shift from benthic assemblages to fauna associated with mangrove plants, such as insects and spiders (Morrissey et al. 2003b). Ellis et al. (2004) quantified macrobenthic assemblages at Mangemangeroa and Waikopua estuaries in the Whitford embayment in

regards to the impact of terrigenous sedimentation. Sampling sites encompassed a range of sedimentation rates and biotic factors, ranging from high depositional environments characterised by fine mud in the sheltered, upper parts of both estuaries to sandy sites that had no net accumulation of terrigenous sediment in the lower parts of the estuaries. Benthic assemblage compositions differed significantly between sites, with upper estuary sites dominated by corophiid amphipods and Paracalliopidae sp., oligochaetes, the crabs *Halicarcinus whitei* and *Helice crassa*. Lower estuary sites were characterised by several bivalve species, *Paphies australis*, *Macomona liliana*, *Austrovenus stutchburyi* and *Nucula hartvigiana*, the limpet *Notoacmea helmsii* [helmsi] and the isopod *Exosphaeroma chilensis*. Comparing the mangrove sites to unvegetated habitats in the same estuaries, these authors observed that diversity and abundance of benthic mangrove assemblages were lower than those at intertidal sand flat sites, but comparable to those of adjacent mud flat areas (Ellis et al. 2004).

Macrofaunal assemblages associated with seagrass beds have received considerable ongoing attention for a numbers of years in studies overseas (e.g., Orth et al. 1984, Boström et al. 2006), yet similar research in New Zealand's seagrass habitats has been limited to few studies (Turner et al. 1999, van Houte-Howes et al. 2004, Berkenbusch & Rowden 2007). Two studies examined benthic macrofaunal assemblages associated with seagrass *Zostera novazelandica* [muelleri] across different spatial scales in North Island estuaries (Turner et al. 1999, van Houte-Howes et al. 2004). Turner et al. (1999) studied benthic assemblages associated with *Zostera muelleri* across different spatial scales in two estuaries, encompassing a range of environmental variables. Sites included one sheltered and one exposed area in Manukau Harbour and a sheltered seagrass area in Whangapoua Harbour/Coromandel Peninsula. Their study revealed significant differences in numbers of individuals and species, species richness, diversity and evenness, with generally higher values for all community measures inside seagrass patches. Differences in assemblage compositions were also evident, and estuary assemblages associated with seagrass were generally distinctly different from those associated with bare sediment, at times dependent on the position of the latter in relation to the seagrass area. Species that were consistently important in distinguishing between seagrass and bare habitats were *Macomona liliana*, *Austrovenus stutchburyi*, and *Aonides trifidus* at the exposed Manukau Harbour site, capitellid polychaetes, *Boccardia syrtis* and *Macomona liliana* at the shelter site, *Prionospio aucklandica* and oligochaetes at Whangapoua Estuary. All of these taxa were generally more abundant in seagrass habitat than in bare sediments. Assessment of differences across spatial scales showed that patch-scale characteristics (e.g., patch-size, seagrass biomass and percentage cover) did not affect macrofaunal assemblage composition, but the spatial patterning of the seagrass habitat (e.g., fractal geometry, patch isolation) at the landscape scale played a role in determining assemblage patterns (Turner et al. 1999). Van Houte-Howes et al. (2004) compared macrofaunal assemblage compositions between unvegetated areas and seagrass beds across three different Coromandel estuaries, Whangamata, Wharekawa and Whangapoua harbours, and sampling sites within each estuary were at different distances to the edge of the seagrass bed. The total abundance, number of species and diversity of macrofauna differed significantly between estuaries and sites, but there was no consistent pattern of seagrass beds affecting these community measures. The most abundant taxa at each estuary were similar across estuaries and included the bivalves *Austrovenus stutchburyi*, *Arthritica bifurca*, *Macomona liliana*, *Nucula hartvigiana*, the polychaetes *Aonides oxycephala*, *Aquilaspio aucklandica*, *Heteromastus filiformis*, *Magelona dakini*, Nereidae spp., *Scolecopides benhami*, oligochaetes, Gammaridae spp., *Protophoxus australis*, the crab *Halicarcinus whitei*, *Eliminius* [Elminius] *modestus*, and *Anthopleura aureoradiata*. Macrofaunal assemblage compositions were similar at sites of high seagrass biomass across estuaries and high-biomass sites at the edge of the seagrass bed supported distinctly different assemblages to other sites. Differences in assemblage composition were primarily owing to small changes in the relative abundance of dominant taxa and the authors suggested that the absence of deep-burrowing polychaetes and low densities of bivalves at sites of high seagrass biomass may be related to dense root-rhizome material precluding these animals (van Houte-Howes et al. 2004).

Berkenbusch & Rowden (2007) examined the generality of macrofauna assemblage patterns in relation to the presence of seagrass *Zostera capricorni* [muelleri] and burrowing ghost shrimp *Callinassa filholi* across three tidal inlets in Otago, at Otago Harbour, Blueskin Bay and Papanui Inlet. They recorded a total of 54–64 infaunal taxa (500 micron mesh) in this region of which 41 taxa were present

at each location. Multivariate analysis showed that assemblages were distinctly different between inlets but showed a general pattern of dissimilarity between ghost shrimp and seagrass sites across inlets. Assemblages at sites that contained both organisms were similar to those at seagrass sites with approximately 67% dissimilarity evident between assemblages at ghost shrimp and seagrass sites. Taxa that contributed the most to these differences were the polychaetes *Paraonidae* sp. 1, *Aquilaspio aucklandica*, *Exogone* sp. 1, Capitellidae sp. 1, oligochaetes, the amphipods *Protophoxus australis*, *Paracalliope novizealandiae*, *Paracorophium excavatum*, *Protophoxus australis*, and small bivalves *Nucula hartvigiana*, *Perrierina turneri*, *Puyseguria tani*. Differences in assemblage composition were owing to differences in relative abundances of taxa, with different species showing a prevalence for either seagrass or ghost shrimp sites (Berkenbusch & Rowden 2007).

Alfaro (2006) compared macrofaunal assemblages across different habitat types within unvegetated, mangrove and seagrass areas in Matapouri estuary, northeast of Whangarei and identified a high overall macrofaunal diversity in the estuary. Seagrass beds supported the highest number of individuals and taxa of all habitat types, with mangroves reflecting the lowest values. Each habitat type was characterised by a distinct assemblage composition, with several species commonly occurring at all sites. Common species included the bivalves *Paphies australis* and *Austrovenus stutchburyi* which occurred in all habitat types but with varying densities, with the former species most abundant in sand flat habitats and the latter preferring seagrass beds. Crabs, shrimp (both unspecified) and grazing snails (*Turbo smaragdus*, *Diloma subrostrata*, *Melagraphia aethiops*) were also most abundant in seagrass beds, whereas oligochaetes revealed highest densities in unvegetated habitat types; amphipods occurred at highest numbers in unvegetated areas and were generally absent from mangrove and seagrass sites. Whilst mangrove habitats showed the lowest densities and diversity of macrofaunal species, the author emphasised that interrelations between different adjacent habitats, including food web interactions, need to be elucidated to ascertain the ecological significance of estuarine habitat types (Alfaro 2006). The importance of large-scale habitat complexity has been recognised in overseas studies that examined macrofauna in relation to the spatial arrangement of habitat mosaics (e.g., Skilleter et al. 2005a).

5.2.1.1.7 Recent across-location studies

Recent ecological studies based on New Zealand data have been aimed at developing models to allow predictions about the occurrence and distribution of intertidal macroinvertebrates in relation to environmental variables (Thrush et al. 2003b, 2005). Thrush et al. (2003b) used survey data from 19 different North Island locations to develop species-specific models for the prediction of the probability of occurrence and the maximum density of 13 common macrofaunal species along a sand to mud gradient. They also considered univariate community measures, the number of individuals and taxa, species diversity and taxonomic distinctness. Selected sedimentary locations included a range of estuarine habitats, encompassing estuaries, harbours and embayments from Ahuriri in the north to Porangahau in the South. Of a total of 92 taxa, 13 species were commonly shared amongst sites (present at more than 7 of the 19 locations) and numerically dominant to warrant consideration in the models. The only crustacean species included was the crab *Helice crassa*, with other species representing polychaetes (*Aonides oxycephala*, *Aquilaspio aucklandica*, *Boccardia syrtis*, *Scolecopides benhami*, *Heteromastus filiformis*, *Scoloplos cylindifer* [cylindrifer], *Nicon aestuariensis* [aestuariensis]), bivalves (*Austrovenus stutchburyi*, *Arthritica bifurca*, *Macomona liliana*, *Nucula hartvigiana*), and the anthozoan *Anthopleura aureoradiata*. Modelling efforts related the distribution and abundance of these common species successfully to sediment mud content, indicating the usefulness of such models to predict the distribution and abundance of species following changes in sediment grain size over a large spatial scale (greater than 100m). The models also showed that the response to habitat change in the form of increasing sediment mud content of four closely related spionid polychaete species varied, indicating different levels of sensitivity to an increase in mud content; at the same time, there was no overall response to increasing mud content between feeding types or mobility levels. Maximum density models showed some deviations from the former models, as several species showed increasing probabilities of occurrence with increasing mud content, but maximum densities at low-to-moderate mud content. The authors concluded that these models are useful for ecological and environmental management of estuarine habitats as they indicate long-term consequences of habitat change (Thrush et

al. 2003b). In a subsequent study, Thrush et al. (2005) developed species-environment models to assess the influence of spatial scale for predicting the response of macrofauna to changes in sediment mud content. Using maximum density and probability of occurrence as measures of macrofaunal response, they assessed three different spatial scales, ranging from 2 to 500 km. Their findings highlight the importance of scale when attempting to predict species distribution as different scales resulted in different responses, even though mud content was an important determinant for most species (Thrush et al. 2005).

Another of the few New Zealand studies that evaluated the generality of patterns across habitats was that by Ellis et al. (2006), which also attempted to make predictions about the distribution of common benthic species. These authors examined macrobenthic species distribution in relation to environmental variables in different coastal systems and their broad-scale study showed that different sedimentary habitats support distinct macrofauna assemblages. Using data from different estuaries and embayments in the Auckland region, including Whitford Bay, Manukau Harbour, Puhinui Creek (a sub-estuary of Manukau Harbour), and Mahurangi Harbour, the aim of their study was to develop a model to predict the occurrence of macrobenthic species (less than 500 micron) in relation to small/medium-scale (e.g., sediment content, organic matter) and large-scale environmental variables (e.g., estuary type, catchment area). Estuaries and sites within estuaries were selected to represent distinct habitat types that were characterised by different physical forcing, sediment types and large-scale forcing. Different intertidal habitats within the Whitford embayment (outer sandflats, outer channels, and inner estuary mudflats) were compared to similar habitats in Manukau Harbour, Puhinui Creek and Mahurangi Harbour to encompass differences in estuary type and environmental conditions. [N.B. subtidal sites were also included in the analysis, but are not considered here.] Within the Whitford embayment, a total of 163 taxa were present across the different habitats, with the majority of taxa occurring at low densities. The distribution of 13 representative macrobenthic taxa in relation to sediment silt/clay content, organic content, water depth, wave disturbance and speed showed that sediment type and physical forcing were important factors determining macrobenthic assemblages, with large differences (75–91%) in macrobenthic assemblages between distinct habitat types. Although some dominant species such as the polychaete *Aquilaspio aucklandica* were widespread across varying habitats, most species showed clear differences in abundance as a function of sediment type. Sandy sediment sites were dominated by the bivalve species *Macomona liliana*, *Austrovenus stutchburyi*, *Nucula hartvigiana*, and the crustacean *Colurostylis lemurum*, whereas the amphipod *Paracorophium excavatum*, oligochaetes, nereid polychaetes, *Heteromastus filiformis*, and crab species *Helice crassa* preferred sites characterised by fine silts and clays. In addition, bivalves and one polychaete species, *Aonides oxycephala*, showed greatest abundances on exposed intertidal sandflats and the abundance of bivalves increased with increasing exposure to high wind-wave disturbance. In addition to differences in assemblages between habitats, differences in average diversity and abundance of benthic macrofauna were also evident. In general, upper estuarine habitats that were characterised by high sedimentation rates and corresponding high mud content had the lowest average species diversity in contrast to intertidal sand flats that supported the highest average species diversity and abundances of benthic fauna. Evaluation of macrofaunal assemblages across different estuaries confirmed the findings from Whitford embayment with differences in assemblage compositions reflecting different habitat types between Manukau and Mahurangi harbours, and Puhinui Creek. The exposed intertidal sand flats of Manukau Harbour supported the highest diversity and abundances in comparison with the muddy sheltered habitat of Puhinui Creek, with Mahurangi Harbour representing intermediate levels of disturbance with similar diversity and abundance values to the former estuary. Assemblage compositions differed 64 to 89%, with the highest dissimilarity also observed between Manukau Harbour and Puhinui Creek. Dominant taxa across estuaries were similar to those found at Whitford embayment, with Manukau and Mahurangi harbours sharing three dominant species, *Macomona liliana*, *Nucula hartvigiana*, *Heteromastus filiformis*, but none with Puhinui Creek, where oligochaetes, a capitellid polychaete and *Scolecopides* sp., *Helice crassa*, and a phoxocephalid amphipod were the top 5 ranking taxa. There was a predominance of suspension feeding bivalves at sandy intertidal sites in comparison with muddy sheltered sites that were dominated by oligochaetes, crabs, amphipods, and deposit-feeding polychaetes.

5.2.1.2 Exposed beaches

In comparison with sheltered intertidal soft sediment environments, macrofaunal assemblages of exposed beaches have been largely overlooked in New Zealand. While considerably fewer studies have been conducted in exposed sediments overall, these have been from few locations and mostly focused on individual species, usually surf clams, including exploited species such as toheroa *Paphies ventricosa* (McLachlan et al. 1996, Marsden 2000, Beentjes et al. 2006). As overseas studies present comprehensive assemblage data from exposed beaches including disturbance effects, New Zealand knowledge is greatly lagging behind (Jaramillo & McLachlan 1993, Dugan et al. 1995, Schoeman et al. 2000)

Oliver (1923), describing littoral communities in New Zealand, commented that exposed sandy beaches such as on the west coast only support a few animals such as surf clams, owing to the physically unstable environment, whereas stable conditions of sheltered east coast beaches support higher numbers and a greater variety of animals, including crabs, polychaetes and gastropods. He considered the burrowing bivalve *Amphidesma* [*Paphies*] *subtriangulata* characteristic of exposed sandy beaches where it occurs in high numbers, and also noted that the congener *Amphidesma* [*Paphies*] *ventricosa* reportedly inhabits exposed West Coast beaches. He described the “*Amphidesma* association” from Maunganui Beach near Tauranga, where highly abundant (more than 1000 individuals) *Paphies subtriangulata* were recorded in one area with the equally abundant bivalve *Antigona* [*Tawera*] *spissa*. Also included in this assemblage were large gastropods, *Struthiolaria papulosa*, *Verconella mandarina* [*Penion sulcatus*], *Cominella adspersa*, the swimming crab *Platyonischus bipustulatus* [*Ovalipes catharus*], the hermit crab *Eupagurus novae-zealandiae* [*Pagurus novaezealandiae*] in areas adjacent to the rocky intertidal, and a small un-identified isopod.

One of the few published studies of sandy beach macrofauna in New Zealand was that by Wood (1968), who conducted a qualitative and quantitative survey of macrofauna at Howick Beach/Auckland in the North Island. This study included a suite of environmental variables (e.g., exposure to wave action, tidal height, temperature, sediment size, organic, and water content) and macrofauna (larger than 1.25mm) were grouped into characteristic associations. Macroinvertebrate assemblages at this beach included a range of species from different phyla, e.g., 6 species of bivalve, 5 gastropods, 23 polychaetes, several crustacean taxa, nemertines, acorn worms, echinoderms and holothurians. Although the author noted that many species were ubiquitous, three main assemblages were discernible which were characterised by the high abundance of different bivalves. The “*Amphidesma australe-Nucula hartvigiana* association” was present in relatively coarse sand at mid-tide level and was dominated by *Amphidesma australe* [*Paphies australis*] associated with *Nucula hartvigiana*, *Zediloma* [*Diloma*] *subrostrata*, *Isocladus armatus* and *Platynereis australis*, *Notoacmea helmsi helmsi* [*helmsi*] and *Anthopleura aureoradiata*. Two further assemblages were present on the lower beach and shared a number of taxa, but were located at different tidal levels. These were the “*Chione stutchburyi-Macomona liliana* association” containing *Chione* [*Austrovenus*] *stutchburyi* as the dominant bivalve associated with *Macomona liliana*, *Axiothella australis*, *Notomastus* sp., *Aglaophamus macroura*, *Glycera* sp., *Halicarcinus cookii*, *Pontophilus australis*, *Balanoglossus australiensis*; these eight species were also included in the third assemblage. The crab *Hemiplax* [*Macrophthalmus*] *hirtipes* and the polychaete *Lepidastheniella comma* were part of “*Chione stutchburyi-Macomona liliana* association” at some sites. The third assemblage, the “*Dosinia subrosea-Macomona liliana* association” occurred further down the shore and was defined by the bivalve *Dosinia subrosea*. In addition to the eight species shared with the second assemblage, this association included the gastropod *Baryspira* [*Amalda*] *australis*, the brittle star *Amphiura aster*, the polychaetes *Leanira* sp., *Podarke* sp., a goniadid polychaete, *Nebalia* sp., haustoriids, phoxocephalid and other amphipods, and ostracods. Six polychaete species, *Chaetozone* sp., *Magelona papillicornis*, *Oridia* sp., *Sigalion* sp., *Asychis* sp., and *Travisia olens* were not part of any assemblage and only present at one site on the beach, which was rarely exposed at low tide. The sand hopper *Talorchestia quoyana* was abundant at the top of the beach where it was the only macrofaunal species present. The author concluded that the different assemblages distinguished at Howick Beach were comparable to similar groupings recorded from sheltered beaches in other parts of New Zealand (Wood 1968).

The geographically most comprehensive study of New Zealand beach fauna was by Fincham (1977) who examined 14 North Island beaches but only considered peracarid crustaceans. Study locations covered three main beach types (open surf beaches, beaches with medium levels of protection, and sheltered beaches) and included: Lyall Bay, Paraparaumu, Opunake, Onaero, Bayleys, Ninety Mile Beach at Waipapakauri, Ti Bay at Pahihia, Paikiri, Long Bay, Cheltenham, Mount Maunganui, Ohope, Westshore and Castlepoint Beach. Peracarid crustaceans were moderately abundant throughout these beaches and amphipods were the dominant group (54% of the total), followed by isopods (33%) and cumaceans (13%). Frequency of occurrence followed a similar ranking, with amphipods present at 64% of all sampling sites, isopods at 46%, and cumaceans at 20%. The most dominant amphipod species were *Waitangi chelatus* and *W. brevirostris* reflecting 39% and 24%, respectively of all amphipod species, and *Pseudoegea punctata* was the dominant isopod species representing 58% of this group. Several species showed a clear preference for a particular beach type; the amphipods *Patuki breviuropodus*, *Metaphoxus littoralis*, *Waitangi rakiura*, and the isopod *Actaecia euchroa* preferred open sandy beaches, whereas the amphipods *Proharpinia* sp., *Urothoe elizae* and the isopods *Cumodoce* sp. and *Isocladus armatus* favoured sheltered sandy beaches. The amphipod *Waitangi chelatus*, the isopods *Pseudoegea punctata* and *Macrochiridothea uncinata*, and cumaceans in general were tolerant of a wide range of exposure but tended to favour open beaches, with the exception of cumaceans. The amphipods *Waitangi brevirostris*, *Talorchestia quoyana*, and the isopod *Scyphax ornatus* were found on both open and protected beaches. When comparing findings from this study to those of a previous one of Stewart Island beaches (Fincham 1974), the author points out that North Island beaches reflected markedly lower abundances of peracarid fauna than their southern counterparts (Fincham 1977).

On the west coast, North Island, Wood (1963) compared intertidal macrofauna at an exposed sandy beach with that at an adjacent estuarine sand flat at Marakopa/Kawhia and presents data from a quantitative beach survey conducted between high (mean high water spring) and low (mean low water neap) tide. A total of 13 species (retained on a 1.25mm mesh sieve) were recorded, including *tututua* *Amphidesma subtriangulatum* [*Paphies subtriangulata*], Nemertine sp., the polychaetes *Armandia* sp., *Pseudonerine* sp., *Aglaophamus macrura* [*macroura*], and *Glycera tessalata*, the paddle crab *Ovalipes bipustulatus* [*catharus*], *Callianassa filholi*, two unidentified amphipod species, *Talorchestia* sp., the isopod *Pseudoegea punctata* and *Scyphax ornatus*. Densities differed with tidal levels and some species were restricted to a very narrow tidal zone, which was attributed to the grain size and water content of the sediment. Abundances also varied between species; as only one individual *tututua* was present at the beach, the author considered the absence of an intertidal bivalve population unusual. Overall, the macrofauna species at the lower part of the beach were considered comparable to those at the mouth of the adjacent estuary (Wood 1963).

Two studies by Morgans (1967a, b) document beach macrofauna at Gooch's Beach/Ingles Bay and Jimmy Armer's Beach at Kaikoura (east coast South Island) and reveal a clear zonation pattern with intertidal macrofauna restricted to the low intertidal area. The unstable environment of Gooch's Beach varied in gradient and substrate type, ranging from cobbles and pebbles to areas of fine and very fine sand (Morgans 1967a). Whilst the beach areas dominated by pebbles and cobbles were devoid of fauna, other areas showed a clear zonation patterns between the supralittoral fringe (the upper intertidal limit and above) and the lower intertidal area, with a lack of fauna and no overlap between zones. The supralittoral fringe (the upper intertidal limit and above) typically contained only one species, *Talorchestia quoyana* at high abundance, whereas the lower intertidal zone was characterised by the dominance of polychaetes. Polychaetes were also the most diverse group and included the locally abundant *Lumbrineris brevicirra* [*Scoletoma brevicirra*], *Nerine antipoda* and *Scolecopides benhami*. The ghost shrimp *Callianassa filholi* and the isopods *Isocladus armatus* and *Allorchestes novizealandiae* were common in the lower part of this area. In contrast to Gooch's Beach, Jimmy Armer's Beach, a small sheltered beach on Kaikoura Peninsula reflected well-sorted sediments with over 80% fine sand and a uniform texture throughout different parts of the beach. Macrofauna at this beach showed a similar zonation as that reported from the unstable environment of Gooch's Beach, with *Talorchestia* dominating the supralittoral zone, a diverse macrofauna assemblage in the lower intertidal area, and fauna lacking in-between the two zones. Similar to Gooch's Beach, polychaetes

were prevalent in the macrofauna assemblage at this beach, and the most common species were the polychaetes *Axiothella* sp. and *Scoletoma brevicirra*, and the ghost shrimp *Callianassa filholi*. Considering the contrasting environments at the two beaches, Morgans (1967b) concluded that macrofauna showed the same zonation patterns and low tide assemblages were similar with some differences in the abundance of particular species.

Knox (1969) provides a summary of beach fauna in Pegasus Bay (Canterbury, South Island). In agreement with Oliver (1923) he noted that beach populations have low species diversity, but populations of individual species reach extremely high densities, such as those of tuatua (*Donacilla* (*Amphidesma*) *subtriangulata*) [*Paphies donacina*]. In Pegasus Bay, he reported that the distribution of several congeners of the burrowing sand hopper *Talorchestia* was dependent on the type of substrate at different beaches. Sandy beaches (e.g., Brighton Beach) contained *Talorchestia quoyana* and its congener *T. telluris* occurred on sandy beaches with low salinity, such as on Banks Peninsula. *Talorchestia cookie* was present on shingle beaches in the northern part of Pegasus Bay and south of the peninsula. Another amphipod *Orchestia chilensis* replaced *Talorchestia* species on rock and muddy shores in oceanic and estuarine conditions. Regarding the vertical zonation of species distributions, the isopod *Actaecia euchroa* co-occurred with *Talorchestia quoyana* at the top of the intertidal zone; at mid-tide level, tuatua *Paphies donacina* was the dominant species with two commensal hydroids (*Amphisbetia fasciculata* and *Perigonium robustus*) on its shell, followed by other common species, a small phoxocephalid amphipod and carnivorous polychaetes, including *Aglaophamus macroura*, *Glycera americana*, *Leonira* [*Labiosthenolepis*] *laevis*, and nemertines. The burrowing ghost shrimp *Callianassa filholi* dominated the lower intertidal area, where it co-occurred with the aforementioned polychaete species and *Onuphis*, but also nemertines and the small isopod *Pseudaega punctata*. Considering shingle beaches, Knox (1969) observed that they support very few animals other than in the supralittoral zone, with a small flatworm as the only species living in other areas. A subsequent study in Pegasus Bay examined the colonisation and degradation of beach-wracked kelp by supralittoral fauna at South Brighton Beach (Inglis 1989). As this study focused on supralittoral beach fauna, it does not provide a general description of intertidal macrofauna and the majority of species listed reflect terrestrial macroinvertebrates, predominantly insects (Inglis 1989).

A survey of five different Stewart Island beaches examined the distribution of infaunal peracarid crustaceans in relation to tidal height, sediment type and exposure level (Fincham 1974). Peracarids (larger than 1mm) were generally abundant on all beaches, but showed highest abundances at sheltered sites with lowest densities at exposed beaches. Although only collected at two beaches, cumaceans were the most abundant group (78% of total peracarids), followed by amphipods (19%), isopods (2%), and tanaids (1%). Amphipods led the frequency of occurrence and were present at all stations (100%), with isopods at 53%, cumaceans at 32%, and tanaids at 11% of all stations. The two most abundant amphipod species were *Patuki breviuropodus* and *Paraphoxus chelatus* representing 41% and 20% of amphipod individuals, respectively; *Pseudaega punctata* and *Paravireia pistus* were the dominant isopod species, reflecting 53% and 27% of all individuals in this group, respectively, whereas cumaceans were only identified as a group and tanaids were represented by a single species, *Tanais novaezealandiae*. Sheltered beaches supported higher peracarid densities than exposed sites and some species, such as *Tanais novaezealandiae* were only present at sheltered environments. In light of the close proximity of sites, Fincham (1974) remarked that the peracarid fauna of Stewart Island was remarkably diverse.

5.2.2 Structural and functional diversity

Functional diversity has been defined as “the variety of different responses to environmental change, especially the diverse space and time scales with which organisms react to each other and to the environment” (Steele 1991). Accordingly, species are grouped based on the role they play in the ecosystem and the importance of functional diversity has been recognised in ecological studies, i.e., in regards to imposed external changes to ecosystems processes (e.g., anthropogenic impacts) (Tilman et al. 1997). Studies of the functional diversity of benthic soft sediment assemblages have generally focused on different trophic groups or on species that have a disproportional influence on associated

organisms and ecological processes, and there have been several studies in New Zealand that have considered functional differences within intertidal benthic assemblages.

The most common distinction of functional groups in soft sediment environments has been based on trophic groups, i.e., on suspension- and deposit-feeders in relation to sediment grain size. Recognising the close link between feeding modes and habitat, deposit feeding species have been shown to be often prevalent in fine-grained sediment owing to the higher availability of organic matter; in contrast, suspension feeders appear to dominate in coarse sediments, which are characteristic of high-flow environments and of a grain size sufficiently large as to not interfere with filter feeding activities (Rhoads & Young 1970, Whitlatch 1977). Data on trophic groups in New Zealand benthic assemblages indicate a prevalence of deposit-feeders in sheltered intertidal habitats (Grange 1977, Healy 1980, Read 1984, Ellis et al. 2006). The majority of macroinvertebrates in Manukau Harbour and Pauatahanui Inlet were deposit-feeders, constituting more than 70% and 95% of individuals, respectively (Read 1984, Pridmore et al. 1990). Similarly, Ellis et al. (2006) who considered trophic differences in benthic assemblages in Whitford embayment also reported a high proportion of this trophic group across different habitat types; benthic mangrove assemblages and non-vegetated mudflats were dominated by deposit feeders and only sandflat habitats supported a relatively high percentage of suspension feeders, corresponding to the lower mud content of this habitat (Ellis et al. 2006). As coastal environments receive an increasing amount of fine-grained terrigenous sediments, the proportion of deposit- and suspension-feeders present in an area has been considered a good indicator for sediment-related disturbances to assemblage structures. In both Manukau Harbour and Pauatahanui Inlet, the proportion of deposit-feeders was closely related to fine sediment grain sizes across sites, and assemblages digressing from this were considered unstable and/or under stress (Grange 1977, Healy 1980).

A study of the functional role of large suspension- and deposit-feeding bivalves in Whitford embayment demonstrated a significant effect of both types of organism on intertidal assemblage patterns (Thrush et al. 2006). Removal of suspension-feeding *Austrovenus stutchburyi* and deposit-feeding *Macomona liliana* from areas dominated by either species significantly affected the flux of nutrients and oxygen and associated macrofauna assemblages. The influence on assemblage structures was apparent in differences in total abundance and in density of individual species, although not in diversity measures. Removal of *Austrovenus stutchburyi* resulted in the increase of small surface deposit feeders (e.g., polychaetes and juvenile *Macomona*), whereas removal of *Macomona* increased the abundance of sub-surface deposit feeders (e.g., polychaetes and small-sized bivalves). The authors concluded that local extinction of these large, functional-important species would cause a system shift with possibly wide-ranging consequences (Thrush et al. 2006).

Other organisms that have a disproportional influence on associated soft sediment assemblages are those that modify the habitat in which they live; they exert their influence through the provision of habitat and/or shelter or indirectly through their impact on sediment properties, or a combination of both. Burrowing macrofauna, such as crustaceans and large polychaetes, are the most conspicuous group of habitat-modifiers and a number of studies overseas (MacGinitie 1934, Karplus et al. 1974, Reise 1981) and in New Zealand (Berkenbusch et al. 2000, Berkenbusch & Rowden 2007) have highlighted their functional importance in soft-sediment environments. Burrows provide habitat and shelter for associated species and extend the sediment-water interface to sediment depth, reducing spatial competition at the sediment surface (MacGinitie 1934, Karplus et al. 1974). The physical structure of ghost shrimp *Neotrypaea californiensis* burrows supports different commensal macro-invertebrates, including polychaetes and bivalves, and gobies use the burrows of alpheid shrimp as habitat and refuge from predation (MacGinitie 1934, Karplus et al. 1974). Other species benefit from the uneven microtopography associated with the presence of burrows – the small polychaete *Spio* sp. only occurs at sites that are continuously covered by water, such as small depressions at the sediment surface caused by ghost shrimp bioturbation (Bromley 1996). The aforementioned overseas studies highlight the functional importance of biogenic structures, however, there has currently been no New Zealand study that examined direct consequences of such habitat modification for intertidal soft sediment assemblages.

Burrowing and feeding activities can cause substantial sediment disturbance (bioturbation) including sediment resuspension and changes in sediment properties (e.g., organic, water and oxygen content, grain size, nutrient exchange) (Reise 1981, Ziebis et al. 1996), and significant bioturbation activity of New Zealand's burrowing ghost shrimp *Callianassa filholi* has been documented in Otago Harbour (Berkenbusch & Rowden 1999). High densities of deposit-feeding bivalves substantially increase sediment erodibility (Widdows et al. 2000) and a study in Tauranga Harbour showed that a decrease of *Macomona liliانا* abundance resulted in an increase in sediment stability of up to 200% (Lelieveld et al. 2004).

Repercussions of sediment disturbance include both positive and negative effects for the abundance of associated biota. For example, overseas studies have shown that burrowing activity by the polychaete *Pygospio elegans* caused an increase in faecal organic material in the sub-surface layer of the sediment resulting in a high concentration of meiobenthos, and increased oxygenation of sediment below the surface by the polychaete *Lagis koreni* was linked to extremely high densities of another polychaete species (Reise 1981). In contrast, sediment disturbance by lugworms *Arenicola marina* and cockles *Cerastoderma edule* has been linked to a marked decline in tube-building amphipods and bioturbation by the amphipod *Pontoporeia* had a detrimental effect on newly settled *Macoma balthica* bivalves of European tidal flats (Flach 1993, Olafsson et al. 1994). As the impact of sediment disturbance varies among individual species, the influence of bioturbating organisms is evident in the assemblage composition overall. In New Zealand, dense populations of bioturbating ghost shrimp *Callianassa filholi* imposed a distinct macrofauna assemblage composition on an intertidal sand flat and patterns persisted throughout different seasons (Berkenbusch et al. 2000). Assessment of benthic assemblages across three different estuaries in the Otago region confirmed the generality of a distinct macrofaunal assemblage associated with this bioturbating species (Berkenbusch et al. 2007). Furthermore, experimental recruitment of ghost shrimp to previous non-bioturbated areas caused a discernible shift in assemblage composition in a southern temperate inlet (Berkenbusch & Rowden 2007). The functional importance of bioturbating crabs, *Helice crassa*, has also been demonstrated in Okura Estuary, where this species played an important role in habitat amelioration following catastrophic sedimentation (Norkko et al. 2002). Through its bioturbation activity, the crab remobilised thick clay deposits and mixed them with underlying sediment, thereby improving the habitat for other colonising macrofauna.

Early studies overseas demonstrated that in contrast to the destabilising effect of bioturbating species, habitat modification by tube-building species such as small burrowing polychaetes has been linked to the stabilisation of sediment, creating a favourable environment for some species with adverse effects on others (Woodin 1978). As lined tubes protrude above the sediment surface, these structures increase surface roughness and reduce near-bottom currents, thereby stabilising the substrate (Eckman & Nowell 1984). Studies in New Zealand have considered this aspect of habitat modification by examining the role of tube-building polychaetes in the colonisation and survivorship of associated macrofauna (Thrush et al. 1991, 1996, Cummings et al. 1996). In Manukau Harbour, the relative low density of *Macomona liliانا* bivalves in areas characterised by dense tube-mats of the polychaete *Boccardia syrtis* was linked to active settlement avoidance of the former species in *Boccardia*-dominated areas (Cummings et al. 1996). At the same time, survivorship of juvenile *Macomona* was significantly lower in sediments containing tube mats. Thrush et al. (1996) who studied macrofaunal recolonisation following defaunation in sand flat areas in Manukau Harbour observed differences in macrofaunal assemblage structure between areas that had *Boccardia* tube mats removed and ambient ones that still contained the polychaete. Differences in assemblage structure were based on changes in species composition and density with assemblages showing slow recovery following the removal of tube mats, which was attributed to habitat instability (Thrush et al. 1996). At the same time, recolonisation of ray feeding pits by macrofauna was slower at a polychaete- than a bivalve-dominated site in Manukau Harbour, which was linked to the slow movement of *Boccardia syrtis* into disturbed areas, while tube-mats of this species in ambient sediment also restricted the movement of other macrofaunal species (Thrush et al. 1991).

The functional importance of macrobenthic species has also been linked to the ability to facilitate colonisation of conspecifics and other infauna (Thrush et al. 1992). Separate addition of adult bivalves

Tellina [*Macomona*] *liliana* and of the polychaetes *Heteromastus filiformis* and *Aonides oxycephala* to defaunated areas in Manukau Harbour revealed that both *Macomona* and *Aonides* facilitated the colonisation of conspecifics and/or other species. The presence of *Macomona* significantly increased the density of juvenile conspecifics and of common taxa and addition of *Aonides oxycephala* also resulted in an increase in conspecifics. *Heteromastus* did not affect colonisation rates of common taxa, but increased the diversity of colonising species. Owing to their facilitation ability, these species may be important in maintaining dominance patterns in benthic assemblage compositions and may also play a significant role in the rehabilitation of disturbed habitats (Thrush et al. 1992).

Other functional differences in soft sediment assemblages are based on the provision of habitat in the form of hard substrate in an otherwise sedimentary environment. Hard-shelled species such as gastropods and bivalves provide the only available hard substratum for associated species, including hydroids, barnacles, limpets, chitons and sea-anemones (Oliver 1923, Wood 1968, Grange 1977, Pridmore et al. 1990, Anderson et al. 2004). The presence of hard shell substrate facilitates the presence of epifauna and thereby increases the number and abundance of species present in soft sediment assemblages; in addition, algae growing on shells provide food for herbivorous epifauna. A number of New Zealand studies comment on the frequent occurrence of the aforementioned species on hard-shelled molluscs and several studies highlighted the close link between the abundance of gastropods or bivalves and associated epifauna (Oliver 1923, Wood 1968, Anderson et al. 2004). Oliver (1923) commented on the high densities of epifauna on gastropod shells and Wood (1968) considered the polychaete *Polydora* sp. and the anthozoan *Anthopleura aureoradiata* dependent on *Austrovenus stutchburyi* as they colonise cockle shells. Anderson et al. (2004) reported high abundances of the barnacle *Elminius modestus* and of *Anthopleura* living on shells of the similarly abundant bivalve *Austrovenus stutchburyi* in Okura Estuary. These studies indicate the functional importance of hard-shelled molluscs in intertidal benthic assemblages, but there has been no formal analysis of the increase in habitat complexity and species diversity associated with the presence of gastropods and bivalves to date

5.3 Taxonomy and biogeography

Intertidal macroinvertebrates in New Zealand have received relatively little attention in taxonomic and biogeographical studies, with species descriptions generally concentrated in early literature (e.g., polychaetes – Estcourt 1967a, b, amphipods – Hurley & Cooper 1974). Former NZOI memoirs provide species descriptions and distributional information on some macroinvertebrate groups, for example cumaceans (Jones 1963) and isopods (Hurley & Jansen 1977), and other literature include publications on New Zealand molluscs (Powell 1979), crabs and crab-like anomurans (McLay 1988), and general naturalist publications (Morton & Miller 1968, Jones & Marsden 2005). The majority of early publications are difficult to access (i.e., out of print) and outdated, and there are currently no comprehensive identification guides, such as dichotomous keys and/or detailed descriptions of New Zealand macroinvertebrates available. In the absence of New Zealand specific publications, researchers rely on individual papers and on taxonomic publications from overseas (e.g., amphipod and polychaete information from Australia - Barnard & Karaman 1991, Beesley et al. 2000) to identify benthic macroinvertebrate species. As a consequence, confident and consistent species identifications, which are crucial for ecological studies, are hampered by the lack of information, which is often evident in the low taxonomic resolution of species or species groups (i.e., to genus or family level only) in a large number of soft sediment studies in New Zealand. Similarly, biogeographical information concerning soft sediment macroinvertebrates are scarce and usually restricted to anecdotal comments or to a few biological studies on particular species (e.g., Jones & Simons 1983, Berkenbusch & Rowden 2000).

5.4 Threats and vulnerability

As intertidal soft sediments are at the interface between land and sea, they are threatened by predominantly land-derived influences, generally associated with human activities (Edgar & Barrett 2000). Sheltered embayments in New Zealand are considered particularly vulnerable owing to their less

dynamic physical environment (Ellis et al. 2000) and estuaries regarded as polluted include Waitemata, Manukau, Kaipara, Tauranga and Porirua harbours, Whanganui River mouth, Ahuriri Estuary, Pauatahanui Inlet, Wellington Harbour, Waimate Inlet, Brooklands Lagoon, Waimakariri River mouth, Avon-Heathcote Estuary, Lyttleton Harbour, and New River estuary (Knox 1980).

Detrimental effects on intertidal soft sediment assemblages have been linked to changes in land use, physical disturbance, input of pollutants, nutrients and waste, and invasive species. Global climate change has also been implicated as a potential threat, through changes in sedimentation patterns resulting in habitat degradation (Thrush et al. 2003b). In New Zealand, most research efforts regarding the threats and vulnerabilities of intertidal macroinvertebrates have been centred on land-derived disturbances, in the form of increased nutrients, pollutants, and sediment. Industrial and urban runoff contains organic matter, sewage and a variety of pollutants including hydrocarbons and heavy metals, and inputs to estuaries in particular are often large (Heip et al. 1995), including estuaries in New Zealand (Glasby et al. 1988). Individually and/or in combination, these substances significantly impact sedimentary environments, with sublethal and lethal effects for individual species and repercussions for benthic assemblages. A number of field and laboratory studies have examined the effects of pollution, including behavioural responses on intertidal macroinvertebrate species, and examples from New Zealand include studies on trace metals in amphipods (Marsden et al. 2003), the effect of tributyl tin (an anti-fouling agent) on oysters and oyster borers (King et al. 1989), copper- and chlordane contamination in bivalves (Roper & Hickey 1994), bioaccumulation of chlordane in molluscs and polychaetes (Wilcock et al. 1993), and the colonisation rates of macroinvertebrates in unpolluted and polluted areas (Thrush & Roper 1988).

Assemblage-level pollution studies include mensurative and experimental evaluations, which have been geographically focused in the Auckland region, predominantly Manukau Harbour. Whilst these studies reveal some disturbance effects at the assemblage-level, they often also highlight the difficulties in providing conclusive evidence of a cause-and-effect relationship. With few exceptions (e.g., experimental field studies), ecological impact assessments have been conducted *post hoc*, using comparisons between supposedly affected areas and ambient reference sites, based on the assumption that the latter represent natural conditions and that the ecosystem has not been affected on the whole.

5.4.1 Contaminants

A small study of intertidal macroinvertebrates at polluted (sewage and industrial inputs) and non-polluted sites in Manukau Harbour showed the same prevalent species at all sites, but lower species numbers at polluted sites (Henriques 1980). Densities of *Chione stutchburyi* [*Austrovenus stutchburyi*] were also lower at the latter sites, and the author linked the observed differences in macrofauna to the discharge of toxic chemical and sewage wastewater, the decrease in sediment grain size and nutrient additions associated with the sewage oxidation ponds (Henriques 1980). An assessment of benthic macrofauna in regards to runoff at upper Manukau Harbour mud flats revealed high concentrations of hydrocarbons and metals in surficial sediments (Roper et al. 1988). Macrofaunal assemblages were dominated by opportunistic species (tubificid oligochaetes, the polychaete *Heteromastus filiformis*, and the amphipod *Proharpinia hurleyi*) and large long-lived ones (the burrowing crabs *Helice crassa* and *Macrophthalmus hirtipes*, and the pulmonate snail *Amphibola crenata*). Although only one site was considered heavily polluted which was evident in the notably low numbers of species and of individuals, other sites also appeared to be affected as benthic assemblage compositions were correlated with several sediment properties, including contaminants. All sites were characterised by marked within-site homogeneity, which the authors considered to be related to high mobility of resident fauna or the influence of pollution, facilitating the establishment of opportunistic species only. At the same time, the authors noted that large between-site variability in assemblages made the detection of pollution effects difficult, as natural unknown factors may have contributed to the variability in benthic assemblage structure (Roper et al. 1988).

Another study of (stormwater) runoff in four different estuaries (or sub-estuaries of larger systems) in the Auckland region also indicated that assessment of contamination effects is complex (Morrissey et al. 2003a). The authors showed that contaminant concentrations (copper, lead and zinc and DDT) were markedly higher in urban than in non-urban estuaries and benthic assemblages differed accordingly, but differences in assemblage patterns were not only correlated with contaminant levels but also other natural variables, such as sediment characteristics and location in the estuary. Nevertheless, as macrofaunal assemblages in the two urban estuaries were similar but distinctly different to the two non-urban ones, the authors considered the similarities in macrofauna evidence for contamination from runoff. At the same time, they point out that their study, as with similar pollution studies, fails to demonstrate cause and effect. In conclusion, they suggested the additional use of toxicity tests in an integrative assessment of stormwater-derived contaminants on estuarine macrobenthos to strengthen correlative findings (Morrissey et al. 2003a). Nipper et al. (1998), who studied benthic assemblages in relation to sediment contamination across different intertidal locations also highlighted the difficulty of assessing pollutant effects. These authors evaluated concentrations of a range of organic chemicals and heavy metals in sediment (whole-sediment and pore-water toxicity) in parallel with benthic assemblages at contaminated and/or uncontaminated sites in Aotea, Raglan, and Manukau harbours, and Okura and Tamaki estuaries. Their findings showed no significant differences in individual and species abundances and diversity between contaminated and control sites and there was no consistent pattern in assemblage compositions in regards to sediment toxicity. At the same time, assemblage compositions differed significantly between sites, including a contaminated and uncontaminated one within Manukau Harbour. As assemblages were correlated with a combination of sediment variables including total organic carbon, the toxicant DDT, acid-volatile sulfide (an indicator of toxic trace metals) and ammonia, subtle pollution effects seemed to be evident. In light of significant sediment contamination at some of the sites, failure to detect clear contamination effects on benthic assemblages prompted the authors to suggest the development of more suitable chronic effects tests, including the assessment of functional instead of structural ecosystem health (Nipper et al. 1998).

Experimental studies conducted in Manukau Harbour to assess the impact of the organochlorine pesticide chlordane, revealed obvious adverse effects on benthic macrofauna (Pridmore et al. 1991, 1992). The pesticide had been previously reported from surficial sediments in the harbour, and experimental application of chlordane to intertidal sand flats resulted in similar pollutant concentrations as those recorded from areas of the harbour directly exposed to pollution (Fox et al. 1988, Hume et al. 1989). Experimental contamination of the sediment significantly affected the population density and structure of two common bivalves, the suspension-feeder *Chione* [*Austrovenus*] *stutchburyi* and the deposit-feeder *Tellina* [*Macomona*] *liliana* (Pridmore et al. 1991). Population densities of both bivalves declined to 30 and 40% of their initial values, respectively, primarily owing to the loss of juveniles. Although the underlying mechanism for this decline could not be determined, the authors suggested that avoidance behaviour by highly mobile juveniles might have been responsible, with bivalves actively avoiding settlement and/or emigrating from contaminated areas. This suggestion was supported by the finding that juvenile bivalves gradually re-colonised polluted sites following a marked decrease in chlordane concentrations in surface sediment after a storm (Pridmore et al. 1991). When considering all resident macrofauna, the pollutant also had an adverse effect on population densities of other common species, the bivalve *Nucula hartvigiana*, the sea anemone *Anthopleura aureoradiata* (commonly attached to *Austrovenus* shells) and the polychaete *Heteromastus filiformis* (Pridmore et al. 1992). In contrast, the abundance of two species, the crustaceans *Paracalliope novizealandiae* and *Colurostylis lemurum*, increased temporarily, which was attributed to their possible response to an increased food supply at contaminated sites. In spite of the effect on individual species, benthic assemblage structure and composition showed no detectable change following chlordane application. The reason for this outcome appeared to be three-fold: the most abundant species *Aonides oxycephala* was not noticeably affected by chlordane; those common species that showed an adverse response did not decline sufficiently to change their dominant position within the assemblage; and there was no emigration or immigration of new species at contaminated sites. The authors concluded that in addition to assemblage analyses it is important to assess the response of individual macrofaunal species to pollution (Pridmore et al. 1992).

5.4.2 Nutrients and organic matter

In addition to contamination, an increase in nutrient input and organic matter, generally in the form of sewage or fertilisers, has been shown in studies overseas to adversely affect soft sediment environments (e.g., Pearson & Rosenberg 1978, Grizzle 1984, Bonsdorff et al. 1997). High concentrations of nutrients, such as nitrates and phosphates, stimulate the growth of micro- and macroalgae, resulting in substantial increases (“blooms”) of algal standing stock (Steffensen 1976, Raven & Taylor 2003). The most severe repercussions from microalgal blooms are those linked to toxin-producing species which cause mass mortality of associated fauna, as has been demonstrated for subtidal assemblages in Wellington Harbour (Wear & Gardner 2001, and see Chapter 6). The prolific growth of macroalgae such as *Ulva* and *Enteromorpha* caused by eutrophication enables these species to outcompete other seaweeds and seagrasses which in turn can lead to shifts in associated benthic assemblages (Raffaelli et al 1998 and references therein for overseas examples). More dramatic effects have been observed overseas which include the direct smothering of macrofauna by dense macroalgal mats on the sediment surface and deoxygenation of underlying sediment through the bacterial breakdown of large amounts of organic matter (Diaz & Rosenberg 1995). Regardless of the origin of organic material, sediment enrichment and associated oxygen depletion can dramatically alter benthic assemblages, resulting in the prevalence of small, opportunistic species, such as oligochaetes and capitellid polychaetes (Pearson & Rosenberg 1978). In extreme cases, severe deoxygenation results in anoxic sediments causing mortality of all resident macroinvertebrates.

Morgans (1969) describing macrofaunal assemblage in Avon-Heathcote Estuary commented on the input of pollutants by the Heathcote River which killed resident infauna on the lower shore level in one area and turned the substrate to anoxic mud. The only species present at this site were *Amphibola crenata*, *Helice crassa*, and *Potamopyrgus antipodarum* at the surface, with the polychaetes *Nicon aestuariensis* and *Scolecopides benhami* within the sediment (Morgans 1969).

Regarding sediment burial of macroalgae, there has only been one New Zealand study that examined intertidal macrofauna associated with sediment enrichment. Ford et al. (1999) experimentally buried algal mats in defaunated areas in Papanui Inlet/Otago and monitored subsequent recolonisation rates of benthic macroinvertebrates. Colonisation of algal-enriched cores was slow and varied with seasons, with higher rates in summer than in winter. Common taxa exhibited lower densities in algal-enriched than in control sediments, and seasonal differences in colonisation rates were mostly influenced by the varying response of the most abundant species, the amphipod *Paracorophium excavatum*. Their study showed that buried algal mats have a considerable influence on benthic assemblages, which they attributed to the differences in oxygen availability (Ford et al. 1999).

Determining the sources and sinks of organic carbon in Manukau Harbour, Vant et al. (1998) observed a significant input of organic carbon and depleted dissolved oxygen levels close to the discharge of sewage wastewater. Their findings were confirmed in a subsequent ecological study by Ellis et al. (2000) who observed increased organic levels in sediments within 1400 m of the sewage outfall. At the same time, abundance of macroinvertebrates decreased with distance from the outfall, with high densities of a few small tolerant species (e.g., the polychaetes *Heteromastus filiformis*, *Aquilaspio aucklandica*, *Boccardia syrtis*) in the vicinity of the outfall. Macrofaunal assemblages were distinguished by environmental factors, such as physical and organic disturbance, and organic loading accounted for 22% of variability in assemblage structure. Species that contributed to dissimilarities were those that were tolerant of sediment enrichment and occurred at high abundances in enriched areas (Ellis et al. 2000). Similarly, Pridmore et al. (1990) in their macrobenthos study of Manukau Harbour attributed some of the variation in assemblage structure between sites to differences in sediment enrichment. As capitellid polychaetes are considered indicative of disturbance effects, the authors suggested that the disproportionate dominance of the capitellid *Heteromastus filiformis* was caused by increased organic loading at the site closest to the sewage treatment plant.

In a short note on biota in Blaketown Lagoon (Greymouth, South Island) Knox (1976) described anthropogenic alterations to the inflow and outflow of the lagoon, which caused high nutrient levels,

organic enrichment, lowered salinity and a change from sandy to predominantly muddy sediments. The author found that macrofauna was exclusively represented by species that are tolerant of low salinities, and he concluded that true estuarine benthic invertebrates had been replaced by species characteristic of brackish and freshwater (Knox 1976).

5.4.3 Sedimentation

Changes in land use such as reclamation have been shown to have a substantial influence on benthic assemblages (Harrison 1987) and a number of studies in New Zealand have been focused on the effects of accelerated sediment input on coastal environments.

Increased urbanisation and changes in land use have led to an increase in sedimentation and terrestrial sediment deposits pose a considerable threat to marine coastal environments (Gray 1997), including those of New Zealand. Extreme rainfall and landslides can cause catastrophic sedimentation events with severe impacts on benthic assemblages, and disturbance effects through low sediment inputs have also been shown to profoundly influence intertidal macroinvertebrates. Repercussions for associated macrofauna include detrimental effects on individual species, mass mortality of all resident macrofauna and long-term changes in assemblage compositions (e.g., Peterson 1985).

Early studies in Manukau Harbour and Pautahanui Inlet related the assemblage structure of benthic invertebrates to sediment characteristics indicated by a close relationship between deposit feeders and fine sediment grain size (Grange 1977, Healy 1980). Assemblages anomalous to this general pattern were considered unstable or under stress, with long-lasting changes in sediment grade predicted to impose marked changes in assemblage structure (Grange 1977). In Pautahanui Inlet, a significant impact of sedimentation on benthic assemblage structure was reported at a site that had received considerable sediment runoff through land development of a subdivision, resulting in the deposition of large amounts of silt and clay (Healy 1980). The input of fine sediments seemed to have greatly reduced densities of suspension feeders (mostly *Austrovenus*), and only a few mud crabs *Helice crassa* and mud snails *Amphibola crenata* were present, which was in sharp contrast to diverse and abundant benthic fauna in areas of the inlet unaffected by sedimentation (Healy 1980).

Subsequent mensurative and experimental studies have been explicitly focused on sedimentation effects on resident macrofauna and clearly indicate the detrimental impact of different sedimentation scenarios (Norkko et al. 2002, Hewitt et al. 2003, Thrush et al. 2003a, Anderson et al. 2004, Lohrer et al. 2004b). Anderson et al. (2004) demonstrated that macroinvertebrate assemblages in areas that were predicted to be in different depositional environments in Okura estuary were distinctly different, i.e., those that were located in high deposition areas. In these areas, benthic assemblages were dominated by small polychaetes and burrowing crabs and bivalves that constituted a significant component of assemblages at low- and medium-deposition sites were conspicuously absent. The close relationship between trapped sediment – total amount and grain size fractions – and assemblage patterns confirmed the significant influence of sedimentation levels on benthic macrofauna (Anderson et al. 2004).

Experimental field studies of sedimentation in coastal environments have been based on the application of terrestrial sediment deposits of different thicknesses to examine ecological repercussions of catastrophic and also less severe sedimentation scenarios. The rapid deposition of catastrophic amounts (several cm thick) of terrigenous clay was the focus of field studies in different northern estuaries (Norkko et al. 2002, Hewitt et al. 2003, Thrush et al. 2003a). In Okura Estuary, experimental deposition of thick clay layers at a sheltered and an exposed site had detrimental effects on benthic fauna, irrespective of the location within the estuary (Norkko et al. 2002). Macrofaunal densities were reduced by more than 90% immediately (within 10 days) after clay deposition and this defaunation was attributed to the physical smothering of underlying sediments and the onset of anoxia. Following the initial collapse of benthic assemblages at both sites, recovery rates between sites differed as the storm-induced fragmentation of clay layers led to a faster recovery at the exposed site. Nevertheless, macrofaunal recovery was still regarded as incomplete after 151 and 408 days at the exposed and the sheltered site, respectively. One important factor contributing to recovery at the latter site was sediment

mixing through mud crab *Helice crassa* bioturbation (Norkko et al. 2002). A catastrophic sedimentation event was also mimicked in Whangapoua Harbour (Coromandel Peninsula) to elucidate macrobenthic recovery pattern along a gradient of wave exposure (Hewitt et al. 2003). As in the aforementioned study, terrestrial sediment deposits resulted in the immediate defaunation of all experimental plots and subsequent long-term monitoring showed that benthic assemblages did not recover fully within 20 months of sediment deposition, although recolonisation was site-specific. After 20 months, the total number of taxa and individuals were consistently lower at experimental than control sites and most taxa exhibited lower abundances in deposited sediment than in ambient areas. The lack of recovery appeared to indicate that the habitat had been significantly altered by the chronic deposition of terrigenous sediment with corresponding changes in macrofaunal assemblages (Hewitt et al. 2003). Thrush et al. (2003a) also demonstrated site-specific responses of benthic assemblages to catastrophic sedimentation within Whitianga Harbour, but the deposition of sediments did not result in defaunation of underlying sediments, although it had an immediate and adverse effect on macrofauna. Recovery rates varied between sites but were slow, and the most affected were deeper-dwelling species at 2–15cm sediment depth, which the authors linked to their restricted mobility. Sediment properties returned to pre-experiment values within approximately 50 days, but macrofaunal recovery lagged substantially behind across all sites, indicating the long-term impact of chronic sedimentation events (Thrush et al. 2003a). In association with the experimental sedimentation study in Whitianga Harbour, these authors used data from this estuary, and from Okura and Whangapoua estuaries to conduct a meta-analysis of macrofaunal recovery rates across different estuarine environments, allowing them to infer general patterns (Thrush et al. 2003a). Meta-analysis confirmed consistent negative effects of terrigenous sediment deposits on benthic assemblages and recovery rates were influenced by site-specific factors including the composition of resident macrofauna and local hydrodynamic conditions. Regarding the overall findings from the three aforementioned sedimentation studies in New Zealand estuaries, Thrush et al. (2003a) concluded that catastrophic sedimentation events have the potential to lead to broad-scale degradation of macrobenthic assemblages.

In contrast to catastrophic, one-off sedimentation scenarios, Lohrer et al. (2004b) examined the impact of thin (less than 1 cm) sediment deposits on infaunal assemblages in the Whitford embayment and also considered repeated sedimentation events in their field experiment. Their findings show that even small amounts of terrigenous sediment significantly impact benthic assemblages with a consistently negative response to clay deposits regardless of assemblage type. Although single and repeated application of thin clay deposits did not result in complete defaunation, negative effects on benthic macrofauna at different sites in the embayment were evident in changes in assemblage structure. The number of individuals and taxa and the densities of common species showed a significant decline following clay deposition and taxa at the sediment surface were the most strongly affected. Repeated application of thin layers of clay led to a notable shift in assemblage compositions and assemblages did not fully recover between sedimentation events. In view of their findings, the authors warned that chronic sediment input even at low levels leads to habitat degradation in estuarine and coastal ecosystems, i.e., as small amounts of sediment are likely to be deposited more frequently than large, catastrophic amounts (Lohrer et al. 2004b).

5.4.4 Freshwater input

There has been no research in New Zealand on the influence of increased freshwater input/lowered salinity on intertidal macrobenthic assemblages in isolation from other disturbances, such as organic matter and pollutants. One study that assessed an *Austrovenus stutchburyi* population in Doubtful Sound in relation to lowered salinity through the input of freshwater from an electrical power plant documents a severe decline in cockles influenced by freshwater (Tallis et al. 2004).

5.4.5 Introduced species

A different threat to intertidal soft sediment environments is that posed by introduced or non-indigenous species. In a global context, marine habitats accrue non-indigenous species at what appears to be an

increasing rate and estuarine ecosystems have been singled out as common sites of invasions (Cohen & Carlton 1996, Ruiz et al. 1997). In regions where introduced species have been exclusively surveyed, such as North America, a large number of non-indigenous species have been recorded - in coastal environments along the Pacific, Atlantic, and Gulf coasts of continental United States, approximately 400 introduced species have been identified (Ruiz et al. 1997). San Francisco Bay, the largest estuary in North America, has been considered the most invaded estuary in the world with 212 non-indigenous species reported at this location; in a sub-environment of this bay, the brackish-water Lake Merritt, 37 of 46 invertebrate species were non-indigenous (Carlton & Geller 1993, Cohen & Carlton 1998). In the Southern Hemisphere, Port Philip Bay, southern Victoria, Australia was determined as one the most invaded marine ecosystems, based on the identification of 160 non-indigenous species following an extensive review of existing data and field surveys (Hewitt et al. 2004). Whilst comparisons between habitats and regions are hampered by scarcity of data, limited information that is available indicate that open coast habitats are less frequently invaded than estuaries and embayments; for San Francisco Bay, fewer than 10 non-indigenous species were identified from the outer coast in comparison to the large number of introduced species within the estuary (Ruiz et al. 1997). Non-indigenous species include a wide range of taxonomic and trophic groups, such as filter- and deposit-feeders and originate from different regions throughout the world. Although systematic studies are still few, it is becoming apparent that non-indigenous species can potentially have significant ecological impacts over broad spatial scales (Pollard & Hutchings 1990, Cohen & Carlton 1996). Following its introduction in San Francisco Bay, the Asian clam *Potamocorbula amurensis* reached extremely high population densities (greater than 12 000 individuals/m²), where it replaced the native estuarine bivalves *Macomona*, *Mya* and *Corbicula* in areas they had dominated previously (Nichols et al. 1990). In the New Zealand context, a study of the introduced Asian date mussel *Musculista senhousia* documented the detrimental effect of this bivalve on associated infauna in Tamaki Estuary (Creese et al. 1997). Intertidal areas that had extensive *Musculista senhousia* mats supported significantly fewer macroinvertebrates than areas without mussels; the effect on species richness was small, but species abundances were greatly affected and native infaunal bivalves showed the most dramatic decrease (8-fold) in population densities. The adverse effect on macrofaunal assemblages was considered to be localised and short-lived, however, as dense mussel beds appeared to be ephemeral. In concluding, Creese et al. (1997) did not expect this introduced species to expand outside the Auckland region, even though its rapid spread had been reported at other (subtidal) sites in Hauraki Gulf (Willan 1985, 1987). Another introduced bivalve, *Theora lubrica* has been predominantly reported from subtidal areas (e.g., Gardner & Wear 2006), but is also present in intertidal sediments as evident from ecological survey data (e.g., Ellis et al. 2006). Both introduced bivalve species were the subject of a recent modelling study to identify the suitability of different habitats for these invasive species; although the models had some value, their applicability was limited by the low spatial accuracy for predicting the likely distribution of these bivalves (Inglis et al. 2004).

Read (2006) reported the occurrence of the introduced polychaete *Paralepidonotus ampulliferus* from a number of intertidal sites in the Auckland region, including Waitemata and Manukau harbours, the Tamaki River Inlet and Weiti River (north of Auckland). This species was collected during several quantitative intertidal benthos surveys and was widespread in Waitemata Harbour and also occurred subtidally in Whangarei Harbour. The author noted that the earliest record of this species was from 1998, but suggested that it is likely that the polychaete had been missed in earlier surveys. Read (2006) also mentioned the presence of several other non-indigenous polychaetes in Waitemata Harbour and highlighted the difficulty of detecting non-indigenous marine species as the majority are small, non-aggregating, inconspicuous marine invertebrates that are easily overlooked in non-targeted surveys. Read (2006) echoed the earlier comments of Ruiz et al. (1997) who noted that although numbers of non-indigenous species for some estuaries and regions are large, they are likely to underestimate the true extent of invasions, as studies tend to focus on species for which historical distribution records and taxonomic identities are available, thereby excluding many small and inconspicuous species. Adding to the complexity of determining that a species is introduced is the uncertain taxonomic status of a large number of marine invertebrates; as these are considered “cryptogenic” (of uncertain origin) it is likely that a number of non-indigenous species are not recognised as such (Ruiz et al. 1997). As a consequence, although the threat of invasions in marine habitats has been recognised globally, the

magnitude of invasions and the long-term impact on native biota remain unstudied in a large number of regions. For New Zealand's intertidal soft shores, there have been no systematic reviews or assessments published to date that include detailed information on non-indigenous species similar to those available for other regions (e.g., Australia, Pollard & Hutchings 1990, Hewitt et al. 2004), although a surveillance programme including marine organisms has been established by Biosecurity New Zealand, included a list of "unwanted species" (<http://www.biosecurity.govt.nz/pest-and-disease-response/surveillance-risk-response-and-management/overview>).

5.4.6 Harvesting and aquaculture

Commercial/recreational fishing activities and aquaculture involve considerable disturbance on intertidal macroinvertebrates (Simenstad & Fresh 1995, Brown & Wilson 1997, Piersma et al. 2001). The harvesting of natural populations and aquaculture are predominantly focused on bivalves, but recreational and commercial bait collections also target other species of infauna, such as crustaceans and polychaetes (Beukema 1995, Contessa & Bird 2004, Watson et al. 2007). Overseas studies document the profound impact of intertidal fishing activities on associated macrobenthos, including direct and indirect effects caused by the physical disturbance of mechanical harvesting methods (Piersma et al. 2001, Watson et al. 2007). Commercial dredging for cockles *Cerastoderma edule* in the Dutch Wadden Sea revealed long-lasting negative effects on recruitment and settlement of bivalves (including the target species), with significant changes in sediment grain size (Piersma et al. 2001). Similarly, a comparison between protected marine reserve beaches and those open for recreational clam harvest in the United States demonstrated considerably greater bivalve abundance, richness and a larger number of polychaete species in protected areas (Griffiths et al. 2006). Bait-collection of crustaceans and polychaetes in the United Kingdom, United States, Australia, and South Africa has also been shown to have a notable influence on infaunal assemblages, generally resulting in lower densities and/or biomass of all or particular species most-impacted by the disturbance (Wynberg & Branch 1991, Brown & Wilson 1997, Skilleter et al. 2005b, Watson et al. 2007). In the Wadden Sea a study on the effects of large-scale mechanical harvesting of intertidal lugworms revealed a substantial decline in macrofaunal biomass including the local extinction of a dominant clam species, although short-lived macroinvertebrates were less severely affected; recovery to pre-exploitation level after removal of the dredge took in excess of 5 years (Beukema 1995). In Australia, bait collection of ghost shrimp *Trypaea australiensis* influenced the spatial distribution of several taxa and had an adverse effect on the abundance of a number of infaunal species, including polychaetes and crustaceans (Skilleter et al. 2005b). Associated with the direct impact of physical disturbance by harvesting are indirect effects such as changes in sediment characteristics and increased predation rates, as revealed by studies in Australia and South Africa (Contessa & Bird 2004, Wynberg & Branch 1991). Contessa & Bird (2004) identified bait-pumping and trampling associated with the bait-collection of burrowing ghost shrimp as the cause for a significant reduction in sediment porosity, oxygen and organic content in harvested areas. Furthermore, the assessment of impacts of ghost shrimp bait collection by Wynberg & Branch (1991) showed that substantial declines in macrofaunal densities and biomass were in part owing to increased seagull predation at impacted sites.

In New Zealand, commercial fisheries for cockle *Austrovenus stutchburyi* exist in different inlets in North and South islands, and cockle populations also support recreational and traditional fisheries (Ministry of Fisheries 2007), but the impact of harvesting on associated macroinvertebrates has been largely unstudied. The effects of commercial cockle harvesting on intertidal macrofaunal assemblages in Otago inlets was part of a PhD study (Irwin 2004), but these data are not available in published literature. At the same time, New Zealand's burrowing ghost shrimp *Callinassa filholi* is collected by recreational fishers for bait (Burgess 1995) and it is highly likely that polychaetes such as lugworms are similarly targeted; however, there have been no ecological studies concerning bait collection in New Zealand.

There is little information available regarding the influence of intertidal aquaculture in New Zealand on benthic assemblages, but detrimental effects associated with aquacultural practices in subtidal areas have been related to organic enrichment and deoxygenation of sediment and input of toxicants in the

form of pesticides to control parasites in farmed animals (Grant & Briggs 1998, Hartstein & Rowden 2004, see also Chapter 6). In light of the connectivity of soft sediment ecosystems, it is likely that similar habitat degradation occurs in intertidal areas. Intertidal aquaculture industries in sedimentary environments are uncommon in New Zealand, but it is conceivable that in the future (with the lifting of the moratorium on new aquaculture enterprises) such practices will expand to levels seen overseas. Reviewing the impact of intertidal aquaculture operations on macroinvertebrate assemblages in the Pacific Northwest, Simenstad & Fresh (1995) emphasised the influence of physical disturbance caused by the mechanical harvesting and manipulation of aquaculture farms. In addition, they considered changes in estuarine habitat types through the addition of gravel and acute effects associated with the eradication of functionally important organisms (seagrass and burrowing ghost shrimp), which interfere with the farming of bivalves. They found that the latter practice lead to a significant shift in benthic assemblages, but found that the influence of other aquaculture practices was within the scale of natural variation. At the same time, they highlight the difficulty of making valid comparisons between farmed and unfarmed areas in *post facto* situations within the same ecosystem (Simenstad & Fresh 1995).

5.4.7 Beach-specific stressors

Although research efforts concerning threats to beach environments have been limited, a similar range of stressors has been suggested for exposed beaches, including pollution, mining, fishing, urban development, and physical disturbance (Schoeman et al. 2000, Brown & McLachlan 2002). Overseas research shows that some of the most dramatic pollution effects regarding intertidal soft sediment assemblages have been linked to catastrophic oil spills causing the decline in abundance and diversity of macroinvertebrates (Teal & Howarth 1984), often with long-lasting effects (Mille et al. 1998). Toxic dispersants used for clean-up operations also have the potential to cause mass mortality of sediment macrofauna, as has been documented for rocky shore assemblages (Southward & Southward 1978). Although New Zealand has not experienced large-scale oil spills, smaller incidents occur occasionally and usually involve commercial vessels (e.g., bulk carriers, fishing vessels) (e.g., Maritime New Zealand 2006). Furthermore, the transport of fossil fuels to and from Marsden Point refinery via a tanker fleet and the presence of offshore oil developments such as the Tui Area Project off Taranaki are potential sources of oil pollution along New Zealand's coasts.

Overseas, physical disturbance effects have received the most attention in ecological beach studies. Human disturbance through recreational beach users was the subject of a study conducted on a beach in Chile, which showed unexpectedly that exclusion of beach users from part of the beach did not result in a change in macrofaunal abundances (Jaramillo et al. 1996). The authors suggested that natural disturbances at the highly dynamic beach were likely to outweigh those caused by beach users, resulting in a negligible impact of the latter on beach macrofauna (Jaramillo et al. 1996). The most recent research on the effects of physical disturbance from recreational activities evaluated the impact of vehicle beach use on macroinvertebrates (Wolcott & Wolcott 1984, Foster-Smith et al. 2007, Schlacher et al. 2007). The influence of off-road vehicles appears to be dependent on the location, frequency and timing of vehicle use. Wolcott & Wolcott (1984) found no adverse effects associated with vehicles on populations of ghost crab and clams in the United States, which they attributed to the low vehicle use at this beach, predominantly during the day when crabs are inactive. Consistent with this suggestion, crab burrows (used as proxies for crab abundance) at an Australian beach declined markedly in areas where off-road vehicle access was high; although the same areas were heavily used for other human activities (walking, horse-riding) and contained significant amounts of litter, the distribution and abundance of crabs were clearly related to vehicle use (Foster-Smith et al. 2007). Similar findings were reported by Schlacher et al. (2007), who showed that crab densities were significantly lower in beach areas that were exposed to heavy off-road vehicle traffic. At the same time, burrows only provided some protection from mortality and mortality rates were high at night, when crabs emerged from their burrows (Schlacher et al. 2007). Throughout New Zealand, beaches are extensively used by vehicles such as four-wheel drives and motorbikes (Environment Canterbury 2006, Northland Regional Council 2007) and other human uses include recreational and tourism activities; the impact of these activities on New Zealand intertidal beach macrofauna has not been examined.

Mechanical beach cleaning is currently not common practice in New Zealand, but occurs regularly at beaches overseas to remove macroalgae and litter (Llewellyn & Shackley 1996, Lavery et al. 1999). Ecological effects such as the physical disturbance by cleaning equipment and repercussion from the removal of algal material have received little research effort to date, but studies indicate that beach cleaning has a marked influence on intertidal macroinvertebrates (Llewellyn & Shackley 1996, Lavery et al. 1999, Dugan et al. 2003). In the United Kingdom, Llewellyn & Shackley (1996) examined the impact of mechanical beach cleaning on associated macroinvertebrates and reported severe adverse effects on species abundance and diversity. An Australian study considered short- and long-term effects of macroalgal removal on benthic assemblages in an estuarine system and showed that the one-off removal of macrophytes resulted in a decline in epifaunal densities, but did not affect infaunal abundances or species richness (Lavery et al. 1999). The same study compared benthic assemblages at two beaches, which differed in the occurrence of macroalgal removal and revealed that beach cleaning resulted in significantly different assemblage compositions relating to the long-term (i.e., several years) removal of algal material (Lavery et al. 1999). At the same time, a study across 15 beaches in the United States highlighted the importance of macroalgal beach wrack to benthic macroinvertebrates and documented significant declines in species richness, abundance and biomass associated with beach grooming (Dugan et al. 2003).

In addition to bivalve fisheries in sheltered locations, traditional, recreational and commercial fishing activities also occur on exposed New Zealand beaches, which support populations of surf clams, such as tuatua (*Paphies subtriangulata* and *P. donacina*) and toheroa (*Paphies ventricosa*) (McLachlan et al. 1996, Marsden 2000, Beentjes et al. 2006). Clam harvesting is associated with significant physical disturbance, but only a single study, in South Africa, has focused on the influence of beach fishing activities on associated intertidal assemblages (Schoeman et al. 2000). Experimental assessment of physical disturbance caused by the excavation and removal of sand to simulate clam fishing showed no consistent effects on macrofauna, which the authors attributed to their inability to distinguish between experimental and natural variation. As their study was the first of its kind, they suggested that more conclusive results would require a higher replication of experimental treatments in space and time (Schoeman et al. 2006).

Physical changes to the beach environment in the form of sediment erosion or accretion can also have severe repercussions for intertidal macrofaunal assemblages (Brown & McLachlan 2002, Defeo & McLachlan 2005). Two New Zealand studies highlight the close relationship between the distribution and abundance of dominant bivalves and habitat characteristics on exposed beaches, with changes in sand habitat significantly affecting the resident surf clam populations (Marsden 2000, Beentjes et al. 2006). In a survey of tuatua *Paphies donacina*, Marsden (2000) related the downward shift in the species' distribution in relation to tidal height to geomorphological changes in Pegasus Bay, where parts of the beach were markedly affected by sediment accretion. In contrast, beach erosion at Bluecliffs Beach/Southland between 1997 and 2005 resulted in a significant loss of sand, exposing gravel and cobbles substrates (Beentjes et al. 2006). The physical changes in sand habitat had an adverse effect on the abundance and distribution of toheroa *Paphies ventricosa* populations and the authors warned that continuing erosion of the beach habitat may lead to the collapse of the local bivalve population (Beentjes et al. 2006).

5.5 Biodiversity “hotspots”

The concept of “biodiversity hotspots” was initially proposed for terrestrial ecosystems by Myers et al. (2000) to enable the identification of areas in which conservation efforts should be concentrated. Accordingly, areas have to fulfil two criteria to be considered hotspots – a high level of endemism and a high rate of habitat loss (Myers et al. 2000). In marine systems, the concept has been applied to coral reefs (Roberts et al. 2002), but not to soft sediment environments. Ecological studies of the latter ecosystems in New Zealand and overseas do not provide sufficient information to identify potential hotspots, but highlight the importance of macrobenthic assemblages in sedimentary habitats. At the same time, the application of the concept remains untested in soft sediment environments and may not be applicable to coastal sedimentary systems. In order to identify biodiversity hotspots in sedimentary

habitats, a greater understanding of the functional role of macroinvertebrates is required in the context of defining habitat loss and diversity measures.

5.6 Gaps in knowledge

The current review of existing literature on intertidal macroinvertebrates highlights substantial gaps in the knowledge of New Zealand soft sediment ecosystems. Although detailed information is available for a few North Island estuaries, including comprehensive assessments of sediment disturbance, there is no general baseline data for a large number of locations and habitat types. Exposed sedimentary environments have received little to no research attention and remain largely unstudied. As a consequence, descriptive information of intertidal macrofaunal assemblage composition is scarce for most regions and there have been no biogeographical studies to systematically examine the distribution of intertidal benthic macroinvertebrates throughout New Zealand. Furthermore, there has been little research regarding the local distribution of benthic fauna (including recruitment patterns and natural structuring forces), trophic interactions, productivity measures and the impacts of human activities other than sediment input. These kinds of data are required to identify areas that may be considered “biodiversity hotspots”. Regardless of this term, a classification system incorporating comprehensive ecological data sets is ultimately required for the effective management and conservation of New Zealand’s intertidal soft sediment environments.

5.7 Recommendations for future research

To address the gaps in knowledge of intertidal macroinvertebrate assemblages it is recommended that the following areas be considered for future research:

- Meta-analysis of existing data sets to assess generalities in distribution and abundance patterns.
- Compilation of taxonomic information into a centralised, authoritative identification guide to allow consistent and confident species identification across locations and research institutions; including complementation of existing information with data on species for which taxonomic information is currently missing.
- Ecological surveys to obtain distribution and abundance data of coastal habitats that have received little or no attention to date, with a particular focus on exposed beach environments.
- A systematic biogeographical study that examines the distribution of intertidal macroinvertebrates throughout New Zealand.
- Examination of trophic interactions across different habitat types within the same ecosystem with consideration to the contribution of benthic assemblages to overall ecosystem productivity.
- Assessment of natural structuring forces (e.g., hydrodynamics, intra- and interspecific interactions) on benthic assemblages across different spatial scales with an emphasis on occurrence, density and recruitment patterns.
- Research of disturbance effects (other than sedimentation) on macroinvertebrate populations in sheltered and exposed environments, including examination of causal relationships.

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6. SUB-TIDAL MACROINVERTEBRATES

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6.1 Introduction

Marine soft-sediments are unconsolidated substrata such as mud, sand and gravels which constitute one of the largest ecosystems on Earth in areal coverage (Snelgrove et al. 1997). Around New Zealand soft-sediments form extensive areas of habitat in the estuaries, beaches and bays of the coast (Goff et al. 2003) and offshore on the continental shelf, slope and deep-sea (Mitchell et al. 1989). Living in and on soft-sediments are macroinvertebrates such as polychaetes, molluscs, crustaceans, echinoderms and many other taxa that form diverse assemblages integral to the functioning of the soft-sediment ecosystem (Snelgrove 1998). The focus of research on macroinvertebrates of sub-tidal soft-sediments around New Zealand has changed somewhat in recent decades, from surveys describing general characteristics of assemblages and biogeography of certain faunal groups (e.g., McKnight 1969a, 1969b), to more process-oriented studies concerned with understanding the links between physical and biological patterns (e.g., Chatham Rise, Nodder et al. 2003), and to studies where the impetus has come from the need for impact assessment and/or attention to fisheries-related issues in coastal waters (e.g., Thrush et al. 1998). Benthic studies at continental slope depths have to a very limited extent concerned human impact, with respect to possible mineral extraction (Dawson 1984), and also, more recently, effects of deep-water trawling (Cryer et al. 2002). Other work has focused on specific 'communities' of special importance for biodiversity, such as 'beds' or 'thickets' of bryozoans (e.g., Otago shelf, Batson & Probert 2000) and beds of horse-mussels (e.g., Mahurangi Harbour, Cummings et al. 1998, 2001).

Spatial differences in the attention given to macroinvertebrate communities around New Zealand exist. Certain sub-tidal soft sediment habitats are well studied, by comparison to other locations, primarily where they are in proximity to a marine laboratory and research base (e.g. Otago Harbour and shelf which are near to the University of Otago's Portobello Marine Laboratory, Rainer 1981, Probert & Wilson 1984, Probert et al. 1997). To a large extent, difficulties in sampling some sub-tidal areas in the past were great, contributing to the spatial pattern of studies undertaken. Certainly, practical resource limitations have contributed to the relative paucity of studies in the deep-sea around New Zealand to date. However, recent advancements in ship technology, positioning, diving, sampling, and photography by still and video imaging techniques have made remote and inaccessible habitats around New Zealand more accessible to quantitative studies (e.g. on seamounts, some of which possess soft-sediment habitat). Basic descriptions of communities (species inventories), including those that are potentially sensitive or 'special' communities, are still lacking for many areas around New Zealand (e.g. for vent and seep communities). However, marine ecologists and marine environmental/resource management agencies in New Zealand are increasingly aware of the importance and sensitivity of soft-sediment communities over varying spatial and temporal scales, to disturbance by fishing at even low but chronic levels (e.g. Thrush et al. 2001) and point-source impacts such as sewage and aquaculture (e.g. Anderlini & Wear 1992, Hartstein & Rowden 2004).

The availability of sufficient and suitable data frequently restricts the spatial extent over which patterns of diversity and threats can be assessed, and suggestions made concerning the need for further research that will allow for a better understanding of biodiversity and management of the environment (Grassle 2000). This impediment has been highlighted by Nelson & Gordon (1997) who indicated the extent of the challenges faced by scientists, environmental managers and policy makers who wished to assess, and utilise information pertaining to, New Zealand's marine biodiversity. Considering the cost-implications of gathering additional information, it is becoming increasingly necessary to exploit

sources of data that have hitherto been under-utilised (Whitehouse 1998). To facilitate the collation, and best utilisation, of such data it is wise to undertake a thorough and documented review of information already available before potentially initiating the collection of new data (Underwood 2000). The present review proposes to provide a useful synthesis of current knowledge, that will also include the identification of particular issues of interest or concern, for the subtidal macroinvertebrate communities of soft-sediment environments of New Zealand. The undertaking of this review is commensurate with some of the objectives of New Zealand's Biodiversity Strategy (produced in response to the Convention on Biological Diversity); to use cost-effective methods for evaluating marine biodiversity (objective 9.2); to improve knowledge of the distribution of marine biodiversity (objective 3.1); and to identify species and habitats most sensitive to disturbance [and put in place measures to avoid, remedy or mitigate adverse effects] (objective 3.4) (Anonymous 2000).

6.1.1 Scope

Traditionally, benthic communities have been recognised and described on the basis of the visually most conspicuous species (their abundance and/or biomass) – often the larger bivalves and echinoderms – as exemplified in the classical pioneering studies carried out in northern European waters by Petersen (Petersen 1914) and others (e.g., Ford 1923). This approach was widely adopted, including in New Zealand, notably in an early study of Powell (1937). In recent decades, however, the concept of community has been refined (e.g. “*community means a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups*”, Mills 1969). More objective statistical means of identifying communities and their diagnostic/characteristic taxa, in particular using multivariate techniques of numerical classification and ordination, are also employed (the first New Zealand study of sub-tidal benthic macroinvertebrates to employ such statistical methods was Knight 1974). These methods usually use numerical abundance rather than biomass data, and the sort of large-bodied (but not necessarily common) species traditionally used as characterising species are less likely to emerge as diagnostic. It can, therefore, be difficult to compare earlier and later studies carried out in the same region (e.g. Hayward et al. 1997). Even in recent times, the use of modern statistical methods has not been taken up by all marine benthic ecologists to identify and describe macroinvertebrate communities of soft sediments around New Zealand (e.g. Hayward et al. 2001) which further impacts the ability to make temporal or spatial comparisons of community composition.

For the purpose of greater completeness this review will consider studies that subjectively describe ‘assemblages’ and ‘associations’ as well as research that objectively identifies and describes ‘communities’. The term assemblage will sometimes be used as the common collective noun. Primarily, this review encompasses studies on the subtidal soft-sediment macroinvertebrate assemblages published in the primary scientific literature rather than the multitude of studies that appear in the grey literature (reports etc) because the latter, while containing potentially useful information, are not always peer-reviewed and are frequently difficult to access. The review aims to synthesize the current state of knowledge of the distribution and composition of assemblages, briefly evaluate the state of subtidal macroinvertebrate taxonomy and benthic biogeography, identify the likely “hotspots” of macrobenthic biodiversity, assess the threats and particular vulnerability of soft-sediment macroinvertebrate assemblages, and distinguish gaps in our knowledge before making recommendations on areas or assemblages that could be the subject of directed research in future years.

6.2 Current state of knowledge

Published studies of subtidal soft-sediment macroinvertebrate assemblages around New Zealand broadly occur in three major environment types: embayments and inlets (which includes estuaries), open continental shelf, and the slope. The review will consider each of these environments separately.

6.2.1 Assemblages of embayments and inlets

Studies of soft-sediment macroinvertebrates have been carried out in several New Zealand embayments and inlets of both the North and South Island. Below are reviewed those descriptive surveys that primarily aimed to identify and describe assemblage compositions and the environmental factors which account for their distributions. However, studies which had other aims (e.g. impact assessment) are also included here where useful information about assemblage composition is recorded.

6.2.1.1 Parengarenga Harbour

Parengarenga Harbour is one New Zealand's more pristine and most northerly large inlets. The survey reported by Hayward et al. (2001) provides the most comprehensive description of the macrobiota of this harbour. As part of this survey Hayward et al. (2001) sampled 147 species from 73 stations in the channels (0–25m), finding that whilst subtidal areas cover less than 25% of the harbour they support nearly 50% of the faunal diversity. Overall, polychaetes were the most abundant and speciose taxonomic group sampled in the subtidal environment. Hayward et al. (2001) recognised four subtidal faunal “associations” in the harbour. The lower harbour association was characterised by variable combinations of bivalves, including the dominant *Tawera spissa* and *Felaniela zelandica*. The upper harbour association, occurring in the upper portions of the four major arms of the harbour, was not subtidally-limited and extended into the low tidal flats throughout much of the harbour. This assemblage was characterised by the common nutshell *Nucula hartvigiana*, the widespread (yet patchy) cockle *Austrovenus stutchburyi*, and the pipi *Paphies australis*. Two “barren” associations were also identified, containing few live macro-organisms; one was at the harbour mouth where coarse sand was swept clean by strong tidal currents, and the other occurred in the northern arms of the harbour between the lower and upper harbour assemblages. Hayward et al. (2001) considered that the distribution of fauna in the subtidal channels reflected a salinity gradient from the mouth of the harbour to the more brackish upper reaches of the harbour arms, and a decrease in wave exposure in the same direction. Within the overall spatial distribution pattern, Hayward et al. (2001) noted that some species exhibited smaller scale distributional patterns between the harbour arms.

6.2.1.2 Auckland and Manukau Harbours

Between late 1927 and mid-1936, A.W.B. Powell of the Auckland Museum undertook a survey of the macrofauna of Auckland and Manukau Harbours. Powell sampled the seabed of these harbours using two types of small bottom dredge at 148 stations from a succession of small motor launches. His research, the first of its kind in New Zealand, was undoubtedly inspired by one of the foremost pioneers of benthic ecology, the Dane C.G.J Petersen, and those who had then recently applied his method for describing communities in Great Britain and the U.S.A. Powell (1937) described the composition of four assemblages (what he termed “formations”), three of which were made up of a number of “sub-associations”. The main assemblages were the “*Echinocardium* formation”, dominated by the heart urchin *Echinocardium australe*, the bivalve mollusc *Dosinia lambata* and the brittlestar *Amphiura rosea*, and found at stations with muddy sediments; the “*Maoricolpus* formation”, dominated by very high abundances of the gastropod *Maoricolpus roseus* found in sediments comprised of coarse shell debris with an admixture of fine sand and silt; the “*Tawera – Tucetona (Glycymeris)* formation” with seven characterising taxa, the most dominant of which are the bivalve molluscs *Tawera spissa* and *Tucetona (Glycymeris) laticostata*. This assemblage was the most species-rich of those found during the study, occurring at stations in the middle of the main channels of the outer harbour where the sediments were mainly composed of a whole and broken shell matrix (with a very small amount of mud); the “*Arachnoides* formation” was only found at four stations in the Manukau Harbour where the substratum was predominantly comprised of fine iron-sand. The fauna of this assemblage was very sparse and the dominant taxon was the cake-urchin *Arachnoides placenta*. Powell (1937) also identified another community, the “*Baryspira* community”, however he felt that insufficient samples had been taken to define this assemblage in the manner he adopted for describing the four “formations”. He did

note that the gastropod *Amalda* (*Baryspira*) *australis* was apparently characteristic of assemblages found in fine clean sand off the outer harbour beaches.

Powell (1937) considered that the assemblages he described were correlated with the texture of the substratum, and represented a ‘succession’ that reflected a gradual accumulation of shells to the original soft mud substrates of the harbour, formed under the influence of tides and wave-action. Powell (1937) made the relatively early observation that harbour works (tide-deflectors, embankments, reclamations) had depleted the seagrass (*Zostera*) beds, which would result in less vegetable detritus and in turn would influence “the distribution and frequency of animals taking this kind of food, as well as the abundance of fish feeding upon such organisms”.

Grange (1979) reported on a survey of macrobenthic organisms (including algae) sampled at 42 stations in Manukau Harbour, which included stations in the vicinity of the nine stations sampled by Powell (1937) in this harbour. Grange (1979) appears to be among the first (the other being Knight 1974) in New Zealand to apply, to data obtained from subtidal soft sediments, the multivariate statistical techniques that are now among those accepted as the standard procedure for identifying and describing macrofauna communities. The analysis undertaken by Grange (1979) discerned four communities, quantifying composition and identifying “indicator species” for each. The four communities were the “*Microcosmus* - *Notomithrax* community” found in the central part of the harbour (1–9 m water depth) with coarse sediment composed of shells and small rocks; the “*Halicarcinus* – *Bugula* community” restricted to deeper water (7–16 m) of the main channels where relatively coarse sediment with very little sand was found; the “*Amalda* – *Myadora* community”, a community that appeared to be fairly extensive in shallow-water (1–8 m) parts of the channels where sediments were largely medium to fine sand with mud or shell; the “*Fellaster* - *Pagurus* community” of relatively low species diversity was restricted to stations in shallow-water (1–2 m) of the outer harbour in clean, well-sorted, fine sand. Grange (1979) commented on the equivalence, or lack of, for the communities he identified with those described by Powell (1937). It is worth making particular mention here of the observations/comments made by Grange (1979) concerning the *Microcosmus* – *Notomithrax* community; that is, stations of this community had the highest average species diversity (including the most diverse station of all), an observation believed to be a consequence of the coarse and variable substrate that provided habitat for a large number of sessile epifaunal suspension feeders (e.g. the ascidians *Microcosmus kura* and *Styela plicata*, the sponges *Callispongia ramosa* and *Halicondria moorei*, and the gastropod *Zegaleurus tenuis*), mobile epifaunal carnivores (e.g. the asteroid *Coscinasterias* [*calamaria*] *muricata*, and the brachyurans *Notomithrax minor* and *Halicarcinus varius*) and grazers (e.g. the chitons *Terenochiton inqinatus* and *Acanthochitona zelandica*).

Hayward et al. (1997) report on faunal changes in Waitemata Harbour soft sediments after comparing assemblage compositions as revealed by monitoring surveys in the 1990s and those described by Powell (1937) from the 1930s. Data from the two study occasions could not be compared using modern statistical methods. Instead, Hayward et al. (1997) describe qualitative differences in the composition and distribution of the harbour’s fauna after “intuitively” deducing contemporary associations in a manner similar to that used by Powell (1937). Whilst some similarities in levels of diversity and spatial pattern exist between the assemblage descriptions made more than 50 years apart, Hayward et al. (1997) also note some significant differences. Some mollusc species appear to have either disappeared or are reduced in abundance, to the extent that two of Powell’s assemblages (*Tawera-Tucetona*, *Amalda*) from the outer harbour no longer exist. Conversely, some mollusc species have colonised the harbour or have increased in abundance. The most significant of these changes include the establishment of an extensive horse mussel (*Atrina zelandica*) bed, and the introduction of three “exotic” bivalves (*Limaria orientalis*, *Theora lubrica*, *Musculista senhousia*) which now characterise six of the eight faunal assemblages recognised in the 1990s. Hayward et al. (1997) speculate that the causes of the observed changes are likely to be both natural and anthropogenic.

6.2.1.3 Whangateau Harbour

The macrofauna assemblages of the soft-sediments at the entrance to Whangateau Harbour were subjectively distinguished by Grace (1966) in a manner apparently similar to that applied by Powell (1937). Grace (1966) recognised ten assemblages found in a range of substrate types from mud to coarse shell-gravel, and considered salinity, tidal currents and wave action to be the main physical factors responsible for the structure of the observed assemblages. These environmental conditions changed over short distances and apparently corresponded to the heterogeneous distribution of the assemblages at the harbour entrance (Grace 1966). This relatively early study of macrofauna assemblages of New Zealand is noteworthy for its suggestion that knowledge from the survey could be used to “predict with some degree of accuracy the general bottom communities which will be found” at other harbour entrances on the Northland and Coromandel east coasts.

6.2.1.4 Tutukaka Harbour

Benthic sampling in Tutukaka Harbour on the east coast Northland revealed via “intuitive, non-statistical analyses” four “associations” and two “sub-associations” of soft-sediment macrofauna in this shallow-water (0–12 m) embayment (Brook et al. 1981). A “*Chione – Nucula – Tellina (Macomona)* association” characterised the inner muddy sediments of the harbour; a “*Nucula – Tellina (Macomona) – Leptomya* subassociation” occurred on shelly muddy fine sand in channels approximately 2 m water depth; a “*Theora* association” was found at the head of the harbour in shallow-water (1–2 m) muds and sandy muds; a “*Corallina – Maoricolpus – Notomithrax* association” characterised gravelly sands and gravelly muddy sands where they occurred (1–7 m water depth) adjacent to rocky areas throughout the harbour; a “*Gari – Myadora – Nucula* association” was found throughout most of the harbour at depths of 0.8–11 m in muddy fine sand and fine to medium sand; an “ascidian – *Gari* subassociation” occurred in fine to medium sand and gravelly sand in the outer part of the harbour (7–12 m water depth). Brook et al. (1981) considered that of the assemblages they identified, the distinction of which could not be attributed to any one physical factor such as sediment type, all but one could be recognised as being the same or similar to those observed elsewhere in embayments and inlets around New Zealand. The ‘unique’ “ascidian – *Gari* subassociation” was apparently restricted to clean sand and gravelly sands and had only previously been observed to occur off Mayor Island (14–20 m water depth) in the Bay of Plenty (Brook et al. 1981).

6.2.1.5 Mahurangi Harbour (and adjacent Martins Bay)

The horse mussel *Atrina zelandica* is a large, suspension-feeding bivalve that occurs patchily in muddy to sandy shallow subtidal (less than 50 m) soft-sediments around the coast of New Zealand. *Atrina* lives partially buried in the substrate and can provide complex physical structure to soft-sediment habitat. It is for this reason that Cummings et al. (1998, 2001) examined the influence of this bivalve on the composition of associated macroinvertebrate infaunal assemblages at muddy sites in Mahurangi Harbour and at a contrasting (sandy) adjacent coastal site in Martins Bay. The study of Cummings et al. (1998) found clear differences in the macroinfaunal assemblages in and out of *Atrina* patches at both study sites. Differences in the assemblages were largely driven by differences in the abundance of infauna at the harbour site, whilst species composition as well as abundances differed in and out of *Atrina* patches at the coastal site. Phoxocephalid amphipod, the cumacean *Hemileucon uniplicatus* and the polychaete *Cossura* sp. were found both inside and outside *Atrina* patches at the harbour site, a paracalliopid amphipod, the polychaete *Minuspio cirrifera* and the bivalve *Nucula hartvigiana* also dominated the “*Atrina* community”, and an exogonid polychaete was also a dominant component of the “bare” sediment assemblage. The burrowing anemone *Edwardsia* sp., phoxocephalid and haustorid amphipods were common taxa found both inside and outside *Atrina* patches at the coastal site, whereas the polychaetes *Heteromastus filiformis* was more abundant in assemblages inside, and *Boccardia* sp. and *Euchone* more abundant outside the patches. Cummings et al. (1998) considered that whilst their study had demonstrated that the presence of *Atrina* influenced the composition of assemblages at the study sites, there was no one process controlling the distribution of macrofauna relative to the horse mussel and further research was required. Follow-up field experiments were carried out at sites (in the

same area) with different current velocities/sediment types, where the density of *Atrina* was manipulated (Cummings et al. 2001). These authors found that the influence of the mussel on the associated macrofaunal community was not generally simple, because interactions between *Atrina*, site hydrodynamic regimes and sediment type influenced the macrofauna assemblages. Cummings et al. (2001) concluded that, despite the robust nature of their experimental design and the fact that it demonstrated that *Atrina* does influence macrofaunal communities, “specific experiments may not alone lead to generalisable results, simply because the system is too complex”.

In the same harbour and adjacent coastal area Lohrer et al. (2004, 2005) conducted studies examining populations of the heart urchin *Echinocardium australe (cordatum)* in order to understand its functional role in coastal soft-sediment ecosystems. These studies demonstrated that considerable sediment reworking by *Echinocardium* (Lohrer et al. 2005) enhances the flux of organic nutrients from sediments to bottom water which improved conditions for production by microphytobenthos (Lohrer et al. 2004). Whilst examining for confounding effects in their manipulative experiment Lohrer et al. (2004) noted that there were “no consistent effects of *Echinocardium* density on faunal variables [community composition, taxonomic richness, diversity and abundance] over time”. Nonetheless it is possible, because some macroinvertebrate fauna feed on microphytobenthic organisms, that bioturbation by this common species of the New Zealand shelf and slope benthos (which also alters the topography of surficial sediments) could have an influence on the composition of associated macrofauna assemblages.

6.2.1.6 Wellington Harbour

Rather surprisingly, considering the proximity of Victoria University (and its Island Bay Marine Laboratory) and the New Zealand Oceanographic Institute (NZOI) (the latter now part of National Institute of Water & Atmospheric Research), there is no published account that describes ‘whole’ macroinvertebrate assemblages throughout Wellington Harbour. This is not to say that many samples of soft sediment macrofauna have not been taken in this locale, rather the efforts in this direction of both the aforementioned scientific institutes have either not been reported upon in the accessible literature or data obtained even formally analysed. In 1964 a benthic survey comprising over 100 stations was undertaken by NZOI, however, the only harbour-wide descriptions to appear in the literature were for the harbour’s sediment composition (van der Linden 1967). Simple lists of the species sampled during this early survey were eventually published in a review of scientific and technical studies of Wellington Harbour (see Appendix 12 by E. Dawson, EHEA (1998)). Students of Victoria University and the university’s Coastal Marine Research Unit were particularly active in carrying out a number of studies and surveys in the harbour in the 1970s and ‘80s. McKoy (1970) published a description of macrofauna assemblages sampled at four sites, whilst Booth (1972) presented in his PhD thesis a multivariate analysis of data for molluscs obtained from over 50 stations in the harbour. Both these authors emphasised the relationship between the composition of fauna observed and the distribution of sediment type. Whilst much of the work of academics from Victoria University on macroinvertebrate assemblages is documented only in unpublished reports, more recently research has begun to be published in the primary literature. Wear and Gardner (2001) examined the influence of a naturally occurring toxic algal bloom on macrofauna assemblages by comparing data obtained post-bloom from six subtidal sites (and one intertidal site) with unpublished pre-bloom data from the same locations. These authors described the relative impact of the bloom on macrofauna assemblage composition as depending upon the geographic and environmental properties of the study sites. Assemblages at low-energy deeper-water locations with silty sediments were apparently impacted more severely than a shallower high-energy site with sandy sediments (Wear and Gardner 2001). Subsequently, further studies of macroinvertebrate assemblages were undertaken with a focus on the recovery of assemblages from the effects of the toxic algal bloom disturbance (Kroger et al. 2006 a,b).

6.2.1.7 Marlborough Sounds

The earliest study undertaken in the Marlborough Sounds was by Dell (1951) who sampled at three stations using a naturalist dredge in Queen Charlotte Sound. Dell described a brachiopod (*Calloria* and *Tegulorhynchia*) – *Chlamys* “formation” from one site, and considered it similar to assemblages, i.e. *Mariocolpus* and *Tawera* – *Tucetona* (*Glycymeris*), found in Auckland Harbour habitats by Powell (1937) and certain other high-current areas in Fiordland by Fleming (1950). At the other sites sampled, two different *Echinocardium* “formations” were identified, one of which was deemed similar to the *Echinocardium* assemblage previously described from Auckland Harbour (Powell 1937), whilst the other (*Echinocardium* – Scaphopod “formation”) was considered somewhat different and to represent “a deeper water community in more open waters” (Dell 1951). Estcourt (1967), reporting on the sampling of over 50 stations (11–140 m) using a large grab, noted an *Asychis* – *Echinocardium* – *Amphiura* “association” (or “sheltered water muddy-bottom association”) at the majority of sites throughout the Sounds. This situation was presumed to be because there were generally only minor differences in environmental factors such as depth and sediment type between sampling stations. However, some differences were noted in the composition of assemblages between Queen Charlotte and Pelorus Sounds, possibly due to higher fresh water input in Pelorus Sound and the supply of algal detritus from intertidal sand and mudbanks (Estcourt 1967). At least two other “associations” were identified in places where tidal currents were strong, and these were considered by Estcourt to be somewhat similar to the Brachiopod – *Chlamys* assemblage previously described by Dell (1951) from the Sounds. Estcourt indicated the difficulties in making comparisons with previous descriptions of assemblages from elsewhere in New Zealand.

6.2.1.8 Lyttelton Harbour

Despite a long history of commercial and recreational use of Lyttelton Harbour, only the study by Knight (1974) provides a quantitative community analysis and comparison with environmental data. This study is notable as being the first study in New Zealand of sub-tidal macroinvertebrate taxa that used largely objective statistical methods to identify and describe communities (Cassie & Michael 1968 had previously examined intertidal communities in Manukau Harbour). Two different statistical techniques were used to identify communities, and their environmental characteristics, from a sub-set of the 71 stations sampled (using three different gear types) in the harbour. Three main benthic soft-sediment communities were identified: *Macrophthalmus* (*Hemiplax*) *hirtipes* – *Virgularia* *gracillima* community of muddy substrata, *Zeacolpus* *vittatus* – *Pectinaria* *australis* community on coarser sandy substrata, *Austrovenus* (*Chione*) *stutchburyi* community in restricted sandy areas. [Also recognised was an “*Ostrea* – *Sigapatella* association” of opportunist species that occurred sporadically on a variety of hard substrata.] Despite using very different techniques to identify communities, Knight (1974) attempted comparisons between the composition of assemblages in Lyttelton Harbour and those described earlier from harbours and embayments elsewhere in New Zealand. Assemblages from muddy areas in Auckland and Manukau Harbours described by Powell (1937) possessed a number of species common to the Lyttelton Harbour muddy substrata community, however, *Echinocardium* (dominant in the former harbours) was not present in the latter harbour. Comparability between assemblages found in sandy substrates described by Powell (1937) and by Knight (1974) was much less obvious. Greater resemblance was noted between the two sandy substrate communities of Lyttelton Harbour and two described by Ralph & Yaldwyn (1956) in Otago Harbour (see below).

Knight (1974) considered that assemblages described by Estcourt (1967) from Marlborough Sounds were “almost totally different” from any in Lyttelton Harbour. It is of interest to note that Knight (1974) is one of the few observers of benthic assemblages in New Zealand to stress the nature of continuums in the distributions of species in soft-sediments and to emphasize that “the fauna changes continuously and is not differentiated, except arbitrarily, into sociological entities”.

6.2.1.9 Otago Harbour

Ralph and Yaldwyn (1956) identified two associations from middle reaches of Otago Harbour in their basic yet informative description of seafloor animals in the vicinity of Portobello Marine Laboratory. These authors nominated, on the basis of the most common organisms present at 11 sample stations: an

“*Austrovenus* association” dominated by the bivalves *Austrovenus stutchburyi* and *Macomona liliana* and the polychaetes *Abarenicola* (*Arenicola*) *affinis* (sub-association “A”) and *Algaophamus macroura* and *Aricia* sp. (sub-association “B”); and a “*Maoricolpus* association” dominated by the gastropod *Maoricolpus roseus*, the polychaete *Harmothoe praeclara* and the ophiuroid *Ophiomyxa brevirima*. The former assemblage was found in intertidal sands and presumed to extend into the shallow sub-tidal, whilst the latter assemblage was found in channels on a shell-sand bottom, in places clearly subject to strong tidal currents. Rainer (1981), after quantitatively sampling fauna and sediment at 34 stations in Otago Harbour and Blueskin Bay (the neighbouring embayment to the north), distinguished five assemblages on the basis of environmental criteria (in the sense described by Jones 1950): “harbour mud community”, “harbour fine sand community”, “harbour stable shell-sand community”, “harbour unstable sand community”, “shallow offshore fine sand community”; but overall there is a gradation from clean sand and shelly substrata in the outer harbour to muddier sediment in the upper harbour. Rainer (1981) recognised a number of sub-divisions of his “communities” and noted that the presence of whole or broken shell exerted an influence on assemblage composition by providing a substrate for the growth of macroscopic algae. This author also remarked that species diversity within communities was not only influenced by the presence/absence of algae but also by the grade, stability and degree of sorting of the sediment (Rainer 1981). The two associations previously described by Ralph & Yaldwyn (1956) from the harbour were considered “roughly equivalent” to the harbour fine sand and harbour mud communities, whilst the *Macrophthalmus* (*Hemiplax*) – *Virgularia* and *Austrovenus* communities found in Lyttelton Harbour by Knight (1974) were also considered to be similar, respectively (Rainer 1981). However, Rainer (1981) noted that whilst there was some species overlap between assemblages described from elsewhere in New Zealand, robust comparisons were complicated by the varying selectivity of the sampling methods used in the different studies, and thus had to conclude that “communities recognised [in Otago Harbour] do not accord well with those listed by other authors for the New Zealand area”.

Thrush (1988) in an experimental study of physical sediment disturbance at a shallow subtidal site (6 m) provided some additional information regarding the macroinvertebrate assemblages in the sandy sediments of the harbour and the factors which influence their composition. Polychaetes (belonging to a variety of different feeding “guilds”) were particularly common, other fauna sampled included oligochaetes, amphipods, isopods, bivalves, gastropods, ophiuroids, holothurians and phoronids. The experiment demonstrated that benthic fauna recolonise the sediment relatively quickly after a simulated storm disturbance and that macrofauna composition was different near and away from the burrows of the crab *Macrophthalmus hirtipes*. The study by Thrush (1988) indicated the importance that relatively large organisms which modify their habitat have for the maintenance of diversity in some soft-sediment environments. Grove and Probert (1999) used a similar suction sampler to that used by Rainer (1981) for their study of 15 stations in upper Otago Harbour, which in part aimed to examine the relationship between pollution sources and benthic community structure. Multivariate analysis of resulting data revealed three communities, the most distinct of which was one associated with an area (Sawyers Bay) impacted by sewage and industrial waste (Grove & Probert 1999). The two other communities were located in the lower harbour (“Group 1”), in generally less muddy sediments, and the relatively deeper upper harbour basin (“Group 2”). The Sawyers Bay community was characterised by the gastropod *Thoristella chathamensis* and the crab *Macrophthalmus hirtipes*, Group 1 by nuculid bivalves, maldanid polychaetes, and Group 2 by holothurians, ophiuroids, a chiton and terebellid, polynoid and hesionid polychaetes. Analysis of the relationship between environmental variables and community composition revealed the importance of the sand content of the sediment and the presence of macroalgae – some taxa being directly associated with the algae *Ulva* sp. and *Lenormandia chauvinii* (Grove & Probert 1999).

6.2.1.10 Paterson Inlet

The macroinvertebrate assemblages of soft-sediments in Paterson Inlet, on the north-east coast of Stewart Island, have received relatively thorough attention. Batham (1969) began the study of whole assemblages by qualitatively sampling eight stations in Glory Cove with an Agassiz trawl and dredge. The seafloor of the cove is relatively shallow (6–15 m) and macroalgae were common throughout on a

relatively uniform sandy-mud sediment. Batham (1969) reported that there were no obvious correlations apparent between the slight differences in sediments and the species occurring at given stations. The assemblage was dominated by echinoderms: the urchins *Evechinus chloroticus* and *Echinocardium cordatum*; the seastar *Coscinasterias* [*calamaria*] *muricata*; the brittle star *Ophiopsammus* [*Pectinura*] *gracilis*; and sea cucumbers, including *Stichopus mollis*, *Amphicyclus thomsoni* and *Chiridota nigra*. Other fauna commonly present at most stations included the turrent shell *Maoricolpus roseus*, the hermit crab *Pagurus traverse*, the polychaete *Eunice australis*, the chiton *Terenochiton inquinatus*, and the trochid *Micrelenchus micans*. Batham (1969) didn't consider it useful to compare the assemblage of Glory Cove with those described from elsewhere in New Zealand.

An extensive examination of the benthic assemblages of Paterson Inlet (as a whole) was undertaken by Willan (1981) based on sampling of 53 soft-sediment stations by dredge, diver and photography. Willan (1981) subjectively recognised two “associations” based on the presence of large ‘indicator’ species. Willan (1981) reported a clean sand assemblage in the outer inlet, subject to strong current movement, and dominated by infaunal bivalves (including *Atrina zelandica*, *Pratulum pulchellum*, *Tawera spissa*, *Scalpomactra scalpellum*, *Gari hodgii*, *Thracia* sp., *Myadora striata*, *Offadesma angasi*) and with a sparse epifauna (*Pecten novaezelandiae*, *Neothyris lenticularis*, *Stichopus mollis*, *Ophiopsammus maculata*, *Evechinus chloroticus*, *Xymene ambiguus*). Where shell gravel occurred in areas in the outer part of the Paterson Inlet, bryozoan (particularly *Cinctipora elegans*) ‘mounds’ offered habitat for a diverse fauna of encrusting and nestling species (ascidians, sponges, tubicolous polychaetes, bivalves, chitons, brachiopods) (Willan 1981). The second association of muddy substrata occurred in the middle and inner parts of the Paterson Inlet where current movement was negligible. This area had extensive cover of the red algae *Lenormandia chauvinii* and *Rhodomenia* spp., whilst the characteristic macroinvertebrates were pectinids (*Talochlamys* (*Chlamys*) *gemmulata*, *Pecten novaezelandiae*), brachiopods (*Terebratella sanguinea*, *Neothyris lenticularis*), turritellid (*Maoricolpus roseus*), and the echinoderm species also noted by Batham (1969). Willan (1981) noted the similarity between the muddy assemblage and that assemblage described by Batham for Glory Cove, despite the differences in sampling techniques that Willan noted would favour the recording of epifauna in his study. Willan (1981) did not wish to assign the Paterson Inlet fauna to any soft-bottom assemblages recognised elsewhere in New Zealand, questioning the validity and therefore the value of the ‘community concept’. Nonetheless he made comparisons between the assemblages of Paterson Inlet and elsewhere, finding differences and similarities between the fauna of Marlborough Sounds, and Fiordland (see above). Willan (1981) also indicated the “importance” of bryozoans for the development of specific assemblages, which he noted were recorded by Probert et al. (1979) on the Otago shelf (see below) and which he considered “may be widespread on the shelf around southern New Zealand” (see also below).

6.2.1.11 Fiordland

The soft-sediment assemblages of a number of fiords were qualitatively described by Fleming (1950) based on the molluscan fauna, largely by reference to those assemblages described by Powell (1937) from Auckland Harbour. Five assemblages were identified: “soft mud; sandy mud and muddy sand; shells and sand with little mud; Brachiopod-*Chlamys*; Coralline Algae”. The latter assemblage is worth particular note, for such assemblages or habitats are known as rhodolith or maerl beds and usually possess a diverse fauna (see Chapter 4, section 4.3, and also section 6.2.2.3 below). Whole assemblage descriptions were later provided by Hurley (1964) (Milford Sound), McKnight (1968) (Chalky and Preservation Inlets), and McKnight and Estcourt (1978) (Caswell and Nancy Sounds), all based on qualitative samples. Hurley (1964) recognised three “communities”: a “Brachiopod - *Chlamys* community” at the entrance sill, which he noted had also been observed in Queen Charlotte Sound (Dell 1951) and Cook Strait (Hurley 1959); an “*Echinocardium* community”; and a “mixed community” that possessed faunal components of both the aforementioned assemblages. Seemingly widespread in the fiords on muddy bottoms in less than 200 m is an assemblage that often includes *Pratulum pulchellum*, *Amphiura* spp. and *Echinocardium cordatum*, and was referred to by Fleming (1950) as “soft mud substratum community”, by Hurley (1964) as an “*Echinocardium* community”, and by McKnight and Estcourt (1978) as a “*Nemocardium pulchellum* – *Dosinia lambata* community” (in the sense of McKnight 1969a), and comparable to *Echinocardium* communities farther afield, such as in Queen Charlotte Sound (Dell 1951). In deeper water mud (typically 200–400 m), a “*Neilo australis* - *Brissopsis oldhami* assemblage” was identified characterised by *Neilo australis* (bivalve), *Brissopsis oldhami* (echinoid), *Fissidentalium zelandicum* (scaphopod), *Hyalinoecia tubicola* (polychaete), *Psilaster acuminatus* (asteroid), *Ophiomyxa brevirima*, *Ophiura irrorata* (ophiuroids), *Metanephrops challengerii* and *Trichopeltarion fantasticum* (decapods) (McKnight 1968, McKnight & Estcourt 1978). Hurley (1964) noted the possible influence of periods of bottom water “stagnation” on benthic life and the temporal composition of assemblages in the fiords, whilst McKnight & Estcourt (1978) remarked that each fiord “has a particular physiography, in which the sill depth, bottom topography, freshwater input, and fauna inter-relate to determine the physical and biological environment. The overturn cycle of any one fiord may bear no relationship to that of another and hence the faunas sampled at any time may be expected to show some differences.”

6.2.2 Continental shelf assemblages

Thousands of benthic samples have been taken on New Zealand’s continental shelf (Nelson & Gordon 1997) and it is possible, despite the generally unintegrated nature of some of the surveys, to appreciate the basic pattern of the composition of soft-sediment macroinvertebrate assemblages and some of the environmental factors which influence their distribution.

6.2.2.1 Shelf-wide patterns

The only study to consider the macroinvertebrate assemblages of soft-sediments throughout the entire shelf area of New Zealand is that by McKnight (1969a). Some data discussed in McKnight (1969a) resulted from an ambitious undertaking by New Zealand Oceanographic Institute (NZOI) to conduct a “preliminary” survey of the continental shelf fauna in 1961 and 1962 (three voyages were required and 331 stations were occupied during the survey). McKnight (1969a) augmented data collected by the shelf survey with data obtained from earlier and subsequent sampling (a total of nearly 600 samples) to identify 17 “communities” based on “the larger infaunal bivalves and echinoderms”. Despite the fact that McKnight noted clearly that his communities should be “regarded as provisional and certainly worth closer and more detailed examination” there is, to date, no comparable data, on the scale of the entire shelf, to supersede the assemblage descriptions he presented.

From his (appended) station data, it is possible to evaluate the relative abundance, distribution and sediment affinities of his communities. McKnight recognised four major “communities” on the

continental shelf: "*Venus* communities" (communities 9–12) as occurring at 54% of stations, "*Nemocardium* [*Pratulium*] communities" (communities 13–15) at 37%, "*Amphiura* communities" (communities 1–4) at 8%, and "polychaete communities" (communities 6–8) at 2% ($n = 597$, which excludes communities restricted to harbours (communities 5, 16 & 17), and stations for which faunal and environmental data are inconclusive). Sediment analyses (available for 79% of both *Venus* and *Nemocardium* communities) show that *Venus* communities tended to occur on coarser sediments than did *Nemocardium* communities. For *Venus* communities, 78% of records are from sediments ranging from gravel to sand, whereas 91% of sediment samples from *Nemocardium* communities range from muddy sand to mud. McKnight (1969a) recognised four *Venus* communities: *Scalpomactra scalpellum* - *Maorimactra ordinaria* community (Ss-Mo) (37% of *Venus* records), *Tawera spissa* - *Venericardia purpurata* community (Ts-Vp) (29); *Glycymeris laticostata* - *Venericardia purpurata* community (Gl-Vp) (28%), and *Tawera spissa* - *Diplodonta globus* community (Ts-Dg) (6%); and three *Nemocardium* communities: *Nemocardium pulchellum* - *Pleuromeris zelandica* community (Np-Pz) (64% of *Nemocardium* records), *Nemocardium pulchellum* - *Venericardia purpurata* community (Np-Vp) (29%), and *Nemocardium pulchellum* - *Dosinia lambata* community (Np-Dl) (7%). The *Venus* communities can be divided into two pairs. Ss-Mo and Ts-Vp were predominantly middle to outer shelf communities and occurred mainly on sandy and gravelly substrata respectively. Ts-Dg and Gl-Vp also occurred on sandy and gravelly sediments respectively but, by contrast, they had a shelf-wide bathymetric range and both were best represented off southern New Zealand, though the eponymous species were all widely distributed in the New Zealand region (Spencer & Willan 1995). McKnight (1969a) recorded Ts-Dg only south of 42° S, and 75% of the records of Gl-Vp are from south of 44° S. Gl-Vp was the dominant community of coarse biogenic sediments south of Stewart Island. *Venus* communities would thus seem to have been less well represented at middle to outer shelf depths off northern New Zealand than they were off southern New Zealand. Among the muddy bottom *Nemocardium* communities, both Np-Vp and Np-Pz occurred at all shelf depths and were widely distributed geographically where suitable substrata occur; Np-Pz tended to be found on muddier sediments than did Np-Vp. McKnight (1969a) recorded Np-Dl at only 15, mainly inner shelf stations, but the community appeared to have a reasonably wide geographic distribution. McKnight (1969a) recognised two further assemblages associated predominantly with muddy substrata. *Amphiura* communities occurred predominantly in shallow-water muddy sediments; some 90% of records are from water depths of less than 50 m and 90% from sediments ranging from muddy sand to mud. McKnight assigned 11 samples to two open sea polychaete communities: a *Neilo australis* - *Brissopsis oldhami* community which occurred at outer shelf to upper slope depths on mud, and a polychaete - *Tellinella charlottae* community recorded only from organic-rich mud at depths of 60–70 m off the South Island west coast.

The characterising species listed by McKnight (1969a) broadly indicated the relative importance of predominant feeding groups in these infaunal communities. Thus, the suspension-feeder dominated (Gl-Vp, Ts-Vp) and deposit-feeder dominated (*Amphiura* and polychaete) communities appeared to correspond to a gradation of sediment type, from clean gravelly and sandy sediments to muds. The geographical distribution of the major community types (Figure 6.1) thus tended to reflect the pattern of sedimentation around New Zealand (Carter 1975; Griffiths & Glasby 1985; Mitchell et al. 1989; Hicks and Shankar 2003). *Venus* communities were thus particularly well represented off Northland, off the west coast of the North Island to mid-shelf depths, and off southeastern and southernmost New Zealand. Surface sediments in these areas consist chiefly of modern terrigenous clean sands and coarser-grained relict terrigenous or biogenic sediment, or both (Mitchell et al. 1989). *Nemocardium* communities occurred primarily in areas of mud deposition, such as off the Bay of Plenty, North Island east coast, northeast coast of South Island, and off the west coast of South Island. McKnight's *Amphiura* and polychaete communities were also mainly associated with muddy sediments. This broad-scale pattern indicates that macroinvertebrate assemblages of the New Zealand shelf can differ substantially depending, in particular, on the modern sedimentation regime. At one end of the spectrum are shelves with high modern sedimentation, typified by the North Westland and South Westland (68.5 million tonnes y^{-1}) and East Cape (69 million tonnes y^{-1}) areas (Hicks and Shankar 2003) and covered largely by modern muddy sediments (Mitchell et al. 1989). In contrast, are those shelves with low modern sedimentation covered largely by coarser relict and biogenic sediments (Mitchell et al. 1989), such as

occur off the Northeast coast and Otago (both 1.2 million tonnes y^{-1}) (Hicks and Shankar 2003). The three best studied shelf areas off the South Island west coast, the north-eastern coast of the North Island, and Otago illustrate this contrast in modern sedimentation and associated macroinvertebrate assemblage composition.

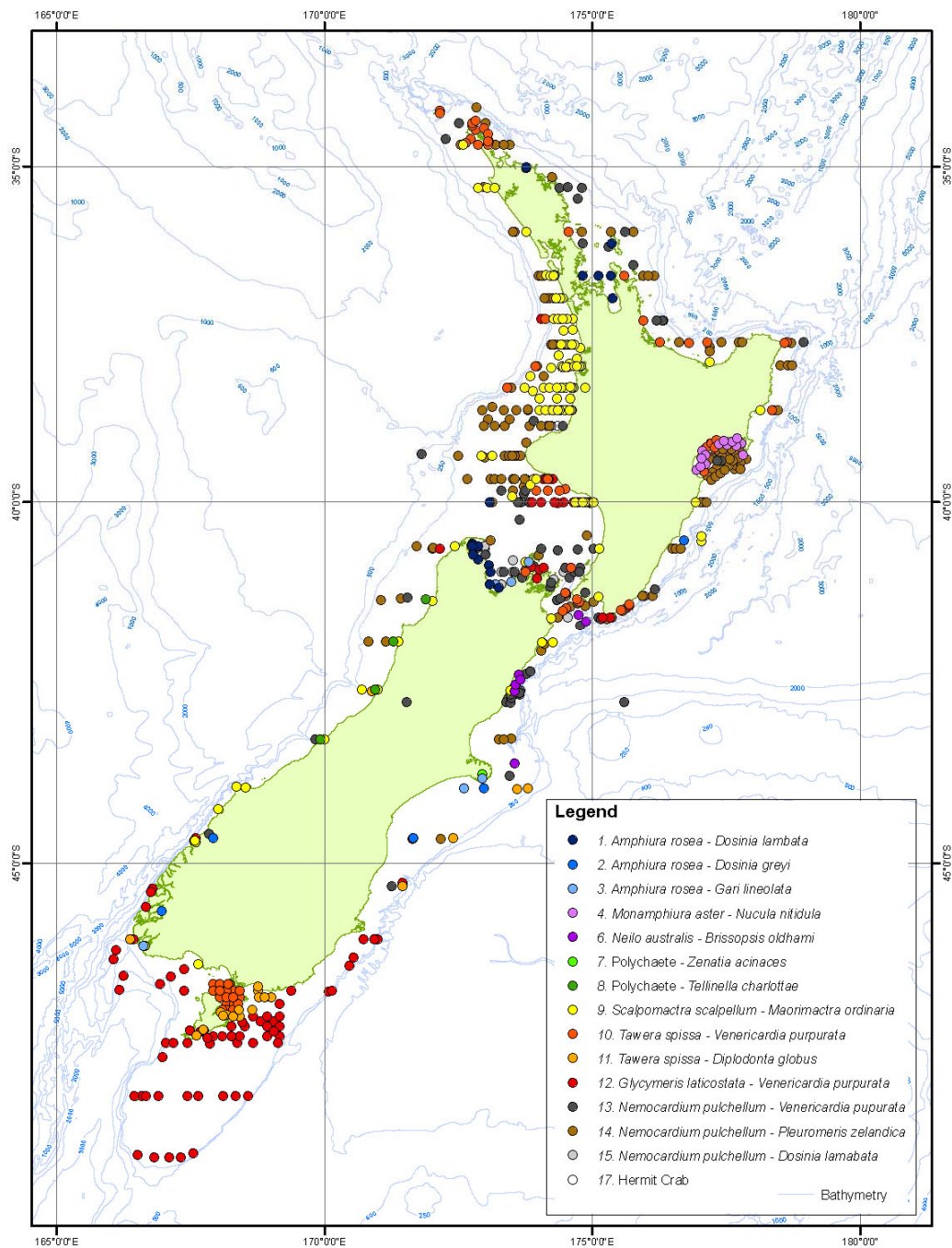


Figure 6.1: Distribution of infaunal shelf communities identified by McKnight (1969a). See text for details and explanation for communities not figured.

6.2.2.2 High-modern sedimentation regime assemblages

A multi-institutional and multi-disciplinary programme of research into the shelf and upper slope ecosystem off the west coast of New Zealand's South Island was undertaken from the late 1970s to the early 1980s. The West Coast Ecosystem Project aimed to achieve a better understanding of relationships between physical environmental factors, nutrient renewal, and plant and animal production in an area that supports important nearshore fisheries. As a result of this project, the relationship between the soft-sediment environment and the composition and production of the area's macroinvertebrate assemblages was revealed. Surface sediments on the continental shelf and upper slope off the west coast of the South Island (from north Karamea Bight to the Whataroa River mouth) consist almost entirely of sands and muds. This area of the west coast shelf experiences a high input of fluvial sediment, probably 12–26 million tonnes y^{-1} , with sedimentation rates of at least 1–2 mm y^{-1} (Probert & Swanson 1985). Surveys of total macrobenthos and polychaetes of the South Island west coast shelf (and upper slope) indicate deposit-feeder dominated assemblages typically dominated by polychaetes, bivalves, peracarid crustaceans and ophiuroids (Probert & Anderson 1986, Probert & Grove 1998, Probert et al. 2001).

Probert & Grove (1998) analysed data from 30 stations using multivariate statistical techniques to identify and describe four macroinvertebrate communities, the composition of which relates most obviously to bathymetry and sediment type, and includes (for the shelf area) an inshore (less than 51 m) silty sand fauna and a mainly sandy mud fauna at mid to outer shelf depths (87–297 m). The inner shelf fauna ("Group 1": characterised by *Sthenelais* cf. *chathamensis*, *Nephtys* sp., *Aglaophamus macroura*, *Prionospio australiensis*, *Paraprionospio* aff. *pinnata*, *Aricidea* sp., *Magelona* spp., *Heteromastus filiformis*, *Ampharete kerguelensis*, *Diplocirrus* sp. (polychaetes), *Austrofusus glans* (gastropod) and *Maorimactra ordinaria* (bivalve)) corresponds mainly to a Venus-type community of McKnight (1969a), described as an open-shelf community widespread around New Zealand and typical of sandy substrata at depths of 20–60 m. However, the mid shelf to outer shelf infauna ("Group 2": characterised by *Aglaophamus verrilli*, *Lumbrineris* ?*brevicirra*, *Paraprionospio coora*, *Diplocirrus* sp. (polychaetes), *Poroleda lanceolata* (bivalve) and *Ampelisca chiltoni* (amphipod)) relates more obviously to *Nemocardium* and *Amphiura*-type communities of McKnight (1969a). The west coast shelf assemblages described by Probert & Grove (1998) were dominated by polychaetes (36% of individuals) and a subsequent survey of the same area of the west coast shelf concentrated solely upon this important component of the macroinvertebrate fauna. Probert et al. (2001) quantitatively sampled 18 stations (up to four replicates per station) with a box-corer, rather than the anchor-box dredge used by Probert & Grove (1998). Multivariate analyses of resulting data revealed two main polychaete communities on the shelf: "inner shelf – Group I (characterised by *Prionospio australiensis*, *Aricidea* (*Acesta*) sp., *Magelona* cf. *dakini*, *Paraprionospio* aff. *pinnata*, *Aglaophamus* sp., *Heteromastus filiformis*, *Magelona* sp.); mid to outer shelf – Groups M and O (characterised by *Levinsenia* cf. *gracilis*, *Prionospio australiensis*, *Paraprionospio coora*, *Aglaophamus verrilli*, *Auchenoplax mesos*). A combination of water depth and sediment clay content provided the best correlation with the biotic pattern (Probert et al. 2001). The spatial distribution of the sediment clay content, which increased in the area from north to south, corresponds with an increase in the rate of modern sedimentation associated with increasing north-south input of riverine sediment (Probert & Swanson 1985). The macroinvertebrate assemblages of the west coast shelf are dominated by deposit-feeders, in particular members of the polychaete family Spionidae (49% of polychaete individuals), which may reflect the scope for opportunistic species in a shelf environment characterised by a high input of terrigenous sediment and episodic upwelling (Probert et al. 2001). However, whilst west coast rivers probably supply large amounts of particulate organic material to the shelf, much of this is likely to be refractory. Benthic productivity of this shelf appears to be low in relation to overlying primary production, possibly due to efficient remineralisation of phytodetritus, its export and/or burial (Probert 1986).

6.2.2.3 Low-modern sedimentation regime assemblages

The continental shelf along the northeast North Island is generally narrow (less than 30 km) except in the region of the Hauraki Gulf (approximately 80 km). Modern-day terrigenous sediment input to the area is low (0.82 million tonnes yr⁻¹), with much of the fine sand and mud from rivers being trapped in the inner Hauraki Gulf. Once beyond the confines of the gulf there is a general coarsening of the substrates (a mosaic of sand and gravel-size sediment). Most of these coarser sediments are relict with some modern biogenic carbonates (Manighetti & Carter 1999). An appreciation of the composition of macroinvertebrate assemblages of New Zealand's north-eastern shelf is possible because of the endeavours of successive expeditions by the Auckland University Field Club/Offshore Islands Research Group (reported almost exclusively over twenty years in the club's non-peer reviewed journal 'Tane'). However, because these surveys were localised around offshore islands they do not permit a shelf-wide appreciation of benthic assemblages in the same way that the studies by Probert and co-workers allow. Nonetheless, considering the large body of work these surveys represent it is worth reviewing them here, and also because they often contain noteworthy observations on particular habitats that occur on the shallowest portion of the shelf.

Grace and Whitten (1974) began with an improvised benthic survey of 41 stations in the vicinity of Slipper Island off the east coast of the Coromandel Peninsula. These authors undertook an analysis of the sampled fauna from the "classical point of view", describing two major and two minor soft sediment "communities"; the major *Tawera spissa* community occurring in 5 to 10 m of water depth, the major *Myadora boltoni* - *Scalpomactra scalpellum* community in 5 to 15 m depth, the minor *Zostera capricorni*-*Nucula hartvigiana* community in 0 to 5 m of water, and the minor *Paphies subtriangulatum* community which was mainly intertidal but which did extend to water depths of 5 m. The distribution of sediments appeared to be related to depth and to the water energy characteristics of the study area (influenced by shelter afforded by the offshore islands), and together these factors were thought to influence the composition of the observed communities (Grace and Whitten 1974). These authors made a comparison between the communities they observed and those identified by others, noting that their major communities probably represented shallow water variations of McKnight's (1969a) *Tawera spissa* - *Venericardia purpurata* and *Scalpomactra scalpellum* - *Maorimactra ordinaria* communities. The minor communities were noted as being typically found elsewhere in New Zealand harbours and open coast sandy beaches, however, the subtidal occurrence (South Bay, Slipper Island) of the *Zostera capricorni* - *Nucula hartvigiana* community was considered rare at the time (Grace and Whitten 1974).

Further north off the east coast of the Coromandel Grace & Grace (1976) sampled the seabed west of Great Mercury Island. Here 36 dredge samples were taken, analysed in the same manner as the previously described study, and used to identify and describe the spatial distribution of three major and three minor soft-bottom "communities". In addition to *Zostera* [*muelleri*] *capricorni*-*Nucula hartvigiana*, *Tawera spissa*, and *Paphies subtriangulatum* (in generally shallow sandy sediments) communities described previously by Grace & Whitten (1974), *Pupa kirki*-*Pectinaria australis*, *Caryocorbula zelandica*-*Pleuromeris zelandica*, and *Tawera spissa* - *Venericardia purpuratara* soft-sediment communities were identified and described (from a range of depths and sediment types). Close parallels were made between the *Caryocorbula zelandica*-*Pleuromeris zelandica* and a number of the communities of McKnight 1969a). Particular note was made of the coarse nature of the substrate (including the presence of algal "rhodoliths") occupied by the *Tawera spissa* - *Venericardia purpuratara* community, and the fact that it had been poorly sampled.

Grace & Hayward (1980) examined an area of the shelf in the vicinity of the Cavalli Islands, primarily southwest of Motukawanui, the largest of the island group. Their study, based on 47 dredge samples, found that the seabed was dominated by coarse shelly sands and gravels in relatively wave-exposed areas, whilst sands (particularly fine sands) were found at shallow depths in sheltered bays and in deeper water (40 m). Some of the coarser grade sediments were comprised of rhodoliths of both living and dead coralline algae, representing a particular unconsolidated biogenic habitat also known as a 'maerl bed' (see Chapter 4, section 4.3). The rhodolith/maerl bed was up to 1 km across and 3 km long. Grace & Hayward (1980) recognized four soft sediment "communities", as per previous studies by Grace, through the use of the "classical" approach of noting the recurring combination of species in a particular habitat, that also demonstrate a degree of spatial continuity. A *Tawera spissa* community was found in

an area (at water depths of 2–15 m) that included the maerl bed, and Grace & Hayward (1980) noted that the rhodoliths and dead shells found there provided attachment surfaces for a number of macroinvertebrate taxa including bryozoans, serpulid polychaetes, chitons and limpets. These coarse sediments in general provided suitable habitat for other epifauna such as amphipods, crabs, isopods, gastropods and ophiuroids. Perhaps not surprisingly then, this community possessed the highest number of species of any of the communities identified. On the sheltered side of Motukawanui, a community characterized by the bivalve *Myadora boltoni* and the sand-mason worm *Pectinaria australis*, occurred from low water to about 5 m water depth. A bed of the seagrass *Zostera* [muelleri] *capricorni* occurs in part of this community. Grace & Hayward (1980) considered that the seagrass bed was less dense and extensive than that previously observed (from aerial photographs), supposing this was why there was not a separate seagrass community with a characteristic fauna similar to those previously observed elsewhere on the northeastern shelf (Grace and Whitten 1974, Grace and Grace 1976). The turritellid gastropod *Zeacolpus pagoda* was a characterizing species, along with the slipper limpet *Zegalerus tenuis*, of a third community. This community was found in fine to coarse shelly sand and gravel in 2 to 30 m water depths over a relatively large area of the study environment. The deepest waters (30–40 m) sampled (insufficiently) apparently contained a community characterized by the bivalve *Nemocardium pulchellum*. Comparing the communities identified in this study around the Cavalli Islands with those undertaken previously and elsewhere, Grace & Hayward (1980) now concluded that “communities with *Tawera spissa* as one of the most important bivalves are common and widespread on the New Zealand shelf”, and that McKnight’s (1969a) *Tawera spissa* – *Venericardia purpurata* community probably most resembled that found at the Cavalli Islands. The *Myadora boltoni*-*Pectinaria australis* community had affinities with two communities recognized by Grace & Whitten (1974) and Grace & Grace (1976), all apparently shallow-water variants of the McKnight’s (1969a) *Scalpomactra scalpellum* – *Maorimactra ordinaria* community. Similarly, the *Nemocardium pulchellum* community, like one of the communities identified by Grace & Grace (1976) at Great Mercury Island, was most likely an inshore variation of one of McKnight’s (1969a) *Nemocardium* communities that occur in fine particle sediments. Grace & Hayward (1980) considered that no community similar to their *Zeacolpus pagoda* – *Zegalerus tenuis* community had been formally recognized before, but believed that it could be considered a local example of McKnight’s (1969a) *Turritella* communities (which only had one representative). Later examining 6 dredge stations off Cuvier Island (40 km east of the north tip of the Coromandel Peninsula), Hayward & Grace (1981) recognized elements of a *Zeacolpus pagoda* – *Zegalerus tenuis* community in some of the samples taken from fine to medium sand in water depths of 10–30 m water.

From a sampling effort in the eastern Bay of Plenty (40 dredge samples from a 3 km² area) in shallow water south of Urupukapuka Island, Hayward et al. (1981) described five subtidal “macrobenthic communities”. On this occasion Hayward and co-workers utilised an objective means (“community score”, which they adapted from Grange 1979) by which to describe the communities they again identified by apparently subjective means. A *Tawera spissa* community was found in mixed sediments in relatively shallow water (1.8–7.5 m) where wave energy was moderate to high. Hayward et al. (1981) noted that the live and dead shells of the characterising species of this assemblage provided attachment surfaces for abundant grazing molluscs and chitons, whilst the coarse sediment component provided habitat for other epifauna species. Occurring in a number of separate areas adjacent to the *Tawera spissa* community was a *Corbula zelandica* community that was associated with somewhat coarser sediments. In the deepest part of the study area (up to 12 m) with moderate wave energy, where there were muddy sands, a predominantly infaunal community characterised by the bivalve *Plueuromeris zelandica* and the polychaete *Pectinaria australis* was found. At a few stations in shallower water (1.5–4 m), where wave energy was low to moderate, a *Zeacolpus pagoda*-*Zegalerus tenuis* community was observed where the former characterising species occurred in very high densities (up to 3500 m⁻²). At three stations in the shallowest water of Urupukapuka Bay Hayward et al. (1981) identified a *Zostera* [muelleri] *capricorni*-*Nucula hartvigiana* community. The seagrass that characterised this community was found by diving and aerial photography to extend throughout the bay (and patchily in adjacent bays). Three of the communities (*Tawera spissa*, *Zeacolpus pagoda*-*Zegalerus tenuis*, and *Zostera* [muelleri] *capricorni*-*Nucula hartvigiana*) were considered by Hayward et al. (1981) to be similar to those previously described from elsewhere (Grace & Whitten 1974, Grace & Hayward 1980), whilst

the other two were considered possible inshore variants of McKnight's (1969a) *Echinocardium*, *Nemocardium* and *Amphiura* communities.

Also on the northeastern New Zealand shelf, sampling (35 stations) an area 10 km² west, northwest and southwest of Rakitu Island (east side of Great Barrier Island), Hayward et al. (1982) recognized four "associations" and one "subassociation". A rather impoverished *Gari stangeri-Felaniella zelandica* association occurred in fine to coarse sand at most shallow (less than 24 m) stations sheltered from oceanic swells. Fauna were also not very abundant at stations where the substrates were gravelly, and the association characterized by taxa (such as bryozoans and polychaetes) that live encrusted or attached to pebbles, cobbles and shells (it is likely, however, that this association was poorly sampled by the dredge used in the study). In deeper water (25–60 m) an association that possessed a number of bivalve species, but was characterized by the more abundant sand-dwelling bryozoan *Selenaria squamosa*, occurred over a large area comprised of a variety of sediment types (fine to coarse sand and sandy pebble gravel). Hayward et al. (1982) identified a *Selenaria squamosa-Zeacolpus* subassociation of the former association, where two species of the gastropod genus *Zeacolpus* also occurred in relatively high abundances. The finest sediments sampled (muddy sands) in the deepest waters sampled (40–68.5 m) northwest of Rakitu Island possessed a *Cuspidaria-Amphiura-Notocallista* association, which Hayward et al. (1982) presumed would "extend across the middle part of the continental shelf in this region". Whilst Hayward et al. (1982) considered that none of the "benthic associations recognised off Rakitu Island have previously been recognised around the New Zealand shelf" they did note that some of the taxa sampled were in "common with described associations". The *Gari stangeri-Felaniella zelandica* association was deemed to have similarities with the ascidian-*Gari stangeri* subassociation of Tutukaka Harbour (Brook et al. 1981) and the *Zeacolpus-Zegalerus* community around the Cavalli Islands (Grace & Hayward 1980) which occur in shallow-water/sand; the *Selenaria squamosa* association was considered somewhat similar to the *Scalpomactra scalpellum-Maorimactra ordinaria* open shelf community of McKnight (1969a) and with at least the *Nemocardium pulchellum* community of Grace & Hayward (1980) where they occur in fine sand in somewhat deeper water (30–40 m); the *Cuspidaria-Amphiura-Notocallista* association showed greatest similarity to the *Amphiura-Dosinia lambata* community of McKnight (1969a) and to a lesser extent another of McKnight's communities and one described off Great Mercury Island by Grace & Grace (1976). Hayward et al. (1982) concluded that the "distribution of benthic macrofaunal associations off Rakitu Island is difficult to correlate with any one physical variable" and stressed rather the "interplay of factors" (i.e. wave energy and sediment type) in determining patterns.

A small area south of one of the Chicken Islands (Lady Alice Island) in the outer Hauraki Gulf was another site at which Hayward and co-workers sampled (15 stations) for benthic macrobiota (Hayward et al. 1984). At this site the seafloor of the shelf slopes quite quickly to depths of 35–40 m before flattening out at 50–60m. The deeper portions of the site have slightly muddy fine sand sediments, whilst the shallower areas have medium sand or coarse sand and gravel substrates (Hayward et al. 1984). Again using "an intuitive, non-statistical approach based partly on associations recognised elsewhere" Hayward et al. (1984) documented four macrofauna "associations" from the study location. The coarse shell and gravel substrate of areas of moderate to moderately high wave energy (12–16 m water depth) provided habitat for an assemblage (*Venericardia purpurata-Corbula zelandica-Talabrica bellula* association) with a wide variety of epifauna and infauna, such as the characterising species of bivalves. At one station in shelly coarse sand (28 m) an assemblage was found that was also characterised by bivalves (*Gari stangeri-Felaniella zelandica* association). However, here it was noted that the most abundant organism was the sand-dwelling bryozoan *Otionellina* [*Otionella*] sp. (350 m⁻²). A *Pupa kirki-Pleuromeris zelandica-Myadora striata* association occurred in the fine sand shallower than 45 m that covered much of the seafloor south of the island. The bryozoan *Otionellina* [*Otionella*] sp. was also a very common component on this association. On the flatter and deeper (42–53 m) area of the study shelf where the sediments were largely composed of fine sand was found a *Nemocardium pulchellum-Notocallista multistriata* association. Hayward et al. (1984) considered that all four associations they described were similar to some of those previously recognised in other study areas sampled by their research group (see above: Great Mercury Island – Grace & Grace 1976, Slipper Island - Hayward & Grace 1981, Cavalli Islands – Grace & Hayward 1980, Bay of Islands – Hayward et al. 1981, Rakitu

Island – Hayward et al. 1982), and commented on the usefulness of associations for recognising areas of similar environmental setting. However, Hayward et al. (1984) did note some disquiet about their designation of associations by highlighting the observation that “the distribution of each species is independently determined by its own physical and perhaps biotic variables”, and mentioned the merit of the study of distribution patterns of individual taxa.

Around the Broken Islands (west of Great Barrier Island, outer Hauraki Gulf) there is a complicated pattern of different seafloor substrate types from mud through sands to coarse gravels and boulders, the distribution of which is controlled by tidal currents (Hayward et al. 1985). In this area of channels (5–10 m water depth) and sloping shelf (to 60 m) Hayward et al. (1985) undertook dredging at 34 stations which revealed the existence of six macrobenthic “associations” (*Scalpomactra scalpellum*-*Dosinia subrosea*, *Felaniella zelandica*-*Talabrica bellula*, Rhodolith-“*Cucumaria*”-*Glycymeris laticostata*, *Pupa kirki*-*Echinocardium cordatum*-*Myadora boltoni*, *Corbula zelandica*, *Amphiura*-*Saccella bellula*-*Nocallista multistriata*-*Cuspidaria willetti*) and three “subassociations” (*Corbula zelandica*-*Limaria orientalis*, *Corbula zelandica*-*Venericardia purpurata*, *Corbula zelandica*-*Pleuromeris zelandica*). Two of the six associations in the study area were considered “very distinctive in their overall biotic composition.” These were the *Amphiura*-*Saccella bellula*-*Nocallista multistriata*-*Cuspidaria willetti* assemblage of deep (31–59 m), quiet water with muddy sediments and the Rhodolith-“*Cucumaria*”-*Glycymeris laticostata* assemblage of shallow (10–15 m), high energy water with coarse sediments. The former association was moderately diverse with a mixture of in- and epi-fauna (including the coral *Kionotrochus suteri*) and was thought to extend a “long way offshore”, the latter association had a rich and diverse fauna reflecting the favourable habitats provided by the live and dead rhodoliths (maerl) for both epi- and infauna (Hayward et al. 1985). Whilst recognising that variants of most of the associations (and subassociations) found off the Broken Islands have been found elsewhere in the vicinity of the offshore islands of the northeastern continental shelf of New Zealand (see above), Hayward et al. (1985) again highlighted observations that support the notion that associations (or ‘communities’) reflect the co-incident distribution of taxa responding individually to a set of environmental factors (in the sense of Gleason 1926).

Hayward et al. (1986) reported on a benthic survey off northeastern Great Barrier Island that extended the appreciation of the distribution of soft sediment macroinvertebrate fauna on this portion of the shelf begun by an earlier survey off Rakitu Island (Hayward et al. 1982). Most of the seafloor of the study area was covered with well-sorted fine sand, although there were patches of coarse sand and gravel in addition to muddier sediments in deep water. Five “associations” and one “subassociations” were recognised by Hayward et al. (1986): Polychaete-crustacean association characterised by fauna living attached to pebbles or large shells of substrates at depths ranging from 6 to 44 m; *Myadora*-*Scalpomactra* association of the fine to medium sand of Rangiwahakaea Bay (3–28 m); an association dominated and characterised by the free-living bryozoan *Otionellina* [*Otionella*] that was widespread in slightly muddy fine sand to coarse shell sand between 33 and 53 m water depth; a variant of the latter association, a *Otionellina* [*Otionella*]-*Zeacolpus* subassociation, that occurred in somewhat shallower (25–34 m) fine to medium sands; the ophiuroid *Amphiura* sp. was found consistently at all stations sampled in the area and the species was one of the characterising taxa of the *Cuspidaria*-*Amphiura*-*Notocallista* association of the muddy sand substrates of the deepest stations; and a *Gari*-*Felaniella* association in a narrow, shallow band adjacent to the northwest shores of Rakitu Island (previously noted in Hayward et al. 1982). Hayward et al. (1986) considered that most of the associations recognised from this portion of the northeastern continental shelf had been previously recognised elsewhere in similar environmental settings (see above). However, these authors did note that whilst high densities of *Otionellina* [*Otionella*] sp. had been observed elsewhere before (Hayward et al. 1984) this was the first time that a specific *Otionella* association (and *Otionella*-*Zeacolpus* subassociation) had been identified. Hayward et al. (1986) conclude their report, apparently the last describing studies by the Offshore Islands Research Group of the northeastern New Zealand shelf, by saying that “It appears that a complex interplay of factors, some of them not easily identifiable, determines the distribution of shallow water, soft-bottom benthos. Among the more significant factors are the degree of exposure to wave and current energy, water clarity, sediment grain size and factors strongly associated with increasing water depth” (Hayward et al. 1986).

Modern sedimentation on the Otago shelf is confined to an inner shelf sand wedge, such that relict and biogenic sediments dominate the middle and outer shelf. Surficial sediments from the relict terrigenous gravel facies are rich in skeletal debris derived from molluscs and bryozoans (Carter et al. 1985). Suspended sediment yields from the two main rivers that supply sediment to the Otago shelf, the Clutha and the Taieri, are 0.39 and 0.32 million tones yr⁻¹ (respectively) (Hicks and Shankar 2003). Powell (1950) was the first to report on the benthic fauna of the relatively narrow Otago shelf, using only records for molluscs he recognized a “*Chlamys* [*Zygochlamys*] *delicatula*-*Fusitriton* community” occurring extensively at approximately 90 to 130 m on sandy or gravelly sediments subject to strong currents. Graham (1962a & b) also documented a single component of the fauna (molluscs and echinoderms, respectively), as did Schembri (1988) (hermit crabs). Andrews (1973) described benthic fauna “assemblages” but largely on the basis of skeletal remains. Descriptions of ‘whole’ macroinvertebrate assemblages of the Otago shelf are relatively few, but were based on extensive sampling and identified with the aid of multivariate statistical techniques. Probert et al. (1979) identified three main “bottom faunas” from station- and species-grouping classification of 111 samples taken with an Agassiz trawl (which introduces an epifaunal bias to the assemblage description) across the entire shelf from just north of the Waikouaiti River mouth to just south of Hoopers Inlet on the Otago Peninsula. These assemblages were: an inner shelf benthos (less than 30 m) associated with sand and neritic water (characteristic macroinvertebrate species include the hydroid *Amphisbetia fasciculata*, the shrimp *Pontophilus australis*, and the gastropod *Zethalia zelandica*); middle-outer shelf and uppermost slope benthos (in places to 370 m) occurring on gravelly sediments in the path of the Southland Current (characteristic taxa included various species of gastropods, anomuran and brachyuran crustaceans, echinoderms and bryozoans); and a submarine canyon benthos of the slope best developed on muddy sediments (greater than 450 m) influenced by Antarctic Intermediate Water (characteristic taxa include the bryozoan *Melicerita angustiloba*, the sponge *Stylocordyla borealis*, and various species of hermit crabs) (see section 6.2.3). The most striking feature of the benthic fauna of the Otago shelf was the preponderance of bryozoans on the middle and outer shelves, the distribution of which was thought to be controlled by the availability of suitable substrata and water currents carrying sufficient food for these suspension-feeding organisms (Probert et al. 1979). The habitat-providing colonies of bryozoans, such as *Cinctipora* [*Filicea*] *elegans*, *Hippomenella vellicata* and *Celleporaria agglutinans*, of the mid/outer shelf assemblages supported a rich and diverse epifauna, whilst the skeletal remains of bryozoans formed a biogenic sediment which itself was thought to provide a complex habitat for both epifauna and infauna (Probert et al. 1979). Probert & Wilson (1984) reported on a complementary survey of the Otago shelf which, because dredges were used to sample the benthos, was able to examine more fully the infaunal component of the shelf assemblages. The combined classification analysis (species and stations) carried out by these authors of samples from 32 stations again revealed the existence of three major benthic “communities”. Characteristic infauna of a inner shelf (14–25 m) sand fauna include the gastropod *Antisolarium egenum*, the spionid polychaete *Spiophanes bombyx*, lyssianassid amphipod *Hippomedon* sp. as well as the lunulitiform bryozoan *Otionellina* [*Otionella*] spp.. Characteristic species of gravelly/sandy sediments of the mid-shelf (mostly 50–76 m) sediments were *Lepidonotus jacksoni*, *Psammolyce antipoda*, *Lumbrineris brevicirra*, *Phyllamphicteis foliata* (Polychaeta), *Terenochiton otagoensis*, *Micrelenchus caelatus*, *Maoricolpus roseus*, *Zegalerus tenuis* (Mollusca), *Ampelisca chiltoni* (Amphipoda) and *Amphipholis squamata* (Ophiuroidea). Outer shelf (87–150 m) sand stations were faunally less distinct but among the more characteristic species were *Euthalenessa fimbriata*, *Sigalion* sp., *Euchone* sp. (Polychaeta) and *Gari stangeri* (Bivalvia). The polychaetes *Nephtys macroura*, *Lumbrineris magalhaensis*, *Owenia fusiformis*, *Phyllochaetopterus socialis*, and the bivalves *Nucula nitidula*, *Tawera spissa* were generally abundant among the three communities (Probert and Wilson 1984).

The inner shelf fauna of Probert et al. (1979) and Probert & Wilson (1984) has similarities to assemblages described elsewhere in sheltered shallow water on the continental shelf of New Zealand by McKnight (1969a) and those described by Hayward and co-workers from one of the other low modern sedimentation shelves, the northeastern shelf (see above). Overall, the mid-outer shelf fauna of sandy/gravelly sediment is allied to McKnight’s *Venus* communities (McKnight 1969a) and the various bivalve-dominated assemblages described from the northeastern shelf by Hayward and co-workers (see

also above). The rich bryozoan structured (largely epibenthic) assemblage of the mid-shelf off Otago (Probert et al. 1979) is similar to that noted from the Foveaux Strait where the shelf is also starved of modern sediment input and coarse sediments (with important relict and biogenic components) provide a substratum for attached epifauna. The dredge fishery for Bluff oyster (*Tiostrea chilensis*) in Foveaux Strait promoted an early study of the benthos by Fleming (1952) who described the faunal assemblage composition of the “oyster-beds”. Fleming also noted that his description of the assemblage was incomplete, the inventory of taxa he provided was impressive and an early testimony to the diversity of a life (including oysters) associated with the mixed, generally coarse sediments of Foveaux Strait. Fleming (1952) related the infaunal component of the shell-sand assemblage he observed to the shell-sand infauna *Tawera-Glycymeris* community of Powell (1937), but including *Panopea smithae* and *Longimacra elongata* among its dominants. Fleming (1952) also noted that “where strong tidal currents prevent the deposition of all but the coarsest shell-fragments, an epifauna develops, dominated by sessile organisms, attached to the coarse substratum, depending for nutriment on plant detritus brought by currents from other areas, and itself supporting an abundant fauna of predatory carnivores. Sessile and encrusting epifauna species of the “patches” identified by Fleming (1952) included sponges, bryozoans, hydroids, mussels and other bivalves, brachiopods, barnacles, tunicates, whilst motile grazing epifauna included gastropods and three species of urchins. Predatory fauna were dominated by the abundant ophiuroid *Ophiopsammus* [*Pectinura*] *maculata*, various carnivorous gastropods, hermit crabs as well as small octopus. Willan (1981) also described similar patches of epifaunal dominated assemblages in Paterson Inlet, of which he considered the bryozoan *Cinctipora elegans* the most important structural component. Cranfield and co-workers have over a number of years examined the benthic assemblages and physical features of this biogenic habitat or “reef” in Foveaux Strait. Those studies focused on the effects of oyster dredging on the occurrence and distribution of the bryozoan reef assemblages (Cranfield et al. 1999, 2003) (see also later section 6.2.3) and the impact on the commercially important blue cod fishery (Cranfield et al. 2001), but they also revealed the relationship between the complexity of the biogenic habitat and the composition and diversity of the associated assemblages in areas of the shelf where modern sedimentation rates are low, current speeds high and soft-sediment substrates are mixed and generally coarse/biogenic (Cranfield et al. 2004).

Bryozoan beds (*Celleporaria agglutinans* and *Hippomenella vellicata*) have also been recorded off Separation Point, between Tasman and Golden Bays (Bradstock & Gordon 1983). The main bryozoan-dominated area is, however, mainly on muddy sediments (Grange et al. 2003, see also later section 6.4).

6.2.3 Continental slope assemblages

A considerable amount of benthic sampling has been carried out at continental slope depths around New Zealand, but few detailed studies have been undertaken of bathyal (200–2000 m) assemblages. In 1874 the H.M.S *Challenger* visited New Zealand waters, on the first global ocean oceanographic survey, taking seabed samples at 12 stations (see summary of *Challenger Expedition* for New Zealand waters by Hamilton 1896). Most of these stations were located at bathyal depths: five were up the slope and across the Challenger Plateau to the shelf edge (from 2011 to 274 m), two were deep on the slope of the east coast of the North Island (1280 and 2011 m), and three were around the Kermadec Islands (951–1152 m). In all, hundreds of benthic taxa were recorded from most of the major marine phyla, with many being “obtained at no other locality” (Hamilton 1896).

Later more comprehensive surveys of macrofauna on the continental shelf of New Zealand have sometimes included sampling of the upper slope, which began to provide a somewhat better indication of slope assemblage composition. McKnight (1969a) began by supposing that the muddy bottom “*Neilo australis* – *Brissopsis oldhami* community” known from deep basins of the fiords may be widespread on New Zealand’s upper continental slope. Probert et al. (1979), in their study of the Otago shelf macroinvertebrate assemblages, identified “upper canyon and deep canyon station groups” on the slope. These two “groups” each possessed particular sets of species (see section 6.2.2.3 for characterising species), and Probert et al. (1979) indicated that a “marked faunal change is evident between the shelf benthos and the canyon benthos, which is best seen at depths over 450 m”. The Otago canyon

community was considered to be similar in composition to the “*Serolis bromleyana*-*Spatangus multispinus* community” of Hurley (1961) described from the Chatham Rise (see below) (Probert et al. 1979). Off the South Island west coast, sampling was carried out of the macrobenthic infauna and of the polychaete component (Probert & Grove 1998, Probert et al. 2001) which also revealed distinctive soft-sediment assemblages on the upper slope. Probert & Grove’s (1998) “Group 4” constituted an assemblage found in deep water (477–1120 m) in the sandy mud of the slope. This assemblage was characterised by the tanaid *Apseudes diversus* and the ophiuroid *Ophiozonella stellamaris*, and below 800 m one of the most conspicuous components of the samples were large agglutinated foraminiferans (*Jullienella zealandica* and komokiaceans). An analysis of separate polychaete data (Probert et al. 2001) also indicated a particular “upper slope group” (or “U group”), best characterised by the spionid *Prinospio ehlersi*. Probert et al. (2001) noted that many polychaete species found on the west coast upper slope were also common on the Chatham Rise (see below, Probert et al. 1996), however, overall at a generic level the polychaete fauna found at comparable depths in these two areas were apparently dissimilar (Probert & Grove 1998).

The Chatham Rise is a prominent submarine feature that extends 100 km from Banks Peninsula eastwards for 1400 km. Five areas with depths less than 200 m occur across the rise: Mernoo, Veryan, Reserve and Wharekauri Banks and the Chatham Islands. West of the Chatham Islands, the rise is generally flat topped at 200–400 m, whilst east, north and south of the feature the water depths increase to over 2000 m (MacKay et al. 2005). Surface sediments on the rise are predominantly fine-grained sands and muds with occasional outcrops of coarser material. Below 150 m the calcareous organic fraction of the sediment is composed mostly of foraminiferan tests, whereas molluscan fragments are more common above 150 m and may dominate the sediments at shallower depth (e.g. the biogenic sediments of the Mernoo and Veryan Banks) (Norris 1964). Of the prominent banks on the Chatham Rise that rise from below 300 m, only the benthic fauna of the Mernoo Bank has been partially described, and then only for molluscs occurring at three shallow (77–104 m) essentially shelf stations (Dell 1951).

Descriptions of the slope/bathyal fauna began with a brief report by Hurley (1961) who examined six stations from depths of 403–604 m from sandy mud on the Chatham Rise. Hurley (1961) described a “*Serolis* [*Acutiserolis*] *bromleyana*-*Spatangus multispinus* community”, which in addition to the isopod and echinoid, was characterised by *Campylonotus rathbunae* (natant decapod), *Nassarius ephamillus*, *Micantapex paregonius*, *Falsilunatia powelli*, *Fusitriton retiolus*, *Cominella alertae*, *Columbarium mariae* (gastropods), *Neilo australis* (bivalve), *Ophiura irrorata* (ophiuroid) and *Hyalinoecia tubicola* (polychaete). Hurley (1961) considered this community to be “sufficiently distinct from any sublittoral communities previously described to warrant distinctive recognition.” Dawson (1984) summarised the taxon-focused studies which were published in the 1960s and 1970s, as well as geologically-focused sampling (grabs and photo/video images) undertaken by NZ-German collaborative studies during the early 1980s, when qualitatively describing the benthic fauna and assessing the possible effects of phosphorite nodule mining on the Rise. The wide expanse of soft-sediments that make up much of the surface of the Rise were deemed to be characterised by large echinoids (*Paramaretia* and *Spatangus*), asteroides (*Zoroaster*, *Astropecten*, *Plutonaster*, *Mediaster*), conical sponges, crabs (*Carcinoplax victoriensis*, *Trichopeltarion fantasticum*), galatheids (*Munida*), gastropods (*Cymatona* and *Fusitriton*), and smaller burrowing polychaetes, bivalves, isopods, amphipods and cumaceans (Dawson 1984). Polychaetes were the most dominant group in terms of frequency of occurrence (by station). Where among the soft sediment there was a concentration of substrate suitable for colonisation (e.g. phosphorite nodules, small glacial erratics), Dawson (1984) noted that a “quite extensive epifauna” of corals such as *Goniocoralla dumosa*, bryozoans, coelentrates, bivalves and brachiopods developed. Dawson considered the “*Goniocorella* clumps” as “epifaunal oases” which “undoubtedly attract small fish as feeding areas and may well be more the centre of energy dispersal than the smoother parts of the rise”.

Probert and co-workers began (from samples recovered in 1989) attempts to appreciate in some detail the composition and distribution of the benthic fauna across the rise in order to understand the influence of the Subtropical Convergence Front (STCF), an oceanographic feature which transects and

characterises the Chatham Rise ecosystem (Probert & McKnight 1993, Probert et al. 1996). Twenty-three stations (244–1394 m) were sampled by anchor-box dredge along three transects that crossed the rise from north to south. Probert and McKnight (1993) reported that the infauna was dominated numerically by polychaetes and peracarid crustaceans and that biomass of the soft-sediment macroinvertebrate assemblages was greater on the south side than on the north side of the rise. Biomass on the north side declined logarithmically with depth, whilst on the south side biomass was unrelated to bathymetry. Probert & McKnight (1993) proposed that the differences in the biomass of benthic assemblages across the rise reflected differences in surface water primary productivity, and the resulting organic flux to the seabed that occurred across the STCF. Probert et al. (1996) reported that the dominant polychaete fauna was composed of 126 species in 37 families and that abundances were higher on the south side than on the north side of the rise. The most abundant polychaete species were *Paraprinospio coora*, *Aglaophamus verrilli* and species of *Notomastus* and *Aricidea*. Half the polychaete fauna were deemed to be surface deposit feeders, with the percentage of total deposit feeders showing a significant relationship with water depth (deeper muddier stations tended to contain more worms of this feeding type). Multivariate analysis of data identified two main polychaete communities, one occurring mainly on the crest of the rise (244–663 m) and a deeper one (802–1394 m) on the slopes of the rise. Species characteristic of the former community were *Aglaophamus verrilli*, *Laonice* sp., *Kinbergonuphi* ?*proalopus*, *Notomastus* sp., *Sthenolepis laevis* and *Euchone* sp., whilst *Aricidea* sp., *Leanira* sp., *Leitoscoloplos* sp., *Poecilochaetus trachyderma*, ?*Diplocirrus* sp. and *Terebellides* aff. *stroemi* were characteristic of the latter community. Community composition also differed between north and south of the rise (to the south of the rise the station assemblages were more homogeneous in composition), and Probert et al. (1996) considered that the differences observed in the fauna were as a result of differences in the quantity and quality of the food supplied to the seabed controlled by the spatial and temporal dynamics of the STCF. Subsequently, McKnight & Probert (1997) described the epifaunal component of the Chatham Rise macrobenthos from samples taken with an small Agassiz trawl at generally the same stations as previous dredging for infauna (Probert & McKnight 1993, Probert et al. 1996), augmented with samples taken in 1993 from a further 16 stations on the central sampling transect. Using multivariate analyses, McKnight and Probert (1997) identified three benthic “community groups” from a subset of 85 species (out of 218 taxa recorded). The shallowest community was characterised mainly by crustaceans and the two deeper water communities were characterised mainly by echinoderms. On mainly sandy sediments on the crest and shallower flanks of the Rise at 237–602 m characteristic species of “Group A” included *Munida gracilis*, *Phylladorhynchus pusillus*, *Campylonotus rathbunae*, *Pontophilus acutirostris* and *Acutiserolis bromleyana* (Crustacea), *Amphiura lanceolata* (Ophiuroidea), *Cuspidaria fairchildi* and *Euciroa galathea* (Bivalvia). At 462–1693 m and associated with muddy sediments, conspicuous species of “Group B” included *Ypsilothuria bitentaculata* and *Pentadactyla longidentis* (Holothuroidea), *Brissopsis oldhami* (Echinoidea), and *Amphiophiura ornata* (Ophiuroidea); whilst at 799–2039 m on muddy sediments major species of “Group C” included *Ophiomusium lymani* (Ophiuroidea), *Porcellanaster ceruleus* (Asteroidea), *Gracilechinus multidentatus* (Echinoidea), and *Aenator recens* (Gastropoda). McKnight & Probert (1997) considered community “A” to be similar to the *Serolis bromleyana*-*Spantangus multispinus* community described by Hurley (1961), and commented that whilst some species of this community and communities “B” and “C” were apparently not restricted to the Rise (being found elsewhere in New Zealand and the globe at bathyal depths) the extent of their respective distributions was poorly known. It was also noted that the bathymetric range of assemblages on the north and south flanks of the Chatham Rise appear to be asymmetric, presumably because of temperature differences caused by the vertical displacement of the Antarctic Intermediate water on the north flank (McKnight & Probert 1997). The previous studies by Probert and co-workers were preliminary to a multidisciplinary study to understand the benthic-pelagic coupling processes associated with the STCF on the Chatham Rise (Nodder et al. 2003). This study confirmed some of the earlier findings and elucidated clearly that the spatial pattern in the make up of benthic communities across the rise mostly reflects variability in the transportation of organic matter to the seabed. This variability was related to the relative position of STCF, where surface waters have seasonally high levels of plankton biomass, and the influence of currents that convey the particles of organic matter that result from the death of planktonic organisms (Nodder et al. 2003).

6.2.4 Abyssal and trench assemblages

There are very few reports of benthic soft-sediment assemblage research carried out in abyssal (2000–6000 m) and hadal (deeper than 6000 m) water depths off New Zealand. Samples were taken in the Kermadec Trench during the 1952 visit by the Danish research ship *Galathea* and the 1958 visit by the Soviet research ship *Vityaz* (Batson 2004). Records of benthic fauna obtained by the former expedition have been, and are still being, published in taxonomic-based volumes. Faunal records from the former Soviet Union are more difficult to obtain, although Belyaev (1960) reports benthic biomass data from stations at water depths of up to approximately 4800 m (from north of North Island, to Tasman Basin and off Campbell Plateau).

6.3 Taxonomy and biogeography

There have been a number of reviews and examinations of specific taxa of communities, and their distributions at the New Zealand-wide scale. However, the content of these reviews is not restricted to soft-sediment specific macroinvertebrate taxa (nor always to New Zealand) and so their usefulness in the context of the present review is limited. However, it is appropriate to note here that such reviews include (among many) those by Dell (1956) (Mollusca), Hurley (1961) (Isopoda), McKnight (1969b) (Echinoidea), Gordon (1986, 1989) (Bryozoa), Glasby & Alvarez (1999) (Polychaeta), Forest et al. (2000), Forest & McClay (2001) (Paguridea), Clark & McKnight (2000, 2001) (Asteroidea). Most of the previous are part of the former NZOI and present NIWA memoir series which have been, and are, periodically published detailing the state of taxonomic knowledge of particular groups. These memoirs are extremely important publications which provide an opportunity to assess New Zealand's marine biodiversity and biogeography of particular macroinvertebrate groups. A full listing of the 107 published (since 1955) biodiversity memoirs published can be found on the NIWA web site (<http://www.niwascience.co.nz/pubs/bm/>). To date, the review by Knox (1975) has been the only New Zealand-wide review of benthic biodiversity and biogeography.

6.4 Threats and vulnerability

New Zealand's soft-sediment benthic assemblages are impacted by various human activities, principally through physical disturbance, contaminant inputs and organic enrichment. Physical disturbance of seabed habitat by mobile fishing gear is the main anthropogenic impact on New Zealand benthic assemblages over extensive areas of the shelf and slope. A review by Jones (1992) summarised (with a New Zealand focus) the likely impact of direct and indirect disturbance by fishing on the seabed and its associated fauna, and urged the undertaking of fishing impact studies that use “experimental designs suitable for assessing transient responses to environmental disturbances”. Thrush et al. (1995) were among the first to take up this baton in a New Zealand context. Their study of the macrofauna of subtidal sand in Mercury Bay (Coromandel Peninsula), which involved experimentally disturbing sites with a commercial scallop dredge, revealed that the density of populations of common fauna decreased as a result of dredging and that assemblage composition was different between dredged and reference sites three months post-disturbance. Thrush et al. (1995) cautioned that their results were conservative and that more robust and extensive studies were required in order to assess the large-scale changes to benthic communities as a result of fishing disturbance. Following their own recommendation, Thrush et al. (1998) conducted a comprehensive study in the Hauraki Gulf in an attempt to examine the disturbance of the marine benthic habitat on the regional scale of commercial fishing. Their study tested a number of predictions (derived from published studies) about how trawling/dredging for snapper and scallop would be likely to impact macrobenthic assemblages. Analysis of data obtained from using a variety of sampling methods (that operated at different spatial scales sampling different components of the fauna/habitat) at a number of different sites throughout the gulf demonstrated that broad-scale changes in benthic communities could be directly related to fishing. In particular Thrush et al. (1998) noted that the removal by fishing of organisms (e.g. *Atrina zelandica*; epifauna such as sponges, bryozoans,

ascidians; *Echinocardium australe*) that add three-dimensional habitat structural complexity is of concern, for such ecological heterogeneity effectively promotes biodiversity. These authors stressed the importance of providing environmental managers with information on the adverse effects of fishing so that appropriate (sustainable) resource management could be enacted (Thrush et al. 1998). Turner et al. (1999) provided a review of fishing impacts and the degradation or loss of habitat structure, complete with examples from soft-sediment environments of New Zealand, and concluded that “The continued loss of habitat structure important in the completion of the life-history of fisheries resources is likely to have significant implications for the fishing industry, and its management and sustainability, as well as dramatic and potentially long-lasting ramifications for the maintenance of habitat diversity, integrity and function.” Thrush and co-workers then undertook research to address the latter concerns. Thrush et al. (2001) extended their fishing impact studies by examining specifically the role of habitat structure (physical and biological) in maintaining macrobenthic diversity in soft-sediment environments. This study demonstrated that habitat structure explained 74–86% of the variance in the diversity of fauna at a number of sites in Kawau Bay (north-eastern New Zealand). The results indicated that the removal by fishing of any habitat structure (e.g. that provided by sponges, hydroids, horse mussels) from generally low-structure soft-sediment environments will decrease biodiversity and most likely have consequences for the wider marine ecosystem (Thrush et al. 2001). Following up on the latter concern, a study by Lohrer et al. (2004) demonstrated that the abundance of the burrowing urchin *Echinocardium australe* (also a creator of habitat structure in soft-sediments around New Zealand) is positively related to primary production because its bioturbatory activities changes nutrient fluxes and improves conditions for microphytobenthos. This study provided the strongest evidence to date (for New Zealand) that the removal of such a species, which is particularly vulnerable to fishing disturbance, will have “potential ramifications for productivity in coastal oceans” (Lohrer et al. 2004).

A particular concern has been raised for the vulnerability from fishing of macrofauna (particularly bryozoans) which form ‘reef-like’ habitat, often in coarse biogenic sediments, at a number of locations around New Zealand (Bradstock & Gordon 1983, Cranfield et al. 1999, Batson & Probert 2000). There are concerns not only about the potential loss of the high benthic diversity that such habitat typically supports, but also their potential importance to commercial fish and shellfish species (Saxton 1980, Cranfield et al. 2001, Carbines et al. 2004). Saxton (1980) initially raised concerns about the loss of one (Torrent Bay), and the potential further loss of another (Separation Point), bryozoan “coral” bed in Tasman Bay (north South Island), and the need for protection of such fish nursery beds from destructive fishing practices. Bradstock & Gordon (1983) described some of the macrofauna associated with colonies of the two main structural frame-building bryozoans, *Celleporaria agglutinans* and *Hippomenella vellicata*, not long after an area off Separation Point was closed to ‘power-fishing methods’. These authors recorded 92 species of other bryozoans, and noted the abundances of polychaetes, molluscs, decapod crustaceans, ophiuroid echinoderms, and ascidians. Bradstock & Gordon (1983) also noted the importance of the recorded macroinvertebrates as diet for a number of fish species (including juveniles) associated with the study bryozoan bed. Subsequently a survey of the Separation Point bryozoan bed was carried out to map its extent and characterise the associated macroinvertebrate assemblage within the protected area (Grange et al. 2003). This survey revealed that the protected area at water depths of 30–40 m possessed a “silt/bryozoan habitat” covering an area of 55 km², where large “multispecies mounds” occur. These mounds (up to 40 cm high and 50 cm wide) were dominated by *C. agglutinans* as well as brachiopods (*Liothyrella neozelanica*), sponges (e.g. *Callyspongia* sp.), hydroids and horse mussels (Grange et al. 2003). Grange et al. (2003) concluded from the form of the mounds that protection had been put into place before any significant destruction of the Separation Point bryozoan bed had taken place. They also surmised that because of the lack of apparent recovery of the Torrent Bay bed, that “once frame-building mounds are broken up, they cannot recover on soft mud sediments.”

In Foveaux Strait, and on the Otago shelf, bryozoan-dominated assemblages occur largely on coarse biogenic sediments. Epifaunal or bryozoan (*Cinctipora elegans*) patch reefs in Foveaux Strait have been progressively modified over more than 130 years of dredging for oysters (Cranfield et al. 1999). These reefs provided habitat not only for oysters but also for blue cod, they have shown signs of some recovery (Cranfield et al. 2001) and could theoretically be regenerated (Cranfield et al. 2003). The reefs

constituted a complex habitat which, with successive regeneration, will support greater biodiversity (Cranfield et al. 2004). What apparently remains then (for this area to achieve a sustainable fishery) is for the implementation of appropriate management strategies, some suggestions for which have been presented on numerous occasions (e.g. Cranfield & Michael 2002).

Bryozoan-dominated assemblages recognised on the mid to outer shelf of the Otago shelf (Probert et al. 1979) were further investigated by a two year survey in order to more precisely map the distribution of the bryozoan “thickets” and determine the species composition of this habitat (Batson & Probert 2000). This study was also to assess the exposure and vulnerability of the thickets to fishing gear and the influence this habitat has on commercial and non-commercial fish and shellfish species. Batson & Probert (2000) indicate that the bryozoan thickets off Otago are different from those bryozoan associations found in Tasman Bay and Foveaux Strait in that the diversity of frame-building bryozoans is much greater, with at least seven structural species being abundant (*Cinctipora elegans*, *Hornera robusta*, *H. foliacea*, *Adeonellopsis*, *Celloporina grandis*, *Hippomenella vellicata*, *Celloporaria agglutinans*). The zone of bryozoan dominance was found to be confined to a relatively narrow band or zone, defined roughly by the 75–100 m water depth contours. Seabed imagery revealed that colonies of bryozoans were patchily distributed on gravel sediments, dense patches or ‘thickets’ were also inhabited by other large sessile epifauna including sponges, hydroids, ascidians and the horse mussel *Atrina zelandica*. The importance of these structurally complex thickets for biodiversity through the provision of habitat was emphasised by Batson & Probert (2000). Batson & Probert (2000) inferred from previous studies overseas, and those from New Zealand, the consequences of fishing disturbance for frame-building bryozoans and their associated fauna. Bryozoans of the Otago shelf are vulnerable to mechanical damage from mobile fishing gear and possibly to smothering/interruption of feeding from sediments suspended by fishing activity, whilst recovery would not be fast owing to slow growth rates and the destabilisation/alteration of sediments on which these organisms settle and grow. Batson & Probert (2000) speculated that, post-fishing disturbance, the complete recovery of a bryozoan-dominated assemblage could not be assumed because of a number of factors which would interact to possibly prevent complete regeneration. In part using anecdotal data from local fishers, Batson & Probert (2000) reconstructed the history of fishing on the Otago shelf and specifically the impact of fishing and other disturbance on the “bryozoan grounds”. The local demersal fishery appears to have largely avoided the bryozoan grounds, although occasionally trawling did take place from the 1960s within the area and large catches of bryozoans occurred. Fishing for scallops took place at water depths greater than the main concentration of bryozoans. Past dredging in the bryozoan grounds for research purposes was not insubstantial. Batson & Probert (2000) concluded that there was no compelling evidence for a range contraction of the bryozoan grounds in the last 30 years, however, they did think it reasonable to assume that fishing had adversely affected the bryozoan grounds (e.g. through changes in colony density and size structure).

A survey of the shallow shelf (20–70 m) of the extreme northern end of New Zealand’s North Island, is to date only reported upon in the grey literature (Cryer et al. 2000). Nonetheless it is worth considering here because of the comprehensive and extensive nature of the study and the significance of the results with respect to the vulnerability of a benthic assemblage dominated by bryozoans. The survey by Cryer et al. in 1999 aimed to specifically determine the extent and composition of this assemblage, whose existence was first revealed by scallop stock assessment surveys, and to assess the effects of fishing upon it. The study (which used a variety of survey and analytical methods) revealed that the substrate of the shelf was largely comprised of a matrix of different soft-sediment types (gravel, mixed sand and gravel, sand, fine sand) and that where sediments were relatively coarse, at water depths of 30–80 m, a diverse assemblage had developed whose species richness was at least in part related to the presence of bryozoans. Other co-occurring colonial organisms (sponges and hydroids) were also considered important for the maintenance of benthic diversity in this assemblage. Sponge species richness was found to have declined in the area and this finding was related to disturbance caused by scallop fishing. Cryer et al. (2000) made particular note of the domination of colonial filter-feeding animals sampled in the area, such as bryozoans and sponges, and the importance of the role that such organisms play in ecosystem functioning and productivity, and the promotion of biodiversity through the provision of structural habitat. Cryer et al. (2000) considered that any changes to the assemblages in the study area

between Cape Reinga and North Cape due to fishing “may be very persistent and take at least decades to restore”. A 1997 voluntary closure to fishing of part of the area was extended in 1999 as a result of the findings of this study. However, Rowden et al. (2004) in their regional assessment of bryozoan biodiversity, noted that not all the sites in the study area which showed high taxonomic distinctness were included in the protected area.

With regards to bathyal benthos in New Zealand, deep-water trawling and mining may significantly impact benthic assemblages of soft-sediments (Dawson 1984, Probert et al. 1997, Cryer et al. 2002). Whilst the fishing disturbance review by Jones (1992) identified that there was an “urgent need to carry out trawling impact studies in deeper water (>500 m) since this is where studies indicate that effects could be severe and that any recovery may be measured in decades”, the first study of any such effects in New Zealand waters came about from the opportunistic analysis of macroinvertebrate bycatch data from a research survey of orange roughy on the Chatham Rise (750–1500 m) (Probert et al. 1997). This study examined the faunal composition of the bycatch from trawls made on “hill” and “flat” areas. The former are generally areas of hard substrate (so will not be considered here), whilst the latter are generally comprised of soft sediment. Common invertebrate groups from the flat areas were Pennatulacea, Natantia, Polychelidae, Asteroidea, Echinoidea and, in particular, Holothuroidea (taken at 53% of flat tows and at no hill tows). Species in these taxa tend to snag easily in the trawl mesh (e.g. spiny species such as brisingid seastars) or are large soft organisms which become pinched in angles of the trawl (e.g. holothurians), which indicates the vulnerability of these particular soft-sediment fauna to fishing disturbance (Probert et al. 1997). Probert et al. (1997) made particular note of the relative importance of the large epibenthic deposit-feeding holothurians to the maintenance of benthic community composition, in that they may promote deep-sea benthic diversity by suppressing competitive exclusion among the smaller benthos in the surface sediment. The study of Cryer et al. (2002) apparently represents the only soft-sediment specific impact of trawling research undertaken in deep-water and published in the primary literature. These authors examined data for macroinvertebrate bycatch from fish research trawls undertaken between 200–600m water depth on the slope in the Bay of Plenty (north-eastern New Zealand) and concluded from their analyses that disturbance from fishing activity in the area was in part responsible for the large-scale patterns in bycatch composition (explaining 11–40% of the variation observed). These authors also noted that “soft-sediment systems of the deep ocean may be enormous in extent, but they are probably fragile and ill adapted to sustain or recover from levels of disturbance commonplace in more dynamic coastal systems.” Furthermore, whilst their study was on a scale comparable with that of the scampi fishery, it could not answer questions about the effects and consequences of trawling on the New Zealand continental slope at the scale of most invertebrate populations and the entire fishery (Cryer et al. 2002).

Whilst mining for phosphorite nodules, which occur extensively on some areas of soft-sediments in New Zealand’s bathyal region, has not been developed into a commercial enterprise, it is thought likely to have major implications for soft-sediment benthic assemblages of the deep-seafloor (Dawson 1984). After reviewing what was known about the macrofauna of the Chatham Rise (see above) Dawson (1984) went on to predict what specific impact mining operations would have for the benthos of the rise. Specifically he noted that: the mining swath would remove the primary consumers (suspension and deposit feeders) and that only the more mobile crustacean predators might be expected to survive; the removal of the rich epifauna of the phosphorite nodules themselves would impact upon the transfer of energy from the pelagos to the benthos; the distribution, breeding and feeding behaviour of fishes might be affected. He proposed that the “trophic structures of the benthic ecosystem would be destroyed”. However, Dawson (1984) considered that mining “may not result in the permanent loss of the benthic ecosystem” depending upon the quantity of nodules removed and the degree of “resilience” to disturbance inherent in the system (he noted in the latter regard that bioturbation by macroinvertebrates and fish was widespread which indicated that assemblages were already experiencing a degree of natural disturbance). Dawson (1984) concluded that “provided the theoretical concepts of resilience and stability can be put to a practical use in monitoring operations, multiple use [mining and fishing] of the Chatham Rise as a resource can be achieved.” There are no studies published in the primary literature that assess the potential threat posed by, or actual impacts from, hydrocarbon exploration and exploitation that takes place on the shelf off Taranaki (west coast of New Zealand). Studies overseas

have demonstrated far reaching spatial effects of oil and gas exploitation for the macroinvertebrate assemblages of soft-sediments (e.g. Olsgard & Gray 1995).

Dredging and associated dredge-spoil disposal in shallow water also physically disturbs soft-bottom benthos and may raise additional concerns where contaminated harbour sediments are being dredged (e.g. Blanchard & Feder 2003). Organic enrichment of seabed sediments as a consequence of sewage disposal (e.g. Conlan et al. 2004) or aquacultural practices (e.g. Findlay et al. 1995) can also influence the composition of macroinvertebrate assemblages. In New Zealand, however, there have been few published studies examining such impacts. In Tasman Bay, dredge spoil (approximately 50 000 m³ y⁻¹) has been dumped at a shallow-water (6–8 m) site off Nelson since 1974. Whilst the spoil is contaminated to varying degrees (trace metals, organochlorines, PAHs), there is little discernible impact on the macrofauna (dominated by small-bodied polychaetes), probably because of the dispersive nature of the site (Roberts and Forrest 1999).

There have also been relatively few published studies concerned with the direct impact of contaminants on soft-sediment benthos in New Zealand. Untreated sewage and industrial waste from Hastings and Havelock North had been discharged for nearly 40 years only 50 m offshore in southern Hawke Bay (east coast of North Island) when Knox and Fenwick (1981) examined the potential organic enrichment effect of the waste for the macrofauna communities of the adjacent shallow subtidal (4–17m). Five macrofauna “community zones” were identified by this study, with macrofauna communities of the two zones nearest the shore (within 500 m) being deemed “polluted” (with high abundances of the capitellid polychaete *Heteromastus filiformis*) and those of the remaining zones (up to 5 km offshore) considered to represent “transitional” communities (to “normal”) according to the organic enrichment scheme of Pearson and Rosenberg (1978). Roper et al. (1989) thought that the sampling regime adopted by Knox and Fenwick (1981) could in part explain the observed faunal changes offshore, and thus considered that the true extent of the “transitional” zone was unclear.

Roper et al. (1989) determined the impact of the then relatively new ocean outfalls that discharged biodegradable domestic and food-processing industry wastes 1.8 km and 2.9 km offshore from Gisborne and Hastings, respectively. The study of these authors indicated that contaminants from the outfalls were responsible for creating zones of “polluted”, “transitional” and “normal” macrofauna communities within 200 m, 400–1600m and more than 1600m from the outfall diffusers, respectively. Anderlini and Wear (1992) examined the influence of sewage effluent discharge on benthic macrofauna, detecting community compositional differences within a 500 m radius of the discharge location in Fitzroy Bay (near Wellington). In a study of macrobenthic community structure in upper Otago Harbour, Grove and Probert (1999) found a distinct benthos in an area (Sawyers Bay) identified as impacted by industrial waste (notably high sediment chromium levels) and sewage.

Organic enrichment under salmon cages and mussel farms may adversely affect benthic communities, however, there are no New Zealand studies of the impact of salmon farming on macrobenthic communities published in the primary literature and only two recent studies that specifically examine the influence of mussel farming on macroinvertebrate fauna and assemblages. Inglis & Gust (2003) assessed the effect of mussel farms on the abundance of the seastar *Coscinasterias muricata* in Pelorus Sound (Marlborough Sounds). These authors found that the abundance of the predatory seastar was much greater where deposits of live and dead mussels existed under farms than on sediments where there were no such shells at unfarmed sites. The study of Inglis & Gust (2003) demonstrated the “potential for significant bottom-up effects of aquaculture on surrounding ecological assemblages.” in New Zealand, which have been observed for macroinvertebrate assemblages in relation to shell drop from mussel farms elsewhere (e.g. Grant et al. 1995). Hartstein & Rowden (2004) quantitatively examined benthic assemblages directly under and adjacent to mussel farms in the Marlborough Sounds and found that at low energy sites, mussel biodeposits (dead mussel shells and particularly organic particulate matter) significantly modified the benthos (notably increased abundance of an opportunistic dorvilleid polychaete), whilst at a high energy site differences in assemblage composition inside and outside the farms were not significant. It would appear from the latter study that the influence of biodeposits from mussel aquaculture activities is dependent upon the hydrodynamic nature of the farm

site. Studies overseas indicate that where there is an effect on the benthos beneath shellfish farms then the impacts are relatively localised (e.g. 40 m, Chamberlain et al. 2001) and can take years to recover post-farm removal (e.g. Stenton-Dozey et al. 1999). Similarly, studies overseas that examined the effects on the benthos of fish farms have often indicated a restricted spatial impact (e.g. 25 m from farm cages, Karakassis et al. 2000), from which communities can take more than a year to recover after farm production ceases (Pereira et al. 2004).

The threat posed by ‘introduced’ ‘exotic’ or ‘alien’ species to native macroinvertebrate assemblages of sub-tidal soft sediments in New Zealand has only relatively recently been assessed (Hayward et al. 1997, Hayward 1997, Hayward et al. 1999). In an examination of faunal changes in Waitemata Harbour (Auckland) sediments from the 1930s to the 1990s Hayward et al. (1997) resurveyed Powell’s (1937) “communities” using similar sampling and analytical techniques and found that three bivalves (*Limaria orientalis*, *Theora lubrica*, *Musculista senhousia*) introduced (possibly via ballast water, but more likely through hull fouling) in the 1960s and 1970s had become abundant enough to be co-dominant species of six of the eight “associations” recognised in the 1990s. The introduction of species from elsewhere was one of a number of factors which Hayward et al. (1997) considered responsible for the overall changes they observed in community composition and distribution that had taken place over 60 years (the others were: closure of sewage outfalls, harbour dredging, sediment and freshwater runoff, land reclamations, erosion retardation schemes and tributyl tin pollution). A review by Hayward (1997) of introduced organisms in Waitemata Harbour and their impact was compiled after the re-survey (Hayward et al. 1997) and a specific monitoring study of four sites in the harbour (the results of the latter were published later – Hayward et al. 1999), detailed the arrival and spread of the three bivalves thought to be bringing about the greatest ecological change to soft-sediment habitats. Hayward (1997) concluded that whilst Waitemata Harbour may be the area of the New Zealand coast most impacted by introduced benthic species, “similar changes are likely to be occurring throughout the country.”

The influence of anchoring by leisure boats on the benthic fauna of embayments and inlets was assessed by Backhurst & Cole (2000) through an investigation of anchoring disturbance at Kawau Island, north-eastern New Zealand. Whilst anchoring scars were observed to persist for up to three months and anchoring could damage beds of the horse mussel *Atrina zelandica*, Backhurst & Cole (2000) could not detect differences in the abundance patterns of benthic fauna between sites of different anchoring intensity. These authors concluded that because “intense anchoring is localised in a few bays over a short time, and macrobenthos can recover over the remainder of the year, benthic impacts are unlikely to require management at present.”

6.5 Biodiversity ‘hotspots’

The term “biodiversity hotspot” has numerous meanings (Myers et al. 2000). From the current state of knowledge, particularly the type and form of data available (see Nelson & Gordon 1997), it is difficult to make other than relatively qualitative assessments of the spatial distribution of biodiversity ‘hotspots’ for New Zealand’s soft-sediment assemblages. However, as detailed previously, increased structural complexity of seabed habitat can provide for a markedly more diverse benthos (e.g. Probert et al. 1997, Cummings et al. 2001) and thus the distribution of such habitat can arguably be used as a useful proxy for identifying biodiversity ‘hotspots’ (here meaning habitat-sized “areas with high species richness”). Therefore, for example, all locations in embayments, inlets and on the shelf where biogenic habitat can be found (such as dense beds of *Atrina zelandica* and bryozoan patches/thickets/reefs) are likely to be areas that support a spatially disproportionate amount of species diversity.

Other types of biodiversity ‘hotspot’ can also be currently identified as existing in the marine environment of New Zealand. Those are areas that feature concentrations of apparently “endemic species and or taxonomically unusual species”, such as locations where chemosynthetic-based communities have been found. Lewis & Marshall (1996) presented (admittedly limited) data in support of the occurrence of seep communities at several locations. Of the thirteen sites that Lewis & Marshall (1996) indicate throughout the New Zealand region, recently shells representative of seep communities (species of *Calyptogena*, *Vesicomya*, *Bathymodiolus*, *Maorithyas*, *?Tentaoculus*, *Provanna*, *?Hyalogyrina*, *Xylodiscula*, *?Pterolabrella*, *Odostomia*) were recovered from three sites, two associated with the Ritchie Ridge (900–1200 m) and one from the slope off East Cape (1675–1803 m). In New Zealand, communities such as these can develop where methane-rich water flows from, or percolates, through soft-sediments as a result of deformation processes near the convergent margin of the plate boundary (as is the case for the Ritchie Ridge sites near the Hikurangi margin), “dewatering” of basin sediments overloaded by a slide of slope sediments (as is the case for the East Cape site), and groundwater aquifers that have been cut by slip-strike faults (as in the case of the apparently fossil seeps at the heads of canyons in Cook Strait and off Otago). This methane-rich water fuels a chemosynthetic-based ecosystem, of which macroinvertebrates such as the endemic and taxonomically ‘special’ molluscs reported by Lewis & Marshall (1996) can be a part. Another potential component of the seep fauna of New Zealand is the endemic pogonophoran worm *Oligobrachia kernohanae* that was described from muddy sediments in the Otago canyons (Batham 1973). Elsewhere in the world, pogonophorans are commonly found in reduced sediments that are not only related to the presence of seeps (including those of fiords) and therefore the occurrence of this relatively inconspicuous species might be more widespread around New Zealand at slope depths.

Macroinvertebrate assemblages of hydrothermal vents, habitats that support another prominent chemosynthetic-based ecosystem, are also only known from a few locations in New Zealand waters. Hydrothermal vents are sites where sulphide-rich water emanates from the earth’s crust generally near or at plate margins as a result of tectonic or volcanic activity (as in the case for New Zealand). The chemical composition of these fluids, and the organismal community that develops, can vary from site to site depending initially on the geochemical processes involved and factors which influence these processes (such as water depth). Sometimes fluids are directly expelled from cracks and fissures in hard substrates at the seabed surface, whilst at other times the fluids percolate through a layer of soft substrate. The macrofauna of soft-sediment vent assemblages were first described from a number of sites (in the vicinity of Whale and White Islands, and a location in between known as the “Calypso” vent field – in water depths of 8 to 200 m) in the relatively shallow waters of the Bay of Plenty (northern New Zealand) by Kamenev et al. (1993). These authors indicated that at sites where relatively high temperature hydrothermal venting (65 °C) was taking place a previously undescribed species of pogonophoran worm (*Siboglinum* sp.), indicative of fauna specially adapted to life in sediments containing reduced compounds, was abundant. Where vent temperatures were somewhat less (17–40 °C) taxa commonly found in ‘typical’ shelf communities (including the dominant bivalve *Tawera spissa*) were also recorded from the vent sites. In 1998 a joint NZ-German investigation that included further study of the “Calypso” vent field (using video/still imagery and a submersible as well as grab sampling) recovered samples and seabed images that demonstrated the occurrence of a vent-specific

soft-sediment fauna (see voyage report, Stoffers et al. 1999). These samples and images were deposited at NIWA, yet have yet to be processed and the macroinvertebrate assemblages are yet to be described for this particular vent field (which is situated near the shelf break).

Clark & O'Shea (2001) and Rowden et al. (2003) reporting on the preliminary results of sampling that took place on seamounts of the Kermadec volcanic arc indicated some of the potentially endemic fauna thought to be associated with the hydrothermal venting on three volcanoes (Brothers, Rumble V, Rumble III) of the arc. These fauna were all thought to be generally associated with hard substrate until a recently completed NZ-American study, using a submersible, revealed that one of the dominant benthic vent-specific taxon (the bathymodiolid mussel *Gigantidas gladius*, apparently forms large 'beds' (tens of metres in size) on soft sediment. Seabed images and limited direct sampling indicated that numerous vent-specific and non-vent taxa are associated with these mussel beds, and that the species of mussels differ between vents along the Kermadec volcanic arc (see voyage report, Merle et al. 2005). However, sufficient funding is yet to be received that will allow sample/image processing to provide a fuller description of the macroinvertebrate assemblages associated with hydrothermal venting that takes place through the soft sediments that in part mantle the volcanoes of the arc. In addition to the formal morphological description/genetic distinction of *G. gladius* (see Von Cosel & Marshall 2003, Smith et al. 2004), a description of the abundant, soft-sediment dwelling lucinid clam (from vent areas in the vicinity of Macauley Island) has been published (*Bathyaustriella thionipta*, Glover et al. 2004). Both of these species have not currently been recorded from outside New Zealand waters.

In the marine environment, chemosynthetic ecosystems are not confined to vent and seep habitat, for soft-sediments with low oxygen levels and high sulphide/methane can also be found in deep water where large pulses of organic matter provided by the carcasses of dead whales, sunken tree trunks or accumulations of kelp come to rest on the seabed (Tunnicliffe et al. 2003). Here, as at vents and seeps, micro-organisms that are able to metabolise sulphide/methane form the basis of an ecosystem that possesses a fauna with high levels of endemism and specialisation, which comprise an assemblage with high species richness. For example, in a comparative study by Baco & Smith (2003) the species richness of whale falls was found to approach levels of those in deep-sea soft-sediments and even exceed those for some shallow-water substrates. Whilst there are a couple of records of fauna (new to science) directly associated with the effectively hard substrate of the whale bones, sunken wood and decaying kelp (e.g. Baker et al. 1986, Marshall 1988, Marshall 1994) opportunistically sampled in New Zealand waters, there is currently no assemblage information pertaining to the fauna of the soft-sediment beneath or surrounding such habitat.

6.6 Gaps in knowledge

The following text provides an assessment of the presently perceived 'gaps in our knowledge' of the macroinvertebrate assemblages of the soft-sediment environments around New Zealand. This evaluation is based upon the review of published studies detailed above, and therefore no specific reference is made to such studies below. The text is ordered generally with respect to the structure of the review treatment above.

Knowledge of the macroinvertebrate composition of soft-sediment assemblages of New Zealand's embayments and inlets is spatially patchy, although where examined, generally comprehensive. Rather surprisingly, some relatively large embayments and inlets have apparently received no attention at all (at least reported upon in the primary literature) or somewhat cursory or qualitative study. For example on the North Island, Kaipara Harbour and the Hokianga have not been the subject of published studies, whilst on the South Island, there are only a few reports (mostly in the grey literature) concerning the soft-sediment fauna of the inlets of Banks Peninsula and Fiordland. Though the inlets of some areas, such as Malborough Sounds and Stewart Island have received historical sampling attention, considering these areas are the subject of present and future marine farming activities, there is a paucity of contemporary baseline data on soft-sediment assemblages for areas where anthropogenic effects may need to be robustly assessed.

There can be marked patchiness in macroinvertebrate assemblage composition within New Zealand inlets and embayments that has been observed to be generally concomitant with the small-scale environmental variability that such environments display. Usually there is a gradation from more hydrodynamic conditions near inlet mouths, where tidal currents may be strong, to increasingly sheltered conditions towards the heads of the inlets, and a corresponding fining in sediment grain size and increase in residence time and freshwater inflow (which influence salinity levels among other parameters). Some within-inlet/embayment studies have indicated the nature of the relationship between varying environmental variables and the distribution of macroinvertebrate fauna, however many have not. Detailed examinations of the differences between environment and macroinvertebrate assemblage composition between inlets/embayments are even more lacking. For example, there has been no thorough study of the relationship between the benthic fauna of the Fiordland fiords and their clearly differing hydrodynamic and physiographic characteristics, let alone studies of the fauna of apparently similar inlet/embayments on the North and South Island. Therefore, there is currently no comprehensive understanding of relationships between environment and soft-sediment assemblage composition for New Zealand inlets/embayments, to the extent that it would be possible to predict the occurrence and distribution of macroinvertebrate fauna in unsampled coastal environments.

It is clear from this review that despite the New Zealand shelf survey described by McKnight and the subsequent shelf-based studies of Hayward and co-workers and Probert and colleagues, there are extensive areas for which there is little or no information on the offshore benthic assemblages of soft-sediments. Much of the continental shelf off the South Island east coast is, for instance, poorly known, especially off Canterbury and Marlborough, where no detailed quantitative studies have been undertaken. Also, few samples of benthic fauna have ever been recovered from the extensive Snares Plateau. For areas of continental shelf off the North Island, information is also notably lacking in places. In particular the shelf between the Mahia Peninsula and East Cape on the east coast has received next to no attention, as have the deeper waters of the Three Kings Plateau off Northland. There has been no New Zealand-wide survey of shelf epibenthic assemblages comparable to McKnight's survey of infaunal assemblages.

Whilst links have been observed between habitat complexity (provided by living and dead biogenic components of the substratum/assemblage) and high faunal diversity, there have been very few studies in New Zealand that have attempted to elucidate the specific mechanisms by which habitat complexity promotes biodiversity. In particular, there have been no examinations of the specific means (e.g. provision of space, additional feeding niches, predatory refuge) by which the habitat complexity offered by bryozoan colonies, and at larger spatial scales their arrangement as thickets/beds/reefs, influences the diversity of the many fauna that either inhabit the colonies themselves or are associated indirectly with them. In addition, no studies have been conducted to determine the precise degree of vulnerability of such physically fragile habitat and the degree of impact such biogenic structures may absorb (e.g. from trawling) before the associated biodiversity declines significantly and/or is unable to recover from natural and/or anthropogenic disturbance.

At continental slope depths, information on benthic assemblages is limited to very few areas: the central portion of the Chatham Rise, an area off the Otago peninsula, and the upper half of the west coast of the South Island. The area of slope off the Otago shelf represents the only place where reasonably robust information on the macroinvertebrate assemblages of canyons has been obtained. Canyons are features that frequently occur on the continental slope (68 canyons/canyon systems are noted in the gazetteer of New Zealand seafloor features, Thompson 2001) and in total area represent a significant slope habitat. Thus, relatively little is known of the fauna of New Zealand canyons and the physical characteristics (including the sediment type of the substratum, the orientation and slope of sub-features such as canyon walls and floor) that may influence the soft-sediment macroinvertebrate assemblages they contain. Canyons are often sites of upwelling and areas of relatively high productivity that support notable fisheries (e.g. hoki fishery of the lower west coast of the South Island), yet no studies have focused on the link between shelf processes (e.g. trans-shelf export of organic matter) and slope patterns of pelagic and benthic production which could support such canyon-focused fisheries.

Whilst it could be argued that there is reasonable information on the species composition, at least at the macroinvertebrate level for the major assemblage types on the New Zealand shelf, there is however still limited understanding of the large-scale environmental factors influencing distribution of offshore assemblages, and of their 'function' in New Zealand's marine ecosystem. There are indications from the studies reviewed that the sedimentation rate experienced by a shelf area influences the composition of the soft-sediment assemblages found therein, however, this and other hypotheses that have been proposed (e.g. influence of primary productivity of overlying water, substrate heterogeneity) to explain large-scale patterns of assemblage composition around New Zealand have not been adequately tested. Studies which aimed to test the influence of different environmental factors in determining such large-scale patterns could be usefully conducted in order to allow the prediction of benthic faunal compositions for unsampled areas of the seabed. With regards to benthic function, further integrated studies, similar to those undertaken on the Chatham Rise and on the South Island west coast, could assist greatly in our understanding of the role of the benthos and benthic processes in marine ecosystems, including the specific links between macroinvertebrate and demersal fish assemblages. Related to the latter perceived gap in our knowledge, there has yet to be any study that examines the effect of bottom trawling on macroinvertebrate assemblages on the scale of the New Zealand fishery (which encompasses almost the entire EEZ).

Knowledge of chemosynthetic-based benthic communities, such as those found at seeps, vents, whale and wood/kelp falls, is sporadic and generally lacking sufficient detail. Considering New Zealand's geological environment, former terrestrial forest coverage and past abundant whale populations, it is likely that such communities occur more extensively than is presently appreciated. Preliminary indications to date suggest that these communities are not only 'special' in terms of their biodiversity for the region but also for the biodiversity of global chemosynthetic ecosystems. A complete understanding of the composition of these assemblages is then particularly desirable, especially as a number of locations where these communities are known to occur off New Zealand are likely to be threatened by future anthropogenic disturbances. That is, seeps occurring in association with the Hikurangi margin are vulnerable to potential mining of hydrocarbon resources, whilst vents associated with the Kermadec volcanic arc are under immediate threat from limited, exploratory mineral mining (with the potential for more extensive drilling in the future).

Appreciation of macroinvertebrate assemblages from samples taken on the abyssal plains and in the hadal trenches is almost non-existent. However, a certain amount of data for these environments remains unexploited. Over 200 photographs of the seabed have been taken at water depths greater than 2000 m from which information regarding the visible and interpreted fauna is yet to be usefully extracted. Sampling (including the use seabed camera systems) of these extensive areas of deep-sea habitats in order to quantify the assemblage composition would be of interest, particularly as fishing technology is likely to develop that will allow exploitation of these hitherto undisturbed environments.

The most meaningful appreciation of the composition of any faunal assemblage (and the biogeography of such fauna) depends upon the ability to identify the components of the assemblage to, as far as is possible, species-level. This ability, therefore, is constrained by the taxonomic knowledge of the various macroinvertebrate groups which comprise the soft-sediment assemblages. In particular, significant restrictions will be imposed upon biodiversity knowledge if the species identity of dominant faunal groups is difficult to ascertain, especially by non-specialist biologists. Among the taxonomic groups which are commonly represented among soft-sediment assemblages, the Polycheta is often dominant in terms of species and abundance. However, there is currently no working New Zealand-specific identification key for this important group, other than for one which deals with species found commonly in the intertidal (see NIWA web page:

http://biocollections.org/pub/worms/nz/Polychaeta/ShorePoly/NZShorePolychaeta_ID.htm).

There are a number of non-trivial taxonomic issues which have perhaps prevented the development of an identification tool that can be used by para-taxonomists in New Zealand who wish to complete polychaete species inventories for macroinvertebrate assemblages. Nonetheless, a more complete understanding of the polychaete fauna of New Zealand is a significant gap in our knowledge which

deserves attention. In addition, the taxonomy of the New Zealand's marine Amphipoda would benefit from further consideration in order to allow for the diversity of this common taxon of the soft-sediment benthos to be fully appreciated. A number of colonial benthic taxa that can be found as epifauna of soft sediment assemblages, but which are more typically considered fauna of hard substrates (e.g. ascidians, corals), also merit taxonomic study.

6.7 Recommendations for future research

- Undertake surveys of the macroinvertebrate soft-sediment assemblages of those inlets and embayments that have received no or limited sampling to date. Such surveys will be resource costly, therefore inlets/embayments should be targeted according to their (1) present or future vulnerability to anthropogenic threats and consequently the need to provide baseline information to assess any disturbance effects, and (2) suitability for providing sites most appropriate for the understanding of the influence of environment on assemblage composition (see following recommendation).
- Carry out studies (mensurative and experimental) that determine the precise nature of the relationship between environmental factors (including habitat complexity) that can vary within and between inlets/embayments, and the occurrence and distribution of macroinvertebrate fauna; such that knowledge of these relationships can be used to model the distribution and composition of assemblages at locations where only environmental data are available.
- Undertake studies that can provide descriptions of the macroinvertebrate soft-sediment assemblages of the continental shelf and slope where little or no information is currently available. Such investigations will be resource costly, therefore the selection of such study areas should ideally be made with reference to testable hypotheses and therefore studies should include sites that: (1) provide a range and replication of large-scale environmental factors thought to influence assemblage composition (e.g. sedimentation rates, overlying primary productivity) (2) comprise of biogenic substrates (live and dead) that provide habitat complexity at a range of spatial scales (3) include canyon features (that could act as conduits for faunal/system linkages between shelf, slope and adjacent deep-sea) as well as relatively simple non-incised slope (4) allow for an assessment of the impact of disturbance from bottom trawling and mineral/hydrocarbon exploitation (e.g. include sites with similar environmental characteristics but which differ with respect to levels of fishing pressure).
- Conduct experimental studies that will determine the mechanisms involved in the promotion and maintenance of biodiversity by habitat of structural complexity (e.g. bryozoan thickets/beds/reefs). Included in these studies should be assessments of the impact of physical disturbance (at different spatial and temporal scales) on such habitat by fishing, specifically evaluations should allow for an appreciation of amount of ecological redundancy inherent in such habitats and the recovery time post-disturbance.
- Examine the role of macroinvertebrate assemblages in benthic-pelagic and benthic processes, as part of integrated, multidisciplinary studies that aim to elucidate and quantify the function of a (preferably large) spatial component of the New Zealand marine ecosystem. Such studies should ideally (1) further augment understanding of specific areas which have already been the subject of an ecosystem-type study (e.g. Chatham Rise) (2) target a specific area that is also known to support important fisheries but has yet to receive detailed attention that is known to be wanting (e.g. Campbell Plateau, Bradford-Grieve et al. 2003) (3) focus on the New Zealand continental slope area as a whole.
- Determine as far as is practically possible (as a first step to appreciating the biodiversity of marine chemosynthetic ecosystems of New Zealand) the macroinvertebrate composition of

those assemblages associated with the vents, seeps, and whale/wood/kelp falls that occur on soft-sediments. Such determinations are characteristically very expensive to conduct (e.g. complete descriptions require the use of Remotely Operated Vehicles and/or human-occupied submersibles for sampling and the use of genetic techniques to support the morphological identification of species) and therefore it would be prudent in the first instance to analyse samples (including video and still imagery), already taken from such areas (specifically vents), for which there is currently no funding to allow for faunal identification processing and assemblage description.

- Collate historical data (including seabed images) that will allow for a preliminary description of macroinvertebrate assemblages found at abyssal and hadal water depths around New Zealand.
- Support taxonomic study of New Zealand's relatively understudied soft-sediment fauna, in particular the Polychaeta, with a view to providing practical information and tools that will allow for the identification of soft-sediment polychaetes by non-expert biologists (parataxonomists).

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7. Conclusions

The extensive and comprehensive review undertaken here for macrophyte and macroinvertebrate assemblages of soft-sediment substrates of the estuaries, inlets, beaches, shelf, slope and deep-sea of New Zealand's marine environment, has achieved the project's objectives and thereby addressed some of the objectives of New Zealand's Biodiversity Strategy. Perhaps the most significant result of this review is the series of recommendations that have been formulated for each of the sub-divisions of the overall review. These recommendations indicate the types of research that is considered necessary in order to address perceived shortfalls in knowledge of biodiversity, its importance to ecosystem function, and the threats and consequences of disturbance by anthropogenic activities.

These recommendations have been gathered here below in order that they may be conveniently viewed in one location.

Seagrass and Mangroves

- Undertake surveys that will establish the current (and as far as possible, the past) distribution of mangrove and seagrass (including subtidal) habitat around New Zealand. Such surveys can be based upon a variety of already available information, but they are likely to also require the acquisition of new data derived using direct (e.g. diver-surveys) and indirect mapping methods (e.g. using aerial photographs).
- Carry out studies of the genetic diversity of seagrass and mangrove populations, as a first step to appreciating the possible ecological significance of any such diversity.
- Determine the spatial and temporal use of seagrass and mangrove habitat by different life stages of fish and 'shellfish' (with an emphasis on commercial species), paying particular attention to understanding any relationship between fish/shellfish utilisation of macrophyte habitat and the presence of their food items (e.g. epiphytic algae, macrofauna).
- Quantify the production of organic matter by seagrass and mangroves and the subsequent transfer of such matter to other systems, in order to begin an understanding of their role in marine ecosystem function of these habitats in New Zealand.
- Examine the dynamics of seagrass recession, mortality, colonisation and expansion processes at the scale of a patch and a seagrass bed as part of studies that attempt to understand the impact of specific anthropogenic activities on seagrass and improve ability to manage this habitat. Studies that consider the effect of anthropogenic impacts on mangrove habitat should also be conducted.
- Determine influence of differing nutrient concentrations on seagrass and mangrove growth in order to understand how regional changes in nutrient inputs to coastal waters will impact these habitats at the 'landscape' scale. An assessment of the influence of likely climate change on the large-scale distribution of these macrophyte habitats could be usefully conducted.

Macroalgae

- Research on rhodolith beds in New Zealand should include the mapping of their geographical distribution and extent, and distribution in relation to environmental parameters (currents/water movement, sediment loads, nutrients) in order to provide missing baseline data, but also to

investigate the diversity of associated assemblages, and assess the relative vulnerability of rhodolith beds to perturbation. This research will result in improved taxonomic understanding of the rhodoliths and associated fauna through the establishment of permanent reference collections for systematic research, and enhanced understanding of the structural and functional components of biogenic reefs.

- Targeted collection of macroalgae in soft sediment environments in New Zealand – resulting in an improved basis for taxonomic studies, permanent reference collections, improved understanding of diversity both geographically and associated with specific environments.
- Ecological studies to examine relationships between macroalgae and associated fauna e.g. the contribution of macroalgae to productivity in nearshore and soft sediment habitats, nutrient relationships, the role of macroalgae in habitat structuring, provision of nursery areas and influence on faunal settlement, resilience to disturbance and to modified sediment regimes, impacts of fishing methods, etc. Temporal (seasonal and inter-annual) variations in assemblages need to be considered, and would be of particular relevance in the case of studies addressing the origins and dynamics of populations of nuisance species.

Intertidal macroinvertebrates

- Meta-analysis of existing data sets to assess generalities in distribution and abundance patterns.
- Compilation of taxonomic information into a centralised, authoritative identification guide to allow consistent and confident species identification across locations and research institutions; including complementation of existing information with data on species for which taxonomic information is currently missing.
- Ecological surveys to obtain distribution and abundance data of coastal habitats that have received little or no attention to date, with a particular focus on exposed beach environments.
- A systematic biogeographical study that examines the distribution of intertidal macroinvertebrates throughout New Zealand.
- Examination of trophic interactions across different habitat types within the same ecosystem with consideration to the contribution of benthic assemblages to overall ecosystem productivity.
- Assessment of natural structuring forces (e.g., hydrodynamics, intra- and interspecific interactions) on benthic assemblages across different spatial scales with an emphasis on occurrence, density and recruitment patterns.
- Research of disturbance effects (other than sedimentation) on macroinvertebrate populations in sheltered and exposed environments, including examinations of causal relationships.

Subtidal macroinvertebrates

- Undertake surveys of the macroinvertebrate soft-sediment assemblages of those inlets and embayments that have received no or limited sampling to date. Such surveys will be resource costly, therefore inlets/embayments should be targeted according to their (1) present or future vulnerability to anthropogenic threats and consequently the need to provide baseline information to assess any disturbance effects, and (2) suitability for providing sites most

appropriate for the understanding of the influence of environment on assemblage composition (see following recommendation).

- Carry out studies (mensurative and experimental) that determine the precise nature of the relationship between environmental factors (including habitat complexity) that can vary within and between inlets/embayments, and the occurrence and distribution of macroinvertebrate fauna; such that knowledge of these relationships can be used to model the distribution and composition of assemblages at locations where only environmental data are available.
- Undertake studies that can provide descriptions of the macroinvertebrate soft-sediment assemblages of the continental shelf and slope where little or no information is currently available. Such investigations will be resource costly, therefore the selection of such study areas should ideally be made with reference to testable hypotheses and therefore studies should include sites that: (1) provide a range and replication of large-scale environmental factors thought to influence assemblage composition (e.g. sedimentation rates, overlying primary productivity) (2) comprise of biogenic substrates (live and dead) that provide habitat complexity at a range of spatial scales (3) include canyon features (that could act as conduits for faunal/system linkages between shelf, slope and adjacent deep-sea) as well as relatively simple non-incised slope (4) allow for an assessment of the impact of disturbance from bottom trawling and mineral/hydrocarbon exploitation (e.g. include sites with similar environmental characteristics but which differ with respect to levels of fishing pressure).
- Conduct experimental studies that will determine the mechanisms involved in the promotion and maintenance of biodiversity by habitat of structural complexity (e.g. bryozoan thickets/beds/reefs). Included in these studies should be assessments of the impact of physical disturbance (at different spatial and temporal scales) on such habitat by fishing, specifically evaluations should allow for an appreciation of the amount of ecological redundancy inherent in such habitats and the recovery time post-disturbance.
- Examine the role of macroinvertebrate assemblages in benthic-pelagic and benthic processes, as part of integrated, multidisciplinary studies that aim to elucidate and quantify the function of a (preferably large) spatial component of the New Zealand marine ecosystem. Such studies should ideally (1) further augment understanding of specific areas which has already been the subject of an ecosystem-type study (e.g. Chatham Rise) (2) target a specific area that is also known to support important fisheries but has yet to receive detailed attention that is known to be wanting (e.g. Campbell Plateau, Bradford-Grieve et al 2003) (3) focus on the New Zealand continental slope area as a whole.
- Determine as far as is practically possible (as a first step to appreciating the biodiversity of marine chemosynthetic ecosystems of New Zealand) the macroinvertebrate composition of those assemblages associated with the vents, seeps, and whale/wood/kelp falls that occur on soft-sediments. Such determinations are characteristically very expensive to conduct (e.g. complete descriptions require the use of Remotely Operated Vehicles and/or human-occupied submersibles for sampling and the use of genetic techniques to support the morphological identification of species) and therefore it would be prudent in the first instance to analyse samples (including video and still imagery), already taken from such areas (specifically vents), for which there is currently no funding to allow for faunal identification processing and assemblage description.
- Collate historical data (including seabed images) that will allow for a preliminary description of macroinvertebrate assemblages found at abyssal and hadal water depths around New Zealand.

- Support taxonomic study of New Zealand's relatively understudied soft-sediment fauna, in particular the Polychaeta, with a view to providing practical information and tools that will allow for the identification of soft-sediment polychaetes by non-expert biologists (parataxonomists).

Clearly more studies are recommended above than can be presently supported by the biodiversity research funds that the Ministry of Fisheries administers. Thus, the question of 'what to do first?' arises. Such a prioritisation of biodiversity research is beyond the scope of the present project. Thus, this report concludes by proposing that a formal and rigorous procedure be adopted to prioritise the recommendations, in order that important and scarce national biodiversity funds are directed towards a research agenda that will best deliver on New Zealand's commitment to the Convention on Biological Diversity (as outlined in the New Zealand Biodiversity Strategy). Ideally, such an exercise will need to involve appropriate researchers from science providers (e.g. universities, crown research institutes, private consultancies or independent research institutes/persons) and science advisors from environmental management agencies (e.g. Ministry of Fisheries, Department of Conservation, Ministry for the Environment) as well as those persons, groups or organisations that possess or claim a 'stake' in the resources of the marine environment (e.g. fishery organisations, Maori). To manage such a process in a way that will prevent 'group think' and/or the 'agendas' of particularly 'vocal' individuals/organisations from potentially prevailing, the use of such tools as the Delphi system are recommended.

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