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Soft-bottom Benthic Communities in Otago Harbour and Blueskin Bay, New Zealand

by

S. F. RAINER

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ABSTRACT

Quantitative sampling of the macrofauna of deposit substrata in Otago Harbour and Blueskin Bay was carried out between May 1965 and January 1967, using diver-operated sampling gear to collect all organisms retained by a 1 mm mesh. Eighty samples, mostly of 0.2 m^2 area, were collected in a large scale survey, with 34 stations arranged in four transects. The samples were ordered into five communities, using environmentally-based criteria (sediment grade and stability, quantity of organic detritus, macroscopic algae and shell). Subdivisions were recognised within each community according to local variations in these characteristics. The presence of whole or broken mollusc shell usually exerted considerable influence on the species composition of a community, particularly in shallow areas, by providing a substrate for the growth of macroscopic algae.

A total of 397 species was collected. Few of these were widely distributed, many species appearing to be restricted to a relatively limited range of environmental conditions. Species diversity (number of species per sample) varied with grade, stability and degree of sorting of a sediment, and with the presence or absence of macroscopic algae. Lowest species diversity was found in samples from unstable fine sand and unconsolidated silt sediments, highest species diversity in samples from stable fine sand sediments with an admixture of shell. Samples from poorly-sorted sediments had a higher species diversity than samples from well-sorted sediments, while the presence of shell or macroscopic algae was usually associated with an elevated species diversity. Dominance diversity, d_r, was highly sensitive to changes in species composition that did not appear to have general significance.

Many of the species found occur in other sheltered or enclosed shallow-water areas in New Zealand. However, the communities recognised do not accord well with those listed by other authors for the New Zealand area, although a *Macoma* isocommunity may be present.

Keywords: benthic communities, Otago Harbour, Blueskin Bay, environmental factors, patterns of diversity.

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Inset 1

INTRODUCTION

Otago Harbour is a long, shallow inlet on the east coast of South Island, New Zealand, at about 48°S 171°E, and lies just to the south of Blueskin Bay (Fig. 1). Previous work on the benthic ecology of the area was on sandbanks and channels in a small area near the Portobello Marine Laboratory (Ralph and Yaldwyn 1956). The present work was carried out to investigate the relationship between a number of environmental variables and the structure and species composition of soft-bottom macrofaunal assemblages in Otago Harbour and Blueskin Bay.

Diver-operated sampling apparatus was used in a general survey of the study area between May 1965 and January 1967 and in an accompanying investigation of small-scale species variability in a subtidal sandflat (Rainer 1969). The general survey included faunal samples from a wide range of soft-bottom environments, from the lower intertidal down to a maximum depth of 28.5 m. Patterns of species distribution indicated by faunal samples have been related in general terms to various environmental properties, including some sediment characteristics, organic detritus, depth, and the amount of macroscopic algae. Similar comparisons were made for changes in species diversity and dominance diversity in the faunal samples.

SAMPLING AND LABORATORY METHODS

The benthic samples were collected by diving, using a suction-dredge (Fig. 2) similar to that described by Brett (1964). The main differences were

(1) the presence of a valve on the high-pressure water intake to regulate the sampling speed,
(2) the use of removable collecting nets, which could be changed and tied off underwater, and
(3) a longer suction end (40 cm), to enable deeper sampling.

The collecting nets were made from 1 mm aperture bolting cloth. High-pressure water was supplied from the surface by a centrifugal pump delivering up to 2000 l/hr, through 3, 6 or 18 m lengths of linked high-pressure water hose. Two sizes of sampling frame were used, of 0.1 m^2 and 0.2 m^2 area, and 25 cm depth. Sampling was taken to a depth at which no obvious macrofauna remained, down to 50-60 cm if necessary. All material was sorted fresh, under a binocular microscope, and sample counts were based on live material only.

Environmental properties measured with each sample included sediment grade and the amounts of organic detritus and macroscopic surface algae present. Sediment samples of at least 100 g equivalent dry weight were collected immediately adjacent to the benthic samples. Grain size analysis was carried out on undried sediment (Morgans 1956) by wet sieving at 0.5 or 1.0 phi unit intervals from $-2\ \varphi$ to $4\ \varphi$ and by the pipette analysis of any remaining sediment at phi unit intervals from $4\ \varphi$ to 7 or $8\ \varphi$ (Barnes 1959). Three statistics were obtained for each sample: the median, the phi decile deviation, and the phi decile skewness. The median (φmd) was obtained as the position of the 50th percentile on a cumulative curve of the sediment fractions expressed in phi units. A measure of the degree of sorting of the sediment, the phi decile deviation (φ_{10} dev), was obtained by

$$\varphi_{10}\ \text{dev} = 0.5\ (\varphi_{90} - \varphi_{10}),$$

where φ_{90} and φ_{10} are the phi values of the 90th and 10th percentiles respectively on the cumulative curve. Skewness in the sediment, the phi decile skewness (φ_{10} skew), was calculated as the difference between the median and the mean (φm),

$$\varphi_{10}\ \text{skew} = \varphi\text{m} - \varphi\text{md},$$

where

$$\varphi\text{m} = 0.5\ (\varphi_{10} + \varphi_{90}).$$

Organic detritus in the sediment was estimated by flotation with carbon tetrachloride. In predominantly coarse sediments this was carried out on the entire fraction retained by the $4\ \varphi$ sieve. In fine sediments, especially those with a considerable proportion of organic detritus, this was carried out on the fraction retained by each sieve separately, and on the pipette analysis fractions. Liquid detergent was used to ensure wetting by the carbon tetrachloride, with subsequent centrifuging to separate the organic detritus from the inorganic material.

Any macroscopic algae occurring at the sample location were collected by the dredge-sieve during sampling. The amount of algae present was measured as the formalin-preserved wet weight.

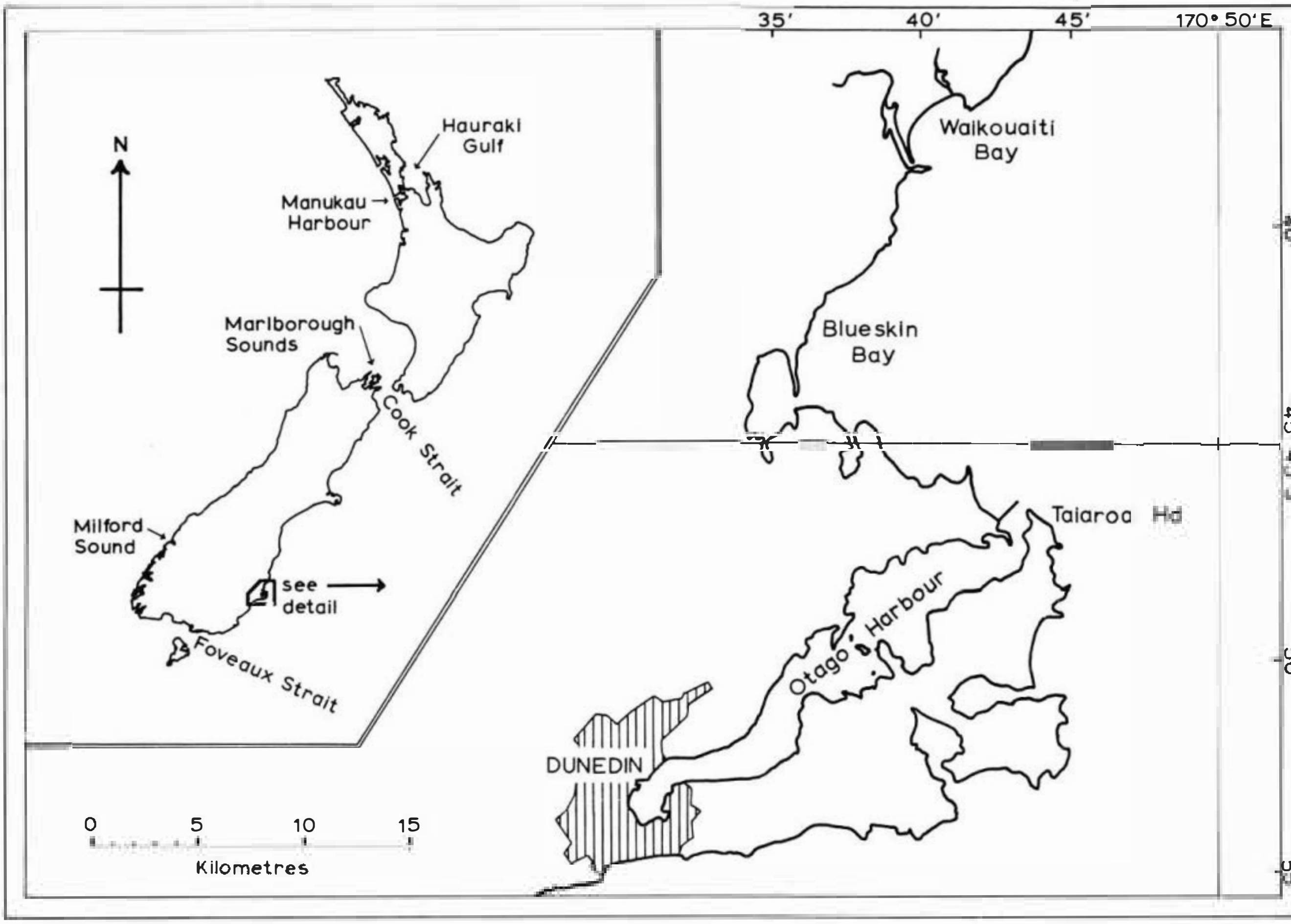


FIG. 1: Map of Otago Harbour and Blueskin Bay area, with localities of other New Zealand benthic studies shown in inset. Bathymetric and sediment data are given in Figs 3–5.

THE BENTHIC ENVIRONMENT

GENERAL DESCRIPTION AND SAMPLE LOCATIONS

Otago Harbour extends some 25 km south-west from Taiaroa Head to the Port of Dunedin, varying from 2 to 4 km in width. A narrow navigation channel, mostly 10–15 m deep, gives access to the Port of Dunedin. The harbour is otherwise shallow, with extensive areas of sand banks exposed at low tide (Fig. 3). Two peninsulas and two islands effectively divide Otago Harbour into inner and outer harbours, connected by the shipping channel and two other shallow channels.

Stations were established at 2 km intervals along two main transects, A and B, the first of 10 km and the second of 22 km (Fig. 4). Transect A comprised six stations along the shipping channel, from Taiaroa Head to Port Chalmers, while Transect B comprised 12 stations along a series of shallow channels on the south-east side of the harbour, from Taiaroa Head almost to the Port of Dunedin. A third transect, C, was located in an area between Quarantine Island and Pudding Island, near Portobello (Fig. 5), and comprised 11 stations which extended 0.7 km in a line between the two islands, from a tidal channel to an intertidal sandbank. Two samples were usually taken from each station in transects A and B while single samples only were taken in transect C. All samples were of 0.2 m^2, except at station A6, which was of 0.1 m^2.

Blueskin Bay is a shallow, relatively sheltered area to the north of Otago Harbour (Fig. 6). Five stations were established in this area. Three of these lie on a line

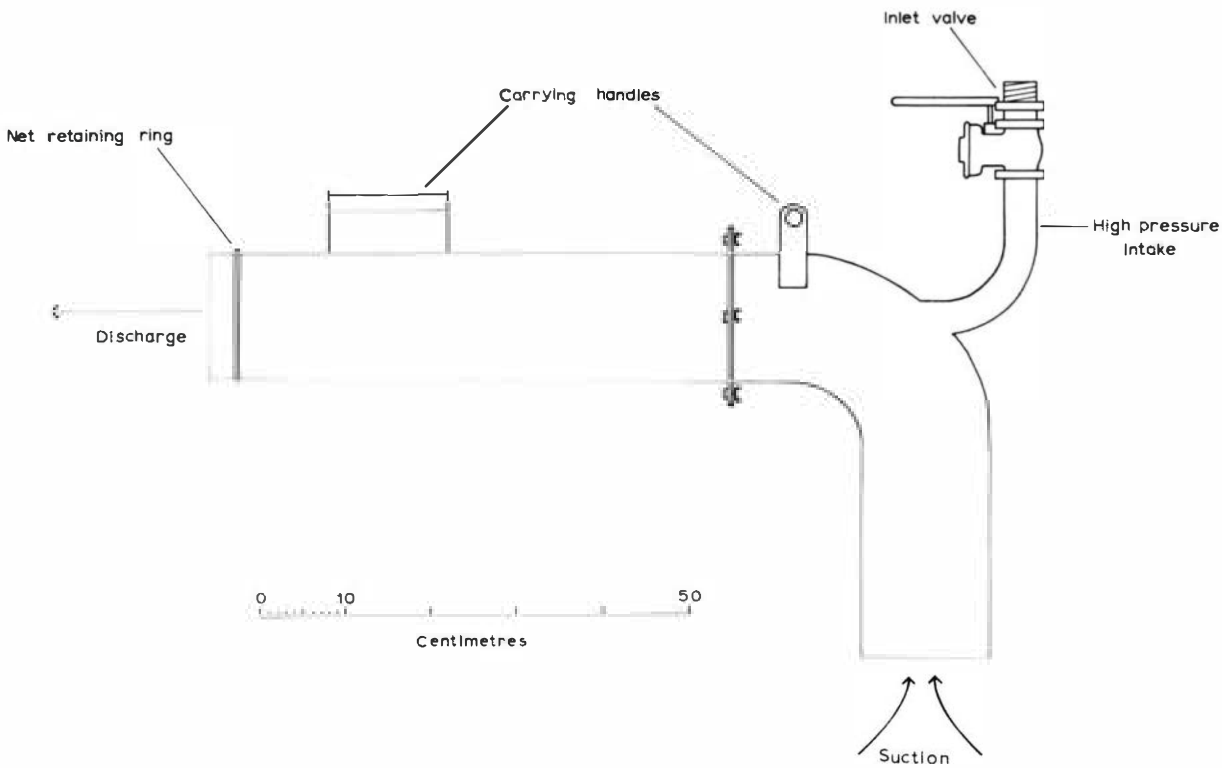


FIG. 2: Side view of dredge sieve. The collecting net is secured to the discharge end in front of the retaining ring; replacement of the net between samples is permitted by closing the high-pressure inlet valve.

running south-west from Waikouaiti (W1, W2, W3), with the other two to the south of this line (W4, W5). Two samples of 0.2 m^2 were taken at W1, W2, W3 and W5, while four 0.2 m^2 samples were taken at W4.

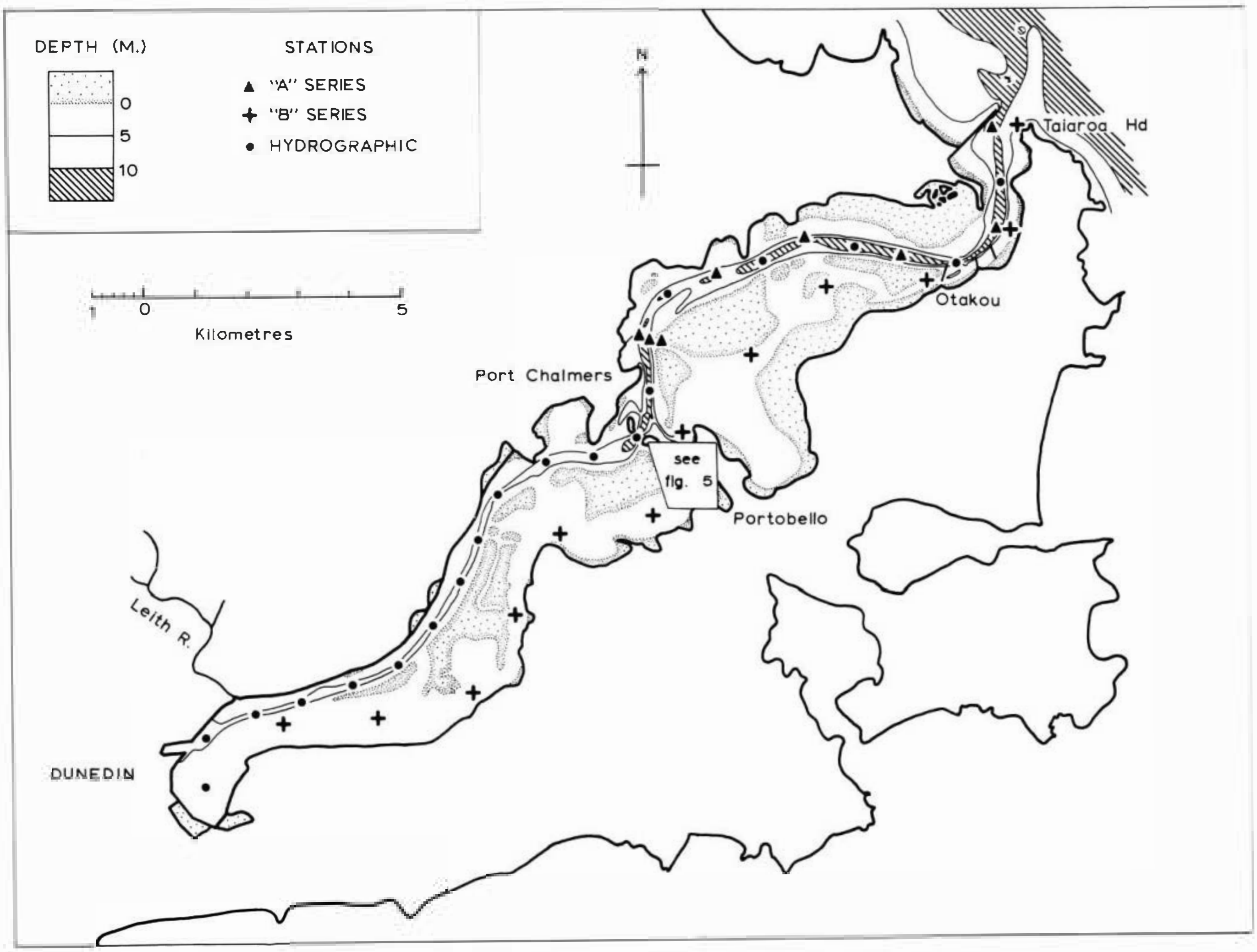
Sediment and other environmental data, including sample depths, are given in Table 1 and Appendix 1. All sample depths have been corrected to Chart Datum, using predicted tidal levels (Marine Division, Ministry of Transport 1964, 1965, 1966).

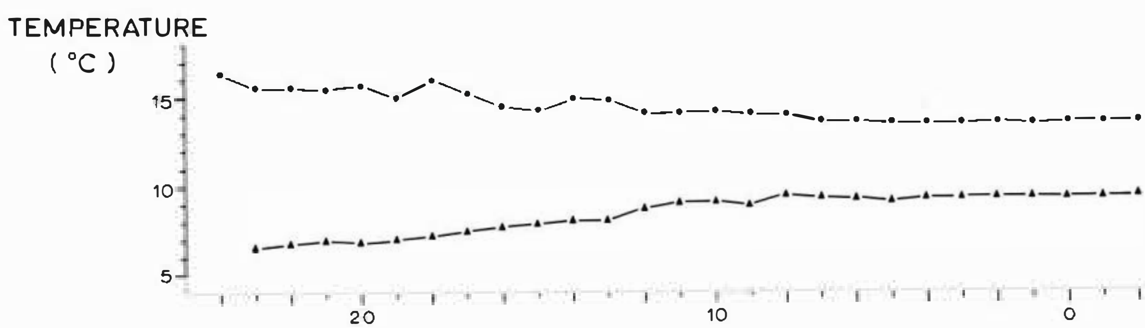
WATER TEMPERATURE AND SALINITY

Surface salinity and temperature gradients were investigated in a number of transects along the harbour, between 10 July 1965 and 16 February 1968. Water temperatures and salinities in the outer harbour were similar to those prevailing just off shore, which vary seasonally from 8.4°C to 14.6°C, and from 33.6‰ to 34.7‰ (Jillett 1969). Salinities were lower in the inner harbour than the outer harbour, but the difference was usually small. The lowest salinity recorded in the inner harbour was 31.4‰, 3.1‰ less than the maximum recorded in the outer harbour on that date (10 October 1966). Data from two transects, one in summer (27 January 1966) and one in winter (15 August 1966), are presented in Fig. 3.

Annual rainfall at the Portobello Marine Laboratory during 1965–1967 averaged 83.1 cm (32.7"), with no consistent seasonal pattern. Periods of high rainfall result in some reduction in salinity, particularly towards the head of the harbour, but the period of depression is probably short, particularly in summer. Otago Harbour and the associated catchment area cover only 15,300 hectares (37,850 acres) (Thomson and Anderton 1921). The largest stream is the Leith, entering at the head of the harbour, and only slight salinity reduction was found at this point in hydrographic transects. The absence of any marked salinity depression over most of the harbour should result in the salinity in any particular area changing very little during a tidal cycle.

FIG. 3 (*opposite*): Otago Harbour – bathymetry and hydrology. The positions of the benthos stations of transects A and B are indicated, those of transect C being given in Fig. 5. The bathymetry is from N.Z. Hydrographic Chart 6612 (Otago Harbour). Surface temperatures and salinities are given from two hydrographic transects made on 27 January 1966 and 15 August 1966 with measurements made at one kilometre intervals from Taiaroa Head (abscissa).


DEPTH (M.)
0
5
10
STATIONS
"A" SERIES
"B" SERIES
HYDROGRAPHIC
N
1 0 5
Kilometres
Taiaroa Hd
Otakou
Port Chalmers
see fig. 5
Portobello
Leith R.
DUNEDIN


TEMPERATURE
(°C)
15
10
5
20
10
0

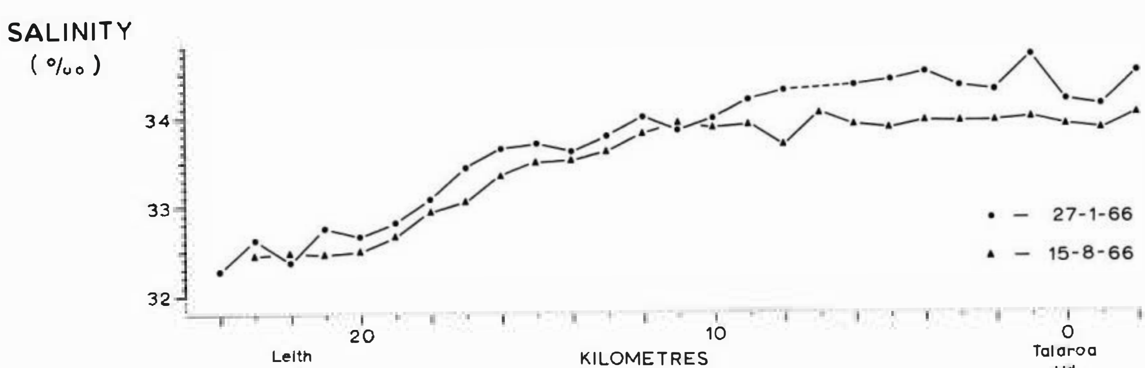

SALINITY
(‰)
34
33
32
27-1-66
15-8-66
20
10
0
Leith R.
KILOMETRES
Taiaroa Hd

TABLE 1: Environmental data for benthic samples, transects A, B and C, and series W.

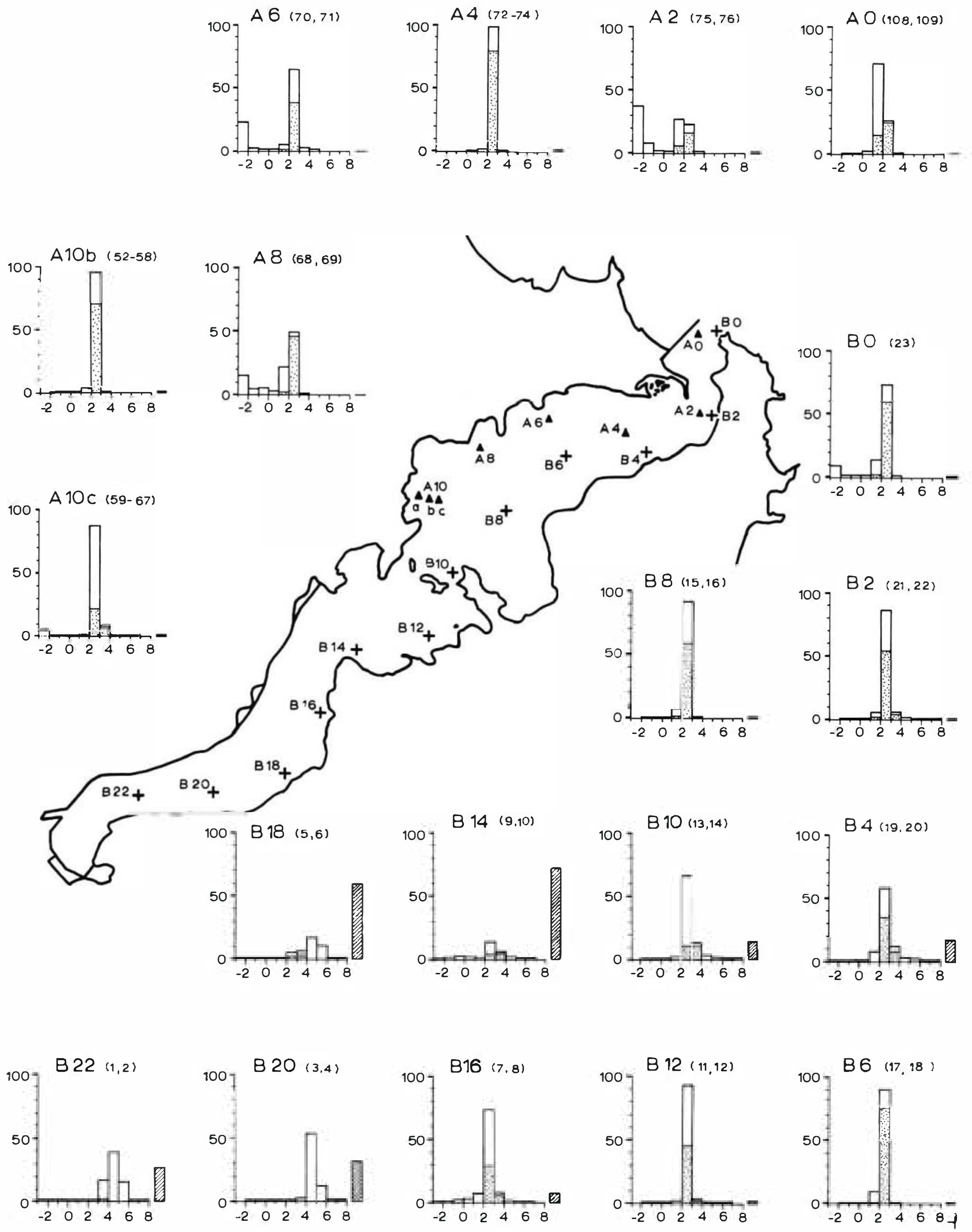
Station	Sample No.	Depth (m)	Sediment Statistics φmd	φ_{10}dev	φ_{10}skew	Sediment Grades (%) <0φ	1–2φ	2–3φ	3–4φ	>4φ	Organic Detritus (%)	Total Algae (g)
Habour mud community												
B4	19,20	3.5	2.47	3.06	−0.53	0.4	8.2	57.8	11.7	4.6	17.1	>100,>100
B10	13,14	4.1	2.77	0.44	0.12	1.1	0.9	65.5	13.2	4.9	14.2	<10,<10
B14	9,10	2.1	2.71	2.21	−0.98	3.9	6.3	14.4	6.0	2.8	71.5	447,738
B18	5,6	1.8	4.53	1.35	−0.47	0.8	0.3	5.4	5.7	28.9	58.8	239,301
B20	3,4	2.1	4.65	0.51	0.04	0.2	0.1	0.4	1.5	66.9	30.7	52,254
B22	1,2	2.6	4.47	0.78	−0.03	0.7	0.2	0.9	17.2	55.6	25.2	287,526
C1	24	2.4	2.44	3.06	−0.53	26.5	3.5	26.8	13.7	2.3	17.3	58
C2	25	2.9	3.51	2.71	1.72	1.7	0.6	34.3	18.1	13.7	31.1	23
C3	26	2.4	3.04	1.87	1.11	0.2	0.5	48.0	17.3	11.2	22.7	4
Harbour fine sand community												
B6	17,18	0.3	2.27	0.26	0.0	0.1	9.5	90.0	0.4	<0.05	<0.05	>100,>100
B8	15,16	0.6	2.37	0.33	−0.01	0.3	6.8	91.7	0.9	<0.05	0.1	<10,<10
B12	11,12	0.9	2.52	0.37	0.0	0.2	1.2	93.3	2.2	1.3	1.7	<10,<10
B16	7,8	2.1	2.54	0.69	−0.29	4.1	6.6	73.0	5.5	1.9	6.5	926,–*
C4	27	2.4	2.58	0.65	0.31	0.1	0.4	83.9	6.9	3.3	5.3	1
C5	28	1.7	2.80	0.48	−0.19	<0.05	0.3	75.9	16.5	3.3	3.8	2
C6	29	0.4	2.72	0.19	−0.02	0.3	0.3	90.2	6.1	1.7	1.2	0
C7	30	0.5	2.64	0.31	0.0	<0.05	0.4	94.9	2.8	1.7	–*	0
C8	31	0.2	2.77	0.45	0.15	1.8	0.6	78.5	11.4	4.7	2.7	1
C9	32	0.0	2.67	0.31	0.0	0.2	0.5	92.2	4.2	1.1	1.5	5
C10	33	−0.3	2.66	0.32	0.01	2.7	0.3	89.0	6.0	0.7	1.0	44
C11	34	−0.5	2.72	0.33	−0.03	7.3	0.3	79.4	11.1	0.5	1.3	39
A10c	67	0.0	2.67	0.32	−0.01	4.8	0.3	86.8	7.6	0.3	0.3	(see note 1)
Harbour stable shell-sand community (see note 2)												
B2	21,22	3.2	2.43	0.46	0.08	0.0	5.0	85.4	6.2	2.6	0.8	0,0
A2	75,76	11.8	1.27	2.71	−1.61	46.9	27.0	23.3	0.9	0.0	0.0	0,0
A6	70,71	13.0	2.31	2.75	−2.34	25.0	4.7	65.0	2.6	0.6	1.6	0,0
A8	68,69	10.6	1.99	2.52	−2.09	25.4	22.3	49.4	0.3	0.0	0.0	0,0
Harbour unstable sand community (see note 3)												
B0	23	6.5	2.20	1.90	−1.55	10.4	14.5	73.3	0.8	0.0	0.0	>10
A0	108,109	12.6	1.78	0.35	−0.01	0.5	71.2	25.8	0.1	0.0	0.0	0,0
A4	72,73,74	10.6	2.30	0.25	0.0	0.0	2.0	97.6	0.3	0.0	0.0	0,0,0
A10b	58	5.3	2.33	0.28	−0.01	0.1	4.1	94.6	0.9	0.0	0.0	0
Shallow offshore fine sand community												
W1	39,40	8.0	2.69	0.51	−0.12	<0.05	8.4	72.5	18.5	0.2	<0.05	0,0
W2	41,42	19.0	2.97	0.36	0.06	0.9	2.0	49.2	45.4	0.8	<0.05	0,0
W3	43,44	28.5	2.97	0.41	0.05	1.4	3.2	45.8	45.4	0.9	0.1	0,0
W4	35–38	13.1	3.05	0.71	−0.32	0.5	6.1	35.7	53.0	1.4	<0.05	0,0,0,0
W5	110,111	19.0	3.09	0.74	0.41	0.4	0.6	36.5	49.6	11.6	1.2	0,0

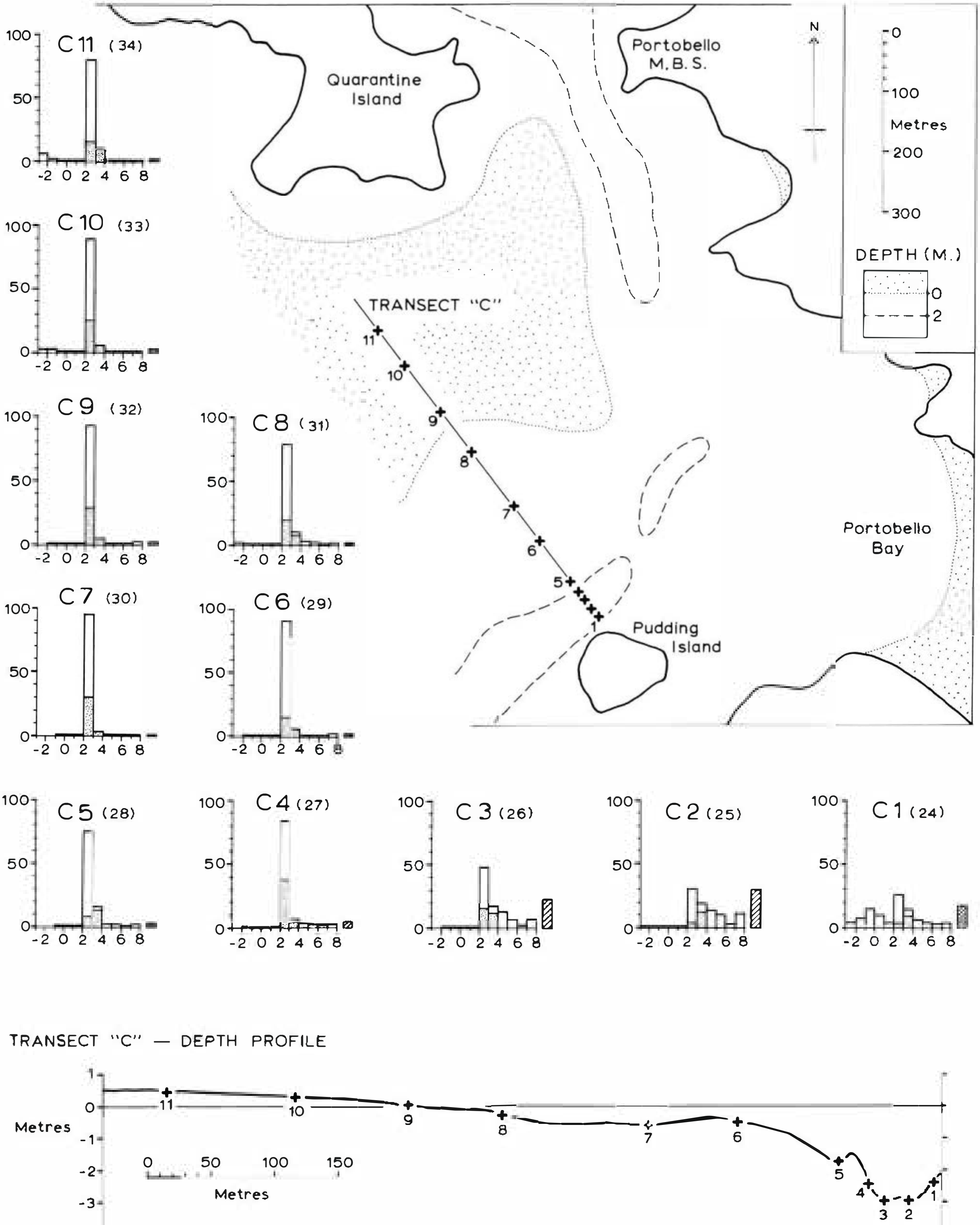
Notes
(1) Harbour fine sand community. Samples 59–66 from station A10c were similar in sediment composition to sample 67. Samples 59, 60, 62, 63, 64, 66 and 67 contained >100 g algae, chiefly *Ulva*; samples 61 and 65 contained <10 g algae.
(2) Harbour stable shell-sand community. Sediments from station A10a (samples 45–51) were similar to those at stations A6 and A8.
(3) Harbour unstable sand community. Samples 52–57 from station A10b were similar in sediment composition to sample 58.
(4) Depths from samples mentioned in Notes 1, 2 and 3 are given in Appendix 1.
*Sample data not available.

This is also suggested by two transects along the shipping channel on 13 February 1968 and 16 February 1968 at high and low tides respectively, in which the maximum salinity reduction at any particular station at low tide was 0.19‰.

Temperature differences between the inner and outer harbours may be more marked than salinity differences. At high tide, the water in the outer harbour is more or less uniform in temperature; in the inner harbour a marked horizontal gradient may be present, particularly in summer and winter. In summer, water temperatures at the head of the harbour may be at least 3.8°C higher than in the outer harbour (27 January 1966). Outer harbour temperatures at high tide varied through the year from 7.9°C to 14.0°C, and inner harbour temperatures from 5.3°C to 17.4°C, ranges of 6.1°C and 12.1°C respectively. Data from the daily 0900 h readings at the Portobello Marine Laboratory during 1965–1967 give a mean annual range of 13.1°C. This figure is probably exceeded in the inner harbour.

FIG. 4 (*opposite*): Otago Harbour, transects A and B – station locations and sediment data. Sediment fractions are given in phi units (abscissa), as a percentage of total sediment weight, including organic detritus (hatched). Each histogram is identified by station number, with benthos sample numbers given in brackets. Where sediment fractions have been expressed in half-phi intervals, the coarser of the two fractions is stippled. Sediment coarser than $-2\ \varphi$ is not subdivided further.


A 6 (70, 71)
A4 (72-74)
A 2 (75, 76)
A 0 (108, 109)
A10b (52-58)
A 8 (68, 69)
B0 (23)
A 10c (59-67)
B 8 (15,16)
B 2 (21, 22)
B 18 (5,6)
B 14 (9,10)
B 10 (13,14)
B 4 (19, 20)
B 22 (1,2)
B 20 (3,4)
B16 (7, 8)
B 12 (11,12)
B 6 (17, 18)
B0
A0
A2
B2
A6
A4
A8
B6
B4
A10
a
b c
B8
B10
B12
B14
B16
B18
B20
B22



Quarantine Island
Portobello M.B.S.
N
0
100
Metres
200
300
DEPTH (M.)
0
2
TRANSECT "C"
Portobello Bay
Pudding Island
C11 (34)
C10 (33)
C9 (32)
C8 (31)
C7 (30)
C6 (29)
C5 (28)
C4 (27)
C3 (26)
C2 (25)
C1 (24)
TRANSECT "C" — DEPTH PROFILE
Metres
0
50
100
150
Metres

FIG. 5 (*opposite*): Otago Harbour, transect C – station locations, sediment data and depth profile. Sediment histogram conventions are the same as in Fig. 4.

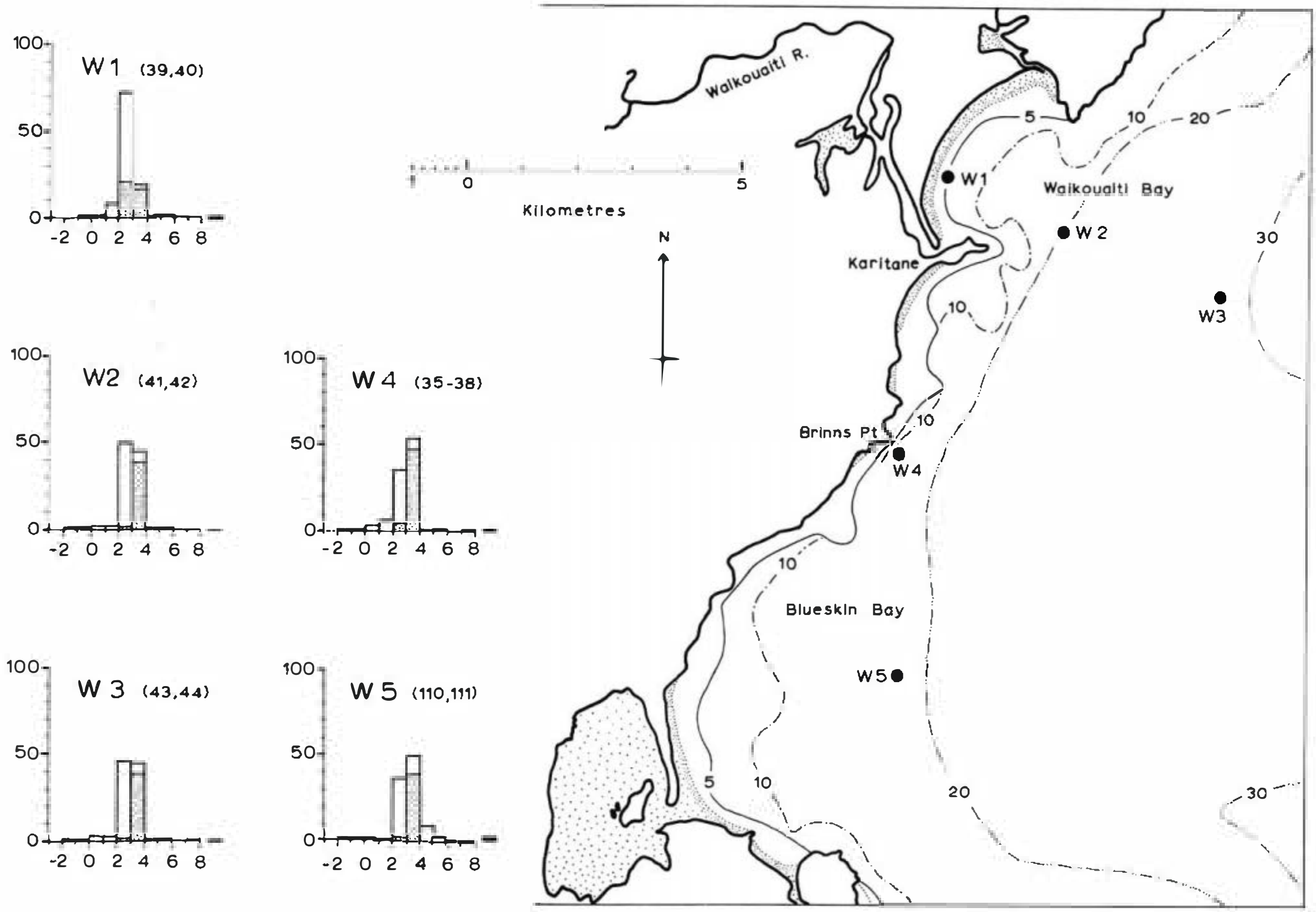


FIG. 6: Blueskin Bay area – bathymetry, station locations and sediment data. Sediment histogram conventions are the same as in Fig. 4. The bathymetry is from N.Z. Hydrographic Chart 66 (Taiaroa Head to Nugget Point), with isobaths in metres.

A considerable volume of the water in the Otago Harbour is replaced at each tidal cycle, the water flushed from the harbour at low tide being carried away from the harbour entrance by the northward-flowing Southland Current. At high tide, unmixed water may extend into the harbour almost to Quarantine Island (Fig. 3), and it is probable that there is also a rapid turnover of inner harbour water. This, together with the small catchment area of the Otago Harbour, is presumably responsible for the relatively unmodified salinity of the inner harbour water.

TIDES AND CURRENTS

Tides are semi-diurnal, with mean sea level in the Otago Harbour 1.1 m above Chart Datum. Mean low water springs are 0.1 m above Chart Datum and mean high water springs 1.8 m above Chart Datum, giving a spring tide range of 1.7 m (Marine Division, Ministry of Transport). No detailed observations have been made on current speeds in the harbour. Benson and Raeside (1963) give a speed of up to 100 cm/sec for tidal currents in the narrow channel between Quarantine and Goat Islands. This is almost certainly approached at the harbour entrance, with maximum surface current speeds of 50–75 cm/sec in the main channel in the outer harbour. In the inner harbour, surface current speeds are probably less than 50 cm/sec in the main channel, and less than 25 cm/sec in the subsidiary channels to the south-east of the main channel. Off shore, there is a strong northerly current of up to 100 cm/sec passing just off the Otago Peninsula (Benson and Raeside 1963). However, surface current speeds in Blueskin Bay are low, generally less than 10–20 cm/sec.

SEDIMENTS

Sediment samples in the Otago Harbour varied from silt to coarse shell-sand (Figs 4, 5). The coarsest sediments were found in the shipping channel, particularly near the mouth of the harbour (e.g., station A0). Sediments from transect B ranged from fine sand at station B0 ($\varphi_{md} = 2.20\ \varphi$) to silts at stations B20 and B22 ($\varphi_{md} = 4.5$–$4.6\ \varphi$). Sediments from stations in more sheltered situations were generally finer and contained more organic detritus. In general, sediments from these stations consisted of a mixture of sand and silt, the proportion of silt tending to increase with distance from the harbour entrance. This trend is clearly shown by the sequence B4, B10, B14 and B18 (Fig. 4). Station B16 was intermediate in type, having an appreciable quantity of organic detritus in a sediment that was otherwise similar to, for example, station B12.

The sediments of the five off-shore stations in Blueskin Bay (Fig. 6) were finer than those of the outer harbour. The finest sediment was found at station W5 ($\varphi_{md} = 3.09\ \varphi$), indicating the relatively sheltered nature of Blueskin Bay. North of station W5, the Otago Peninsula provides less shelter from the prevailing south-westerly winds and the sediment is coarser, particularly close inshore, as at station W1 ($\varphi_{md} = 2.69\ \varphi$).

POLLUTION

There is some degree of industrial pollution in the inner harbour, but this is mostly limited to areas close to the Port of Dunedin and to Port Chalmers. Sewage pollution at the time of the survey was low. Sewage discharge from Dunedin takes place on the outer coast, but minor discharges occur from Port Chalmers and small settlements along the harbour. Measurements in 1963 of dissolved oxygen, phosphates and nitrites in sea water samples taken at the Portobello Marine Laboratory produced little evidence of organic pollution (Slinn 1968).

THE BENTHIC COMMUNITIES

Eighty samples were collected, from 34 stations. Five assemblages, or communities, were distinguished, using subjective criteria of environmental similarity which enabled samples with a similar species composition to be arranged together. These are:

- Harbour mud community (16 samples),
- Harbour fine sand community (24 samples),
- Harbour stable shell-sand community (15 samples),
- Harbour unstable sand community (13 samples),
- Shallow off-shore fine sand community (12 samples).

Within each community, differences in species composition occurred that could be related to environmental differences not considered in the primary division into communities. The species were therefore considered in three categories:

- a, species common throughout the community,
- b, species whose distribution could be related to environmental differences within the community,
- c, species locally abundant only, and not considered under b.

Quantitative species analysis for transect A samples was generally restricted to annelids, molluscs, arthropods and echinoderms. Species counts for samples from station A10c were made on annelids and molluscs only, although a qualitative assessment was made for abundant species of other groups. Samples from stations of the other series (B, C and W) were analysed for the abundance of all animal species collected. Listings of species counts for all samples collected have been deposited with the New Zealand Oceanographic Institute, Wellington, New Zealand, and with the Oceanographic Data Centre, Washington, D.C., United States of America.

HARBOUR MUD COMMUNITY

Characteristics

1. Sediments predominantly either very fine sand or silt (3–4 φ, >4 φ).
2. Organic detritus at least 10% of total sediment weight.
3. Maximum tidal current speeds generally less than 25 cm/sec.
4. Algae sometimes present in abundance, particularly red algae.

Sixteen samples from 10 stations were placed in this community (Table 1A), the samples ranging from subtidal mudflats at the head of the harbour to shallow tidal channels running along the south-east side of the harbour. Samples taken from the head of the harbour had a high proportion of silt (e.g., B22 $\varphi md = 4.5\ \varphi$, B20 φmd = 4.6 φ). This was replaced by very fine sand towards the harbour mouth (e.g., B4 φmd = 2.5 φ, B10 φmd = 2.8 φ). A large amount of coarse material was found in some samples. At station C1, for example, more than 25% of the sediment consisted of material coarser than 0 φ. Foliaceous red algae often occurred in abundance, as at stations B14 and B16.

Species composition

A total of 161 species was found in the 16 samples referred to the harbour mud community. Nine species were consistently present throughout the community (Table 2A). Variations in sediment type, the amount of organic detritus present, and the quantity of algae and coarse shell, appeared to influence the distribution of some 33 species (Table 2B). The distribution of 19 species was too irregular to be explained in this way (Table 2C).

HARBOUR FINE SAND COMMUNITY

Characteristics

1. Sediments predominantly fine sand (2–3 φ).
2. Organic detritus less than 10% of total sediment weight.
3. Maximum tidal current speeds less than 25 cm/sec.
4. Depth usually less than 5 m.

Twenty-five samples from 13 stations were placed in the harbour fine sand community (Table 1B). This community was extensively represented in Otago Harbour, except at the head of the harbour and near the Otago Heads. The samples fell into two groups, with samples from the inner harbour having more organic detritus and somewhat finer sediments than those from the outer harbour. In particular, stations B16, C4 and C5 (samples 7, 27 and 28) had a relatively large amount of organic detritus present.

Samples also differed in depth and in the quantity of algae and shell present. Stations C4 to C11 formed a series illustrating changes associated with decreasing depth and with variations in shell abundance and algal cover. Stations C5, C6 and C7 afforded examples of the effect of a fairly constant moderate tidal current, while the changes associated with emergence at low tide were illustrated by stations C10, C11 and A10c.

Species composition

One hundred and seventy-five species were found in the 24 samples referred to the harbour fine sand community. Nine species were consistently present throughout the community, including two species of crustaceans (Table 3A). The distribution of 35 species could be related to changes within the community of one or more the following factors: a, amount of organic detritus, b, amount of algae, c, amount of shell, d, sample depth. These species are listed in Table 3B. A further 18 species were locally abundant, but their distribution was not apparently explicable in terms of the above factors (Table 3C).

HARBOUR STABLE SHELL-SAND COMMUNITY

Characteristics

1. Sediments predominantly sand between 1.5 φ and 3 φ, often containing a high proportion of shell and coarse shell fragments.
2. Little organic detritus present.
3. Restricted to areas of high tidal current speeds (maximum between 50 and 100 cm/sec.).
4. Sediment movement by currents low except for surface shell.

Fifteen samples from five stations were placed in the harbour stable shell-sand community (Table 1C). All were from the outer harbour, mostly from areas of the shipping channel with a relatively stable bottom. The samples were considered in three groups, according to the amount of shell and shell fragments in the sediment. Samples 75 and 76, with 47% of the sediment coarser than 0 φ, comprised a group with a considerable quantity of coarse shell in the sediment. The second group consisted of samples with moderate amounts of coarse shell (samples 45–51, 68, 69, 70, 71), while the third group had very little shell (samples 21, 22). The sediment properties of samples 45–51 were not known in detail, but were considered to be sufficiently similar to samples 68, 69, 70 and 71 to be grouped with them.

Other differences between samples were due to differences in current speeds and water turbulence, and to disturbance by dredging. Tidal currents were strongest at station A2, where some surface movement of shell probably occurred. At station B2, situated about 10 m to the SW of a subtidal rock groyne running across the direction of current flow, water flow was fairly turbulent although current speeds were less than at station A2. In some parts of the outer harbour, shipping channel maintenance is carried out by a bucket dredge. Samples from station A10a, off Port Chalmers, and particularly station A8, showed disturbance by dredging.

Species composition

A total of 240 species was found in the 15 samples placed in the harbour stable shell-sand community. The absence of sediment samples from station A10a, and disturbance due to dredging, made it difficult to relate variations in species numbers to variations in particular environmental properties. However, a number of species groups were distinguished, according to their abundance in the groups of samples recognised. Fifteen species were consistently present throughout the community (Table 4A), while 62 species of restricted distribution were classified according to their abundance in the various sediment types (Table 4B). Twelve locally abundant species of restricted distribution could not be classified in this way (Table 4C).

HARBOUR UNSTABLE SAND COMMUNITY

Characteristics

1. Sediments predominantly sand between 1.5 φ and 2.5 φ, generally with little coarse shell or shell fragments.
2. Very little silt or organic detritus present.
3. Restricted to areas of high tidal current speeds (maximum speeds 50–100 cm/sec.).
4. Sediment movement by current action considerable.

Thirteen samples from four stations were placed in the harbour unstable sand community (Table 1D). All

TABLE 2: Harbour mud community – species widely distributed or locally abundant, found in N samples of the community and with mean abundance $\bar{X}$ for the N samples.

Species	N	$\bar{X}$	Species	N	$\bar{X}$
A. Species widely distributed within the community					
Annelids			Molluscs		
Podarke angustifrons	10	2.6	*Arthritica bifurca*	11	4.5
Dorvillea incerta	10	5.3	Arthropods		
Heteromastus filiformis	16	191.5	*Proharpinia hurleyi*	15	20.8
Nicolea maxima	10	3.2	*Bathymedon* sp. 1	11	6.9
tubificid 1	14	38.5	*Aora typica*	13	3.7
B. Species whose distribution can be related to variations in environmental features within the community					
1. Sediment type					
a. Species more abundant in sediments with a predominance of silt					
Annelids			Molluscs		
Harmothoe praeclara	10	9.4	*Acanthochiton neozelanicus*	7	9.9
Streblosoma sp.1	7	7.1	*Thoristella chathamensis*	6	5.7
b. Species more abundant in sediments of mixed sand-silt composition					
Annelids			Molluscs		
Exogone heterosetosa	7	4.3	*Maoricolpus roseus*	13	94.5
Neanthes cricognatha	7	1.9	*Chemnitzea zealandica*	16	75.5
Prionospio aucklandica	7	51.6	Echinoderms		
Prionospio n.sp.1	6	6.5	*Trochodota dendyi*	7	26.1
Notomastus zeylanicus	5	34.4	*Kolostoneura novaezealandiae*	11	2.0
Phisidia sp.1	8	5.1			
tubificid 2	9	11.2			
2. Species more abundant in sediments with a high organic content					
Annelids			Molluscs		
tubificid 2	9	11.2	*Nucula nitidula*	13	20.7
3. Species whose abundance can be related to the amount of algae/shell					
Annelids			Arthropods, cont'd		
Harmothoe praeclara	10	9.4	*Hemiplax hirtipes*	16	13.9
Caulleriella sp.1	8	5.6	*Halicarcinus cooki*	13	10.5
Cirriformia filigera	10	29.9	Echinoderms		
Molluscs			*Ophiomyxa brevirima*	12	26.7
Acanthochiton neozelanicus	7	9.9	*Axiognathus squamatus*	9	18.0
Thoristella chathamensis	6	5.7	*Allostichaster insignis*	4	2.0
Eatoniella kerguelensis	16	292.3	Chordates		
Sigapetella novaezelandiae	9	3.6	*Ascidiella aspersa*	8	4.6
Arthropods			*Botrylloides leachi*	3	–
Cilicaea canaliculata	10	3.1	*Syngnathus blainvillianus*	3	2.0
Parawaldeckia sp.1	9	25.4	*Tripterygium varium*	11	2.2
Paradexamine pacifica	10	2.8			
C. Species of restricted distribution not included in A and B above					
Nematodes			Molluscs, cont'd		
nematode 1	7	10.1	*Paxula paxillus*	2	6.0
Annelids			*Subonoba* cf. *foveauxiana*	2	101.5
Paraonis sp.1	3	8.0	*Odostomia cryptodon*	10	13.2
Euclymene sp.1	3	30.7	Arthropods		
Macroclymenella stewartensis	5	13.6	*Scleroconcha sculpta*	2	25.5
Branchiomma curta	5	4.4	*Tanais novaezelandiae*	11	6.8
Molluscs			*Corophium acherusicum*	2	11.5
Eatoniella pullmitra	3	19.0	*Parambasia rossi*	4	8.5
Estea rekohuana	3	114.3	*Phoxocephalus regium*	2	11.5
Rissoella rissoaformis	6	7.5	*Melita* sp.1	1	14.0
Xymene plebejus	4	3.0			

TABLE 3. Harbour fine sand community – species widely distributed or locally abundant. Distribution data as for Table 2.

Species	N	$\bar{X}$	Species	N	$\bar{X}$
A. Species widely distributed within the community					
Annelids			Molluscs		
Aglaophamus macroura	18	3.5	*Macomona liliana*	17	3.3
Prionospio aucklandica	13	16.2	Arthropods		
Travisia olens	16	3.7	*Haustorius* sp.1	-	-
Capitella capitata	13	8.5	*Pontophilus australis*	-	-
Heteromastus filiformis	22	13.2			
Macroclymenella stewartensis	23	40.2			
B. Species whose distribution can be related to variations in enviromental features within the community					
1.Organic detritus					
a. Species more abundant in sediments with a low organic detritus content (<1%)					
Annelids			Molluscs		
Prionospio n.sp.1	11	7.2	*Chione stutchburyi*	21	61.5
Armandia maculata	8	13.7	*Amphidesma australe*	4	3.5
b. Species more abundant in sediments with a moderate organic detritus content (1–10%)					
Annelids			Arthropods		
Naineris laevigata	12	2.7	*Diastylopsis thileniusi*	10	1.7
cf. *Boccardia* n.g., n.sp.4	12	78.5	*Urothoe* sp.1	10	34.0
Molluscs			*Proharpinia hurleyi*	7	7.9
Nucula nitidula	15	30.8	*Bathymedon* sp.1	6	3.0
			Lembos kergueleni	6	19.8
2. Species whose abundance can be related to the amount of algae					
Annelids			Arthropods, cont'd		
Platynereis australis	15	12.6	*Caprellina longicollis*	4	4.8
Molluscs			*Parawaldeckia* n.sp.1	3	18.0
Micrelenchus huttoni	16	78.9	cf. *Harpinioides* sp.1	4	6.5
Eatoniella kerguelensis	23	148.2	*Paradexamine pacifica*	6	21.3
Arthropods			*Aora typica*	7	12.9
Tanais novaezelandiae	7	15.9	*Hemiplax hirtipes*	8	2.0
Caprella aequilibra	7	6.6	*Halicarcinus cooki*	5	7.2
3. Species whose abundance can be related to the amount of shell					
Coelenterates			Molluscs, cont'd		
Anthopleura aureoradiata	2	313.0	*Micrelenchus huttoni*	16	78.9
Annelids			*Eatoniella kerguelensis*	23	148.2
Nicomache plimmertonensis	3	12.0	Arthropods		
Molluscs			*Isocladus armatus*	2	32.5
Notoacmea helmsi	13	12.1	*Hemiplax hirtipes*	8	2.0
			Halicarcinus cooki	5	7.2
4. Species more abundant in samples with moderate organic detritus content, subject to moderate tidal currents					
Annelids			Annelids, cont'd		
Aglaophamus virginis	3	2.0	*Euchone* cf. *pallida*	10	3.6
Glycinde dorsalis	4	1.5	Molluscs		
Scoloplos ohlini	3	4.3	*Antisolarium egenum*	4	1.5
Aricidea sp.1	9	3.3			
5. Species more abundant in samples subject to various degrees of exposure at low tide					
Coelenterates			Molluscs		
Anthopleura aureoradiata	2	313.0	*Chione stutchburyi*	21	61.5
Annelids			*Amphidesma australe*	4	3.5
Abarenicola affinis	2	2.0			
C. Species locally abundant but not included in A and B above					
Annelids			Molluscs		
Perinereis nuntia vallata	3	15.7	*Maoricolpus roseus*	8	22.1
Notomastus zeylanicus	5	5.6	*Chemnitzea zealandica*	9	6.4
Rhynchospio glutaea	4	17.7	*Arthritica bifurca*	4	4.7
Spio cf. *filicornis*	8	9.2	*Mysella unidentata*	9	11.0
Paraonis sp.1	4	9.0	*Neolepton antipodum*	6	29.8
cf. *Capitomastus* sp.1	9	13.2	Arthropods		
capitellid 1	11	6.3	*Parawaldeckia thomsoni*	3	6.7
Cirriformia filigera	6	8.3	*Pontharpinia australis*	4	17.0
Pectinaria australis	6	3.7	*Melita* sp.1	2	4.0
			Echinoderms		
			Kolostoneura novaezelandiae	8	2.6

TABLE 4: Harbour stable shell-sand community – species widely distributed or locally abundant. Distribution data as for Table 2.

Species	N	$\bar{X}$	Species	N	$\bar{X}$
A. Species widely distributed within the community					
Annelids			Molluscs, cont'd		
Prionospio n.sp.1	12	80.2	*Tawera spissa* (juv.)	14	32.6*
Armandia maculata	12	45.4	*Scintillona zelandica*	8	4.2
Travisia olens	9	4.2	Arthropods		
Molluscs			*Asterope grisea*	13	4.4
Eatoniella kerguelensis	11	8.4	*Nebalia longicornis*	10	5.4
Nucula nitidula	12	38.1	*Parawaldeckia* n.sp.1	9	11.6
Mysella unidentata	9	18.9	*Parawaldeckia thomsoni*	14	22.9
Neolepton unidentatum	14	38.8	*Phoxocephalus regium*	10	7.3
Paphirus largillierti (juv.)	12	20.2*			
B. Species whose distribution can be related to variations in environmental features within the community					
1. Species more abundant in shell sand with considerable coarse shell and shell fragments (proportion of sediment <0 φ about 50%)					
Molluscs			Arthropods, cont'd		
Ischnochiton sp.1	7	18.7	*Pagurus* n.sp. aff. *thomsoni*	7	4.4
Gari stangeri	6	15.8	*Pagurus* n.sp. aff. *cooki*	6	5.3
Arthropods			Echinoderms		
Isocladus armatus	7	22.7	*Axiognathus squamatus*	10	19.6
Lil'jeborgia hansoni	3	26.7	*Monamphiura spinipes*	9	22.9
2. Species more abundant in shell sand with moderate amounts of coarse shell and shell fragments (proportion of sediment <0 φ about 25%)					
a. Species generally present					
Coelenterates			Molluscs, cont'd		
Edwardsia tricolor	–	–	*Linopyrga rugata*	7	14.3
Annelids			*Chemnitzea* sp.3	6	10.2
Podarke angustifrons	10	3.7	*Odostomia cryptodon*	7	19.3
Glycera lamellipodia	9	4.3	*Paphirus largillierti* (large)	12	20.2*
Hemipodus simplex	7	6.0	Arthropods		
Aonides n.sp.1	9	8.8	*Paranthura flagellata*	8	3.0
Prionospio aucklandica	9	51.1	*Cilicaea canaliculata*	7	11.7
Notomastus zeylanicus	7	27.0	*Ianira neglecta*	6	10.0
capitellid 1	9	30.4	*Eusirus antarcticus*	6	3.7
Euclymene sp.1	10	36.5	*Eurystheus* sp.1	8	9.1
Owenia fusiformis	11	404.5	*Achelia* sp.1	8	11.9
Euchone sp.2	8	8.1	Echinoderms		
tubificid 1	10	7.2	*Trochodota dendyi*	9	3.2
Molluscs					
Maoricolpus roseus	10	30.2			
Buccinulum pertinax	7	2.6			
b. Species locally present					
Annelids			Arthropods		
Autolytus monoceros	3	9.0	*Astacilla tuberculata*	4	3.2
Odontosyllis polycera	6	11.7	*Bathymedon* sp.1	4	10.2
Odontosyllis sp.1	2	40.5	*Halicarcinus cooki*	4	3.7
Neanthes cricognatha	5	4.4			
Nereis falcaria	5	4.2			
Spirorbis spp.	4	19.2			
3. Species more abundant in sand with little coarse shell or shell fragments (proportion of sediment <0φ less than 1%)					
Molluscs			Arthropods, cont'd		
Cyamiomactra problematica	3	49.3	*Haustorius* sp.1	3	3.0
Tawera spissa (large)	14	32.6*	*Urothoe* sp.1	2	10.5
Arthropods			*Urothoides* sp.1	3	7.0
Scleroconcha sculpta	15	10.3	*Heterophoxus* sp.1	3	13.7
Diastylopsis thileniusi	3	43.7	*Pontharpinia australis*	15	41.3
Tanais novaezelandiae	12	222.0	*Lembos kergueleni*	4	165.7
Caprella aequilibra	3	28.3	*Photis brevicaudata*	4	327.0
4. Species rare in samples with considerable coarse shell or shell fragments					
Annelids			Phoronids		
Heteromastus filiformis	10	8.6	*Phoronopsis* sp.1	10	9.7
Macroclymenella stewartensis	8	7.6			
Euchone cf. *pallida*	14	101.7			
5. Species rare in samples without moderate or considerable coarse shell and shell fragments					
Molluscs			Arthropods		
Terenochiton otagoensis	9	27.6	*Jaeropsis palliseri*	5	3.6
Estea rekohuana	13	101.0			

TABLE 4—*continued*

Species	N	$\bar{X}$	Species	N	$\bar{X}$
C. Species locally abundant within the community but not included in A and B above					
Annelids			Arthropods, cont'd		
Lanice conchilega	6	14.2	*Maera* sp.1	5	6.8
Molluscs			*Paradexamine pacifica*	4	4.0
Chemnitzea zealandica	4	8.2	*Eurystheus dentifer*	1	16.0
Eatoniella pullmitra	1	173.0	*Jassa* sp.1	5	18.4
Arthropods			*Corophium acherusicum*	7	11.3
Gitanopsis squamosa	1	21.0	Echinoderms		
Stenothoe sp.1	1	75.0	*Allostichaster insignis*	4	6.0
Monoculodes sp.1	5	3.2			

*Distribution data includes both adults and juveniles.

were from the outer harbour, either from the shipping channel itself (stations A0, A4) or to one side of the channel (stations B0, A10b). The environment of this community differs from that of the stable shell-sand community principally in the amount of sediment movement by tidal currents that is taking place.

The stations differed in sediment grade and current speeds: the sediment at station A0 was coarser (φmd = 1.78 φ) than at the other stations (φmd = 2.20–2.33 φ), probably because of higher current speeds at station A0. Although current speeds were lower at station B0, its exposed position made it more liable to disturbance by wave action. A considerable amount of large shell and rock was present at station B0, and algae were growing on the embedded rocks.

Species composition

A total of 64 species was found in the 13 samples classified in the harbour unstable sand community. Four species were considered to be widely distributed within the community, while another four species were less abundant in samples exposed to strong water movement (stations B0, A0). These species, together with other species of a more restricted distribution, are listed in Table 5. A number of species were present only at station B0, probably because of the presence of a hard substrate, but few of these were abundant.

TABLE 5: Harbour unstable sand community – species widely distributed or locally abundant. Distribution data as for Table 2.

Species	N	$\bar{X}$	Species	N	$\bar{X}$
A. Species widely distributed within the community					
Annelids			Arthropods		
Travisia olens	9	2.3	*Macrochiridotea uncinata*	9	7.4
Molluscs			*Achelia* sp.3	8	6.9
Amphidesma forsterianum	12	5.5			
B. Species whose restricted distribution can be related to variations in environmental features					
1. Species less abundant at stations exposed to strong water movement					
Arthropods					
Haustorius sp.1	7	3.0			
Platyischnopus noezelanicus	10	53.5			
Urothoe sp.1	9	22.2			
Urothoides sp.1	11	53.3			
2. Species whose abundance is related to the presence of a hard substrate					
Molluscs					
Micrelenchus huttoni	2	7.5			
mytilid spat	2	-			
C. Species of restricted distribution not included in A and B above					
Annelids					
Sigalion ovigerum	4	1.2			
Aglaophamus macroura	5	1.4			
Magelona cf. *papillicornis*	5	2.4			
Scoloplos ohlini	7	16.9			

SHALLOW OFF-SHORE FINE SAND COMMUNITY

Characteristics

1. Sediments predominantly fine sand between 2.5 φ and 3.5 φ, with little coarse shell or shell fragments.
2. Water movement due to tidal currents limited (maximum current speeds less than 25 cm/sec.).

Twelve samples from five stations have been assigned to the off-shore fine sand community (Table 1E). Most of the differences between stations could be related to differences in depth and degree of shelter. Stations W4 and W5 were more sheltered than stations W1, W2 and W3, and had finer sediments (φmd = 3.05 φ, 3.09 φ). Little silt or organic detritus was present except at station W5, where over 10% of the sediment was finer than 4 φ, and organic detritus comprised about 1% of the sediment. Stations W1 and W4 were subject to greater wave action than the other stations. Station W1, just seaward of the surf line in Waikouaiti Bay, had a coarser sediment (φmd = 2.69 φ) than stations W2 and W3, which were otherwise similar (φmd = 2.97 φ). No algae were present at any station, but a considerable amount of suspended detritus occurred at station W1 at the time of sampling.

Species composition

A total of 91 species was recorded from the 12 samples placed in the off-shore fine sand community. Three groups of species were recognised. The main group consisted of species that were most abundant at station W2, common at stations W3 and W4, and present in reduced numbers at stations W1 and W5. The second group comprised species most abundant at station W1, and the third group comprised species most abundant at station W5. Table 6 lists 26 species belonging to these groups, with a further four species whose distribution did not conform to this pattern.

TABLE 6: Shallow offshore fine sand community – species widely distributed or locally abundant. Distribution data as for Table 2.

Species	N	$\bar{x}$	Species	N	$\bar{x}$
A. Species present at station W2, and usually at stations W3 and W4					
Annelids			Arthropods		
Sigalion ovigerum	9	1.4	*Cyclaspis argus*	7	19.7
Aglaophamus virginis	8	2.7	*Diastylopsis thileniusi*	8	4.5
Aglaophamus sp.1	10	12.7	*Macrochiridotea uncinata*	7	3.6
Goniada sp.1	10	8.6	*Tryphosa* cf. *kergueleni*	7	4.7
Prionospio sp.2	8	17.9	*Hippomedon* n.sp.1	7	4.6
Travisia olens	6	4.3	*Ampelisca acinaces*	6	4.0
			Urothoe sp.1	6	4.0
			Urothoides sp.1	8	3.7
			Pontharpinia sp.1	10	3.8
B. Species most abundant at stations with greater water movement and suspended detritus (stations W1, W4)					
Molluscs			Arthropods		
Zethalia zelandica	4	146.5	*Platyischnopus neozelanicus*	2	6.0
			Pagurus n.sp.1	1	8.0
C. Species most abundant at stations with reduced water movement and increased silt (stations W5, W3)					
Coelenterates			Molluscs		
Peachia carnea	3	2.0	*Antisolarium egenum*	8	56.9
Annelids			Arthropods		
Drilonereis sp.1	5	2.4	*Ommatocarcinus macgillivrayi*	1	2.0
Magelona cf. *papillicornis*	4	6.7	Echinoderms		
Aricidea sp.1	4	8.0	*Heterothyone ocnoides*	4	9.5
Chaetozone sp.1	8	10.0			
D. Species locally or irregularly abundant, not included in A, B or C above					
Annelids			Arthropods		
Langerhansia cerina	2	7.0	*Heterophoxus* sp.3	6	2.7
capitellid 1	4	6.2	*Photis brevicaudata*	4	6.5

DISCUSSION

THE CLASSIFICATION OF BENTHIC COMMUNITIES IN A SHALLOW-WATER DEPOSIT ENVIRONMENT

A close relationship between the composition of the benthos and the benthic environment is generally accepted (Jones 1950, Thorson 1957, Knox 1961, Pérès 1961, Longhurst 1964). The classification of communities has been variously made on the basis of species composition or of environmental characteristics. Classification on the basis of species composition is usually performed by selecting a single species, or a group of species, as being 'characteristic' of the community as a whole. For the concept of characteristic species to have heuristic value, however, it is necessary to consider that the occurrence of a particular set of characteristic species in more than one group of samples implies the existence of other properties in common. This is often assumed to imply a similar overall species composition and hence membership of the same community. This assumption is justified if the community is a unit largely bound by rigid biological interactions, or if its component species have closely similar habitat preferences. While biological interactions, particularly predator-prey relationships, may play an important part in determining the composition of benthic soft-bottom communities, strong interspecific bonds are relatively uncommon.

It has been suggested that a classification by environment is insufficiently sensitive. Thorson (1957), for example, feels that the use of species rather than the environment to describe the communities will give a much finer analysis. Some species are indeed very sensitive to small environmental differences, especially during their larval phase, as has become evident from the work on, for example, *Ophelia bicornis* (Wilson 1953, 1954). However, community classifications taking into account relatively minor changes in species composition very rapidly become unworkable because of the consequent proliferation of communities (e.g., Gislèn 1930). For most purposes, the use of environmental criteria provides at least as satisfactory a subdivision of communities as the use of characterising species.

In the present study, no distinction was made between infaunal and epifaunal species. While the difference between the two is sufficiently distinct to be useful descriptively, their separation as communities is somewhat artificial. This particularly applies in a coarse deposit environment, where the group to which some species are assigned is largely a matter of personal discretion.

The classification of the samples collected in Otago Harbour and Blueskin Bay into five communities was made primarily as a convenient means of assigning species to a particular habitat. Within some communities, the differences in species composition related to differences in environmental properties almost warranted their partition into a number of more narrowly defined communities. If more samples had been obtained from the off-shore fine sand community, it would probably have been more convenient to regard the off-shore samples as coming from three separate communities, corresponding to the subdivisions recognised in Table 6A, B, C. Similarly, if there had been more samples in the harbour stable shell-sand community similar in species composition to the samples from station B2, these could have been assigned to a separate community.

While the limits of the five communities recognised correspond generally to more or less obvious discontinuities in environmental properties, the distribution patterns of some environmental variables measured did not permit a sharp distinction to be made. In particular, the shallow harbour mud and fine sand communities tend to inter-grade, so that the assignment of samples to either community depends on arbitrary criteria. While each community has a reasonably distinct species composition, it is not surprising that many of the commoner species have patterns of distribution which overlap the community boundaries set. Altogether, 93 species were present in at least half the samples assigned to any one community, but 81 of these were present in at least one other community, while 17 occurred in at least half the samples of two or more communities. The wide distribution of these 17 eurytopic species does not seem to be accounted for by differences in size or feeding habits from other species of a more restricted distribution. However, their usually greater abundance, and the greater number of samples in which they were found, enables some generalisation to be made about their distribution, relating them to patterns of environmental variation other than those used in delimiting the communities.

Nine species, typically abundant in the harbour stable shell-sand community and usually present in the less muddy samples of the harbour mud community, seemed to prefer a firm substrate, either with little water movement and considerable organic detritus, or with considerable water movement and a reduced level of organic detritus. These species included two polychaetes, *Podarke angustifrons* and *Prionospio aucklandica,* tubificid 1, the bivalve *Nucula nitidula* and the gastropod *Maoricolpus roseus, Tanais novaezelandiae,* two amphipods, *Parawaldeckia* n.sp.1 and *Proharpinia hurleyi,* and the ophiuroid *Amphipholis squamata.* Seven of the eight remaining eurytopic species had distributions that can be related to environmental properties. The polychaete *Travisia olens* was common in any fine sand sediment, while the amphipod *Urothoe* sp.1 was restricted to fine sand sediments with little organic detritus. Two species, the isopod *Macrochiridotea uncinata* and the amphipod *Urothoides* sp.1, were more or less restricted to samples from well-sorted fine sand sediments with minimal organic detritus. The polychaete *Macroclymenella stewartensis* was common in most stable fine sand samples, and the polychaete *Heteromastus filiformis* was common in most samples with considerable organic detritus in the sediment. The gastropod *Eatoniella kerguelensis* was abundant in most samples with macroscopic algae. The ostracod *Scleroconcha sculpta*, while abundant in most samples in the harbour stable shell-sand community and also in three other communities, did not seem clearly related to any particular environmental properties.

THE EFFECT OF SHELL AND MACROSCOPIC ALGAE ON SPECIES COMPOSITION

Although the benthic samples from the Otago Harbour and Blueskin Bay were restricted to soft-bottom areas, varying amounts of coarse material were present (Table 1). This was occasionally broken rock (station C1) or small boulders (station A0), but generally consisted of whole or broken mollusc shell, and often provided a substrate for the growth of macroscopic algae. Variations in the amount of this coarse material and macroscopic algae present in the samples could be related to the abundance of various species. From these relationships and from observations made while diving it was apparent that shell and other coarse material was directly responsible for the presence of a number of animals otherwise found only on a hard bottom, and indirectly responsible for the presence of others dependent on the algae for food and shelter. In its turn, the presence of such algae has affected sediment composition in some areas by favouring the deposition of silt and organic detritus, with resulting differences in the infauna.

A large group of species directly associated with the presence of shell used it primarily as a hard substrate for attachment, but did not depend on it for the supply of food. In areas of strong tidal currents the bryozoans *Caberea zelandica* and *Flustrella hispida* were found attached to large shell, along with the campanularian *Obelia* sp. (probably *O. geniculata*) and sertularians like *Amphisbetia fasciculata*, *A. trispinosa* and *Symplectoscyphus johnstoni*. Exposed shell surfaces of the southern tuatua *Amphidesma forsterianum*, common in unstable sand substrates, often carried long colonies of *Plumularia wattsi*. In areas less exposed to water movement, the Foveaux Strait oyster *Ostrea lutaria* occurred in small numbers, as well as the mussel *Gregariella barbata*. At low tide *O. lutaria* was commonly found attached to clean shell of the cockle *Chione stutchburyi*, or in small clumps formed from successive spatfalls on older specimens of *O. lutaria*. Occasional specimens of the blue mussel *Mytilus edulis aoteanus* and the ribbed mussel *Aulacomya maoriana* were found attached to oyster or cockle shell, while the small anemone *Anthopleura aureoradiata* was particularly common on cockle shell or the exposed surfaces of live cockles, along with occasional specimens of the acorn barnacle *Elminius modestus*. In areas with some organic detritus another epifaunal species associated with cockle shell was the maldanid *Nicomache plimmertonensis*, constructing thick, orange-tinged sandy tubes in the empty valves. Two further species associated with shell were the saucer limpets *Sigapatella novaezelandiae* and *Zegalerus tenuis*, which occurred in subtidal areas with substantial organic detritus. Both were commonly found on the turritellid *Maoricolpus roseus*, sitting on the basal whorl behind the aperture.

In contrast to these epifaunal species were others which either burrowed in shell or used it in other ways for shelter. The boring sponge *Cliona celata* was common in old *Ostrea* and *Paphirus* shell while a number of polydorids, including some new species, occurred in the shell of various bivalve species. Where entire gastropod shells were present hermit crabs were often found. These included *Pagurus cooki*, *P. spinulimanus* and other undescribed pagurids, living in *Maoricolpus* shell, and another undescribed species of pagurid common in *Zethalia zelandica* shell outside the harbour. Broken shell was used in large amounts by tubicolous polychaetes such as *Owenia fusiformis*, which coats its membranous tube with small shell fragments up to 2 mm in diameter. In the shallow harbour stable shell-sand community this species occurred in closely-packed beds at densities of up to 7500/m^2.

Bivalve shell, in particular, formed a suitable habitat for a number of grazing species, including various chitons. *Acanthochiton zelandicus* occurred in areas with considerable silt and organic detritus while *Amaurochiton glaucus* was found only on intertidal sand flats. The shallow harbour stable shell-sand community was particularly rich in chitons, a species of *Ischnochiton* and the small *Terenochiton otagoensis* being the most abundant, but also including *Ischnochiton circumvallatus*, *I. maorianus*, *Paricoplax* cf. *platessa* and *Anthochiton canaliculatus*. The limpet *Notoacmea helmsi* was common in shallow sandy areas while the rissoid *Estea rekohuana* was often numerous in deeper samples with considerable shell.

The growth of macroscopic algae on shell or other hard substrates provided a favourable attachment surface for a range of sedentary and tubicolous species. The predominant alga in samples from areas of low light penetration was the foliaceous rhodomeleacean *Lenormandia chauvinii*, occurring at a density of up to 4.5 kg wet weight/m^2. Its fronds often carried flat, circular colonies of the bryozoan *Membranipora membranacea*, while the ascidians *Ascidiella aspersa* and *Botrylloides leachi* could be found on the thicker, basal portions, along with occasional tubes of the terebellid *Streblosoma* sp.1. Various tube-building amphipods were common, although more often on other, finely-branching red algae. The more numerous of these were the calliopiid cf. *Harpinioides* sp.1, the dexaminid *Paradexamine pacifica* and the aorid *Aora typica*. In samples from shallow sand flats green algae were often abundant, the predominant algae being species of *Ulva*. These sometimes formed broad sheets a metre or more wide to which the small coiled tubes of *Spirorbis* spp. were attached, while the membranous tubes of *Platynereis australis* were often built between their folded surfaces. Several herbivorous gastropods were often numerous on foliose algae like *Lenormandia* and *Ulva*. These included the trochids *Thoristella chathamensis dunedinensis* and *Micrelenchus huttoni*, *Thoristella* being largely restricted to areas with substantial silt and organic detritus, and *Micrelenchus* to shallow areas of clean sand. A third species, the small eatoniellid *Eatoniella kerguelensis chiltoni*, was usually present in large numbers on both red and green algae. Although most commonly found on algae, these herbivores, and also most of the sedentary and tubicolous species associated with algae, were often found grazing on, or attached to, suitable shell.

Indirectly dependent on the presence of shell or macroscopic algae are epifaunal species living on hydroids, and various predators. The species epifaunal on hydroids include the bryozoan *Celleporina granum*, a number of small, byssus-producing bivalves, including *Neogaimardia minutissima*, *Cyamiomactra* n.sp.1 and the spat of several species of mussels, and various species of pycnogonid which probably feed on the hydroids themselves. Two species of caprellid, *Caprellina longicollis* and the more abundant *Caprella aequilibra*, were irregularly present clinging to hydroids or to fine, branching algae and probably feeding on copepods or other small crustaceans. In algal beds the pipefish *Syngnathus blainvillianus* probably feeds similarly while the tan brittle star *Ophiomyxa brevirima* and the cockabully *Tripterygium varium* appear to feed on larger crustacea. A number of other species are often more abundant in the presence of shell or macroscopic algae, although the nature of the relationship is uncertain. The sphaeromatid *Cilicaea canaliculata* was found in samples with substantial organic detritus or with little organic detritus and high water movement, while another sphaeromatid *Isocladus armatus* was found in cleaner samples with abundant shell. A third isopod, the asellote *Jaeropsis palliseri*, was distributed similarly to *Isocladus* but did not occur in samples exposed at low tide. Two echinoderms, the asteroid *Allostichaster insignis* and particularly the ophiuroid *Axiognathus squamatus*, were often numerous in subtidal shell-sand samples or samples with some shell and organic detritus. The polynoid *Harmothoe praeclara* was found only in samples with considerable amounts of red algae, the lysianassid amphipod *Parawaldeckia* n.sp.1 was often abundant in any samples with considerable shell or red algae, and the hymenosomid crab *Halicarcinus cooki* occurred commonly in any samples with considerable shell or red or green algae.

In areas of low water movement the development of dense beds of foliaceous algae has resulted in the accumulation of fine sediment and organic detritus on the bottom, in part from the reduction in water movement in the algal beds, and in part from the large amounts of faecal material deposited by epifaunal species. The increased amounts of silt and organic detritus in the bottom deposit in an algal bed has consequently affected the composition of the infauna, with deposit- and mud-feeding species replacing those preferring a cleaner or coarser sediment. The cirratulids *Caulleriella* sp.1 and *Cirriformia filigera* were two common deposit feeders, the latter sometimes being particularly abundant in samples with considerable fine sediment. In samples with considerable organic detritus the small capitellid *Heteromastus filiformis* was an abundant mud-feeding species while two oligochaetes, tubificid 1 and tubificid 2, were usually common in mixed silt-sand sediments. Other mud-feeders included the burrowing mud-flat crab *Hemiplax hirtipes*, common in both silty and fine sand sediments containing much organic detritus, and the worm-like holothurian *Trochodota dendyi*, which was usually found in firm sediments with some organic detritus. Two gastropods, the suspension-feeding turritellid *Maoricolpus roseus* and the pyramidellid *Chemnitzea zealandica*, were often abundant in samples with considerable organic detritus. The Pyramidellidae are primarily an ectoparasitic group, but the absence in the samples of any obvious prey species which could account for the occurrence of *C. zealandica* at a density of up to 2000/m^2 suggests that it is in fact a deposit-feeder.

The distribution of macroscopic algae was often variable, areas of dense algae alternating irregularly with relatively open areas. The species composition of these open areas appears to be more or less independent of the fauna in the algal beds. At station B16 for example, two 0.2 m^2 samples were collected, the first (sample 7) from an area of fine sand with some organic detritus and little macroscopic algae, the second (sample 8) 2 m away in an area of dense foliaceous algae with considerable organic detritus. Sample 7 contained less than 5 g of algae while sample 8 contained over 900 g, chiefly *Lenormandia chauvinii*. The species composition of the two samples (Table 7) indicates a high degree of independence for at least the commoner species. Of a total of 75 species only 17 (23%) were found in both samples, and only two of the commoner species, the capitellid *Notomastus zeylanicus* and the phoxocephalid *Proharpinia hurleyi*, occurred in similar numbers in both samples. In more

TABLE 7: Station B16 – samples 7, 8. Species with 5 or more individuals per 0.2 m² sample.

	Sample 7	Sample 8
A. Species more abundant in sample 7		
(Substrate fine sand with some organic detritus and little macroscopic algae)		
Annelids		
Exogone heterosetosa	5	–
cf. *Boccardia* n.g., n.sp.4	95	–
Spio cf. *filicornis*	5	–
Macroclymenella stewartensis	37	–
Molluscs		
Neoguraleus sinclairi	5	–
Nucula nitidula	109	23
Arthropods		
Scleroconcha sculpta	8	–
Urothoe sp.1	15	–
B. Species more abundant in sample 8		
(Substrate silty sand with considerable organic detritus and foliaceous red algae)		
Annelids		
Podarke angustifrons	–	7
Neanthes cricognatha	–	5
Dorvillea incerta	–	11
Cirriformia filigera	–	5
Caulleriella sp.1	1	10
Heteromastus filiformis	82	492
Nicolea maxima	1	6
Streblosoma sp.1	–	5
Branchiomma curta	–	8
tubificid 1	–	52
tubificid 2	–	18
Molluscs		
Eatoniella kerguelensis	15	627
Eatoniella pullmitra	–	6
Molluscs		
Rissoella rissoaformis	–	9
Maoricolpus roseus	6	52
Chemnitzea zealandica	23	140
Arthritica bifurca	1	7
Arthropods		
Halicarcinus cooki	–	6
Hemiplax hirtipes	1	13
Echinoderms		
Ophiomyxa brevirima	–	14
Trochodota dendyi	1	7
C. Species more or less equally abundant in both samples*		
Annelids		
Notomastus zeylanicus	6	2
Arthropods		
Proharpinia hurleyi	19	20

*Species have been assigned to A, B or C on the basis of a two-tailed test of the data, assuming a binomial distribution ($p=q=0.5$), and $P \leq 0.10$. A high probability level was used because the binomial model is a simplification which has the effect of increasing the likelihood that a species will be assigned to C.

closely comparable sets of paired samples the proportion of species found in both samples is about half the total number. At station B18 for example, with 240 g and 300 g of algae in the two samples, the number of species in common was 26 of a total of 51 (51%).

The irregular distribution of macroscopic algae is a feature of both the harbour mud and harbour fine sand communities, and may arise from an irregularity in the distribution of shell or other coarse material similar to that found in the harbour stable shell-sand community. A consequence of the variability in species numbers associated with this irregular distribution is that even closely-spaced samples cannot necessarily be considered to be representative of the same environmental conditions, so that a better understanding of the relationship between particular species and their environment may be achieved by the measurement of local environmental conditions than by considering average conditions in the sample environment.

PATTERNS OF DIVERSITY

In addition to the variations of species composition which benthic assemblages show, meaningful patterns may be found in the more general property of diversity. Thus differences in diversity may result from differences in, for example, environmental heterogeneity (Simpson 1964), environmental stability (Klopfer 1959, Sanders 1968), or the degree of biological competition (Dobzhansky 1950). These and other hypotheses advanced to explain diversity have been summarised by Pianka (1966) and Sanders (1968).

Two components of diversity may properly be distinguished, species diversity and dominance diversity (Whittaker 1965). Species diversity is concerned with the number of species present in an assemblage, dominance diversity with the extent to which species are equally represented. Minimum dominance diversity occurs when an entire assemblage consists of a population of a single species, maximum dominance diversity when all species are equally represented.

Species diversity was measured simply as s, the number of species present in a sample. Dominance diversity was measured as d_r, the value of the information function $H(s)$ compared to H_{max}, the maximum possible value of $H(s)$ for s species, by

$$d_r = H(s)/H_{max},$$

where

$$H(s) = -\sum_{r=1}^{s} p_r \log_2 p_r, \qquad \text{(Shannon 1948)}$$

$$H_{max} = \log_2 s,$$

p_r being the sample proportion of individuals belonging to the rth species. As an index of diversity, $H(s)$ is sensitive both to changes in the number of species present and to changes in their relative proportions. By comparing the sample value of $H(s)$ with H_{max} the dominance diversity measure becomes theoretically independent of the number of species found. However, Lloyd and Ghelardi (1964) have suggested that a better measure of the relative numbers of species may be provided by equitability ε,

$$\varepsilon = s'/s$$

where s' is the number of species in an assemblage following a particular theoretical model required to give the same value of $H(s)$ as that actually observed. In their case, the broken-stick model of MacArthur (1957) was used, but the technique is also valid if the comparison is made with the equivalent number of evenly-distributed species required to give the observed value of $H(s)$.

A comparison was made of the dependence of the two measures of dominance diversity, d_r and ε, on the number of species present in a sample. This was achieved by considering the changes in both measures for replicate samples considered both singly and after pooling. Equitability was computed using the value of $H(s)$ predicted both by the MacArthur model (ε), and by an even distribution of species (ε'). The results for eight stations are presented in Table 8. In all cases the equitability of the pooled samples was substantially lower than the equitability of the samples considered separately, whether computed as ε or ε'. The similar behaviour of ε and ε' is not surprising, since the value of $H(s)$ expected on the basis of the MacArthur model bears a close relationship to H_{max} over nearly all possible values (Fig. 7). The dominance diversity measure d_r, showed a much smaller reduction than ε or ε' when calculated for pooled samples, and would appear to be the more satisfactory measure of dominance diversity where insensitivity to sample size is required.

Species diversity, s

The number of species in each sample, s, ranged from 2 to 114. Higher numbers of species were generally associated with a higher sample density of individuals (Spearman $\rho = 0.82$; $t = 11.9$ and $P \ll 0.001$ for 71 samples), and some of the variation in s can undoubtedly be ascribed to variation in population density. The existence of a factor operating to keep diversity high in the high-density populations is suggested by the absence of any trend in d_r with increasing s (Fig. 7), in contrast to the usual fall in d_r when single samples are pooled (Table 8, Fig. 7).

TABLE 8: Measures of diversity $H(s)$, d_r, ε, and ε^1, for the separate and pooled samples of 8 stations.

Station (sample)		Sample Area (m^2)	$H(s)$ (bits/indiv.)	d_r	ε	ε^1
B18	(5)	0.2	2.66	0.52	0.24	0.18
	(6)	0.2	2.52	0.47	0.19	0.14
	(5+6 – 51 spp)	0.4	2.62	0.46	0.17	0.12
B22	(1)	0.2	2.89	0.55	0.27	0.19
	(2)	0.2	2.36	0.46	0.20	0.15
	(1+2 – 46 spp)	0.4	2.66	0.48	0.19	0.14
A6	(70)	0.1	4.29	0.67	0.34	0.24
	(71)	0.1	4.14	0.63	0.27	0.19
	(70+71 – 120 spp)	0.2	4.36	0.63	0.25	0.17
Al0a	(49)	0.2	4.61	0.71	0.41	0.28
	(50)	0.2	4.25	0.68	0.37	0.25
	(49+50 – 112 spp)	0.4	4.77	0.70	0.36	0.24
A4	(72)	0.2	2.53	0.63	0.49	0.36
	(73)	0.2	2.54	0.60	0.42	0.31
	(74)	0.2	2.23	0.62	0.52	0.39
	(72–74 – 25 spp)	0.6	2.76	0.59	0.38	0.27
W1	(39)	0.2	0.87	0.20	0.11	0.10
	(40)	0.2	1.79	0.43	0.24	0.19
	(39+40 – 24 spp)	0.4	1.21	0.26	0.09	0.08
W2	(41)	0.2	4.29	0.81	0.72	0.49
	(42)	0.2	4.21	0.83	0.82	0.56
	(41+42 – 47 spp)	0.4	4.40	0.79	0.66	0.45
W4	(35)	0.2	3.99	0.77	0.63	0.43
	(36)	0.2	3.29	0.75	0.67	0.47
	(37)	0.2	3.97	0.90	1.08	0.75
	(38)	0.2	3.92	0.76	0.61	0.42
	(35–38 – 49 spp)	0.8	4.26	0.76	0.57	0.39

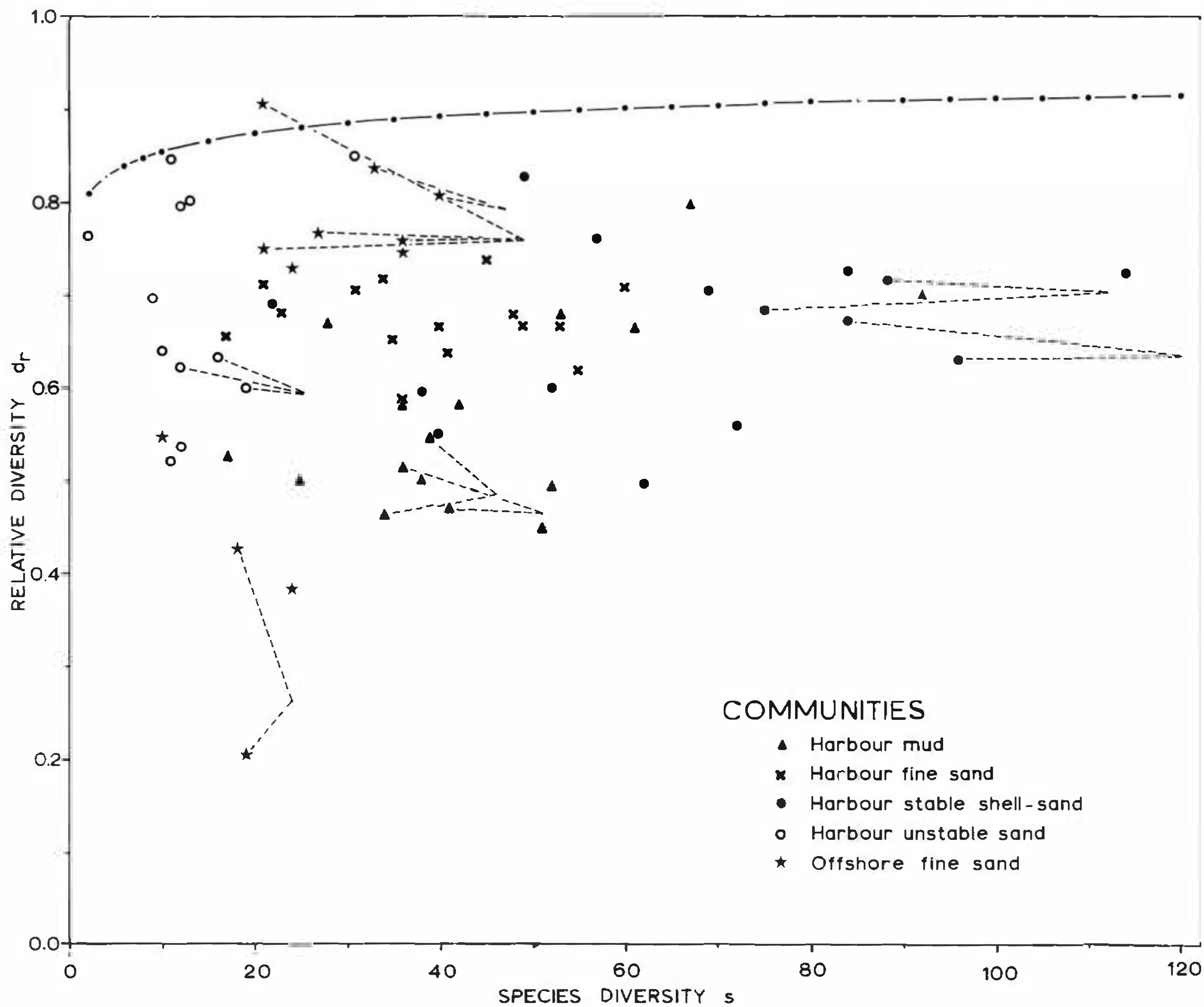


FIG. 7: Species diversity, s, and relative dominance diversity, d_r, for the benthic samples from Otago Harbour and Blueskin Bay area (71 samples). Sample combinations listed in Table 8 are indicated by dashed lines. The values of d_r expected on the basis of the MacArthur broken-stick model are indicated by ·——·

A possible explanation lies in differences in habitat diversity between samples or, more generally, the various communities. A community such as the harbour stable shell-sand community, with a relatively poorly sorted sediment and often considerable shell, has a high habitat diversity, with a wide range of habitats available for occupation by different species. On the other hand, a community such as the harbour unstable sand community, with a well-sorted sediment and little or no shell and algae, has a low habitat diversity. The association of species diversity and habitat diversity was also apparent within the communities. For example, samples within the same community with more surface shell or macroscopic algae usually had a higher species diversity.

The relationship between species diversity and habitat diversity is probably best considered in terms of a basic species diversity associated with the particular sediments of each community. The highest basic species diversity was shown by the well-sorted fine sand sediments of the stable shell-sand community, with $s \sim 60$ (e.g., samples 21, 22). The fine and very fine sand sediments of the harbour and off-shore fine sand communities showed moderate basic species diversity, with $s \sim 20$–40 (e.g., samples 11, 12, 29, 35–44). An unconsolidated silt sediment such as that of sample 3 of the harbour mud community had s = 17, while the lowest values of s were shown by the medium and fine sand sediments of the harbour unstable sand community, in which $s < 15$ in the majority of the samples.

In poorly-sorted sediments the basic species diversity was increased by the admixture of species extending their range from other habitats. The relatively high species diversity of samples 13, 14, 19 and 20 of the harbour mud community was largely due to the occurrence in the same samples of species normally more abundant either in fine sand with little organic detritus or in a silt sediment with considerable organic detritus.

The presence in the communities of even a small amount of very coarse material such as whole or broken mollusc shell may have a very strong influence on the species composition, as was indicated in the previous section on the influence of shell and algae. In shallow samples without strong water movement this material was primarily important as a substrate for foliaceous red and green algae, so that the presence of a moderate amount of coarse material was reflected by the occurrence of species associated with algae. In general, the number of species present in a sample increased with the amount of algae. Thus sample 3, with 50 g of algae, contained 17 species, and sample 4, with 250 g of algae, contained 38 species. Other samples from the harbour mud community whose high species diversity was largely due to the presence of large amounts of algae were samples 1, 2, 5, 6, 8, 9 and 10. Where there was more coarse material present on the surface it was available as a substrate for epifaunal species additional to those associated with the algae. The relatively high species diversity of samples 17, 18, 33 and 34 from the harbour fine sand community is likely to be accounted for in this way. In these samples the coarse material was provided by mollusc shell (noted for samples 17 and 18 at the time of collection, although not revealed by the sediment analysis). The high species diversity of a sample from the harbour mud community, sample 24 with 92 species, is also most likely to be accounted for by the amount of coarse material present, in this case mainly angular rock fragments.

In the deeper samples, or where there was considerable water movement, the development of algae was restricted. A high species diversity was, nevertheless, often found in samples of the harbour stable shell-sand community. For example, samples 70 and 71, of only 0.1 m^2, contained 84 and 96 species each. The high species diversity of these samples was probably due to the presence of epifaunal species directly associated with the occurrence of surface shell in combination with the high basic species diversity of the fine sand sediment of this community. In some samples, however, the species diversity was considerably less than would have been expected on this basis. The harbour stable shell-sand community was subject to interference as a result of maintenance operations on the shipping channel. Evidence of the recent activity of a bucket dredge was noticed at station A8, and samples 68 and 69 had correspondingly low numbers of species and individuals present.

While changes in environmental diversity may provide an explanation for much of the variation in species diversity found, some of the differences in species diversity seem more closely related to differences in sediment grade or stability. The variations in species diversity in well-sorted fine sand are particularly interesting. Sanders (1958) found this type of sediment a most favourable environment for filter-feeding species in Buzzards Bay and Long Island Sound. This would also seem to be true for the fine sand samples from the stable shell-sand community in Otago Harbour, particularly from station B2 (samples 21 and 22). Sample 21 contained 62 species and 3876 individuals, sample 22, 52 species and 1875 individuals, the most abundant species being small, filter-feeding crustaceans. The samples of the harbour unstable sand community form a strong contrast, having considerably fewer species and individuals. For example, the seven samples taken at station A10b contained an average of 11 species and 178 individuals in each sample. The sediment was slightly coarser than at station B2, with φmd = 2.33 φ (0.199 mm) instead of φmd = 2.43 φ (0.185 mm). However, the presence of current-driven sand ridges at station A10b (and the other stations of the harbour unstable sand community) indicates a degree of sediment instability absent from stations such as B2. In view of the known relationship between environmental stability and species diversity (Klopfer 1959, Sanders 1968) the difference in basic species diversity of the harbour stable shell-sand community and the harbour unstable sand community is likely to be due to the difference in sediment stability.

Dominance diversity, d_r

Dominance diversity d_r was computed for the same samples as species diversity s (Table 9, Fig. 7). Although d_r was more variable in samples with low species diversity, the two measures of diversity were uncorrelated (Spearman ρ = 0.03, for 71 samples). Samples from the harbour stable shell-sand and the harbour unstable sand communities had a similar range of values of d_r, between 0.50 and 0.85. For the other three communities some degree of separation on the basis of d_r was possible. Most samples from the harbour mud community had values of d_r between 0.45 and 0.58, while all values of d_r from the harbour fine sand community were between 0.59 and 0.75. The highest values were found for samples from three stations of the off-shore fine sand community (stations W2, W3, and W4), between 0.73 and 0.90.

Within each community, dominance diversity was generally inversely related to the number of individuals present. In the off-shore fine sand community, for

TABLE 9: Numbers of individuals and measures of diversity for samples from Otago Harbour and Blueskin Bay. Species diversity *s* is given as the number of species in a sample, and dominance diversity is given as the Shannon information function $H(s)$ expressed in bits/individual, and as relative dominance diversity d_r.

Station (Sample)	s	No. of Individuals	$H(s)$	d_r	Station (Sample)	s	No. of Individuals	$H(s)$	d_r
Harbour mud community									
B4 (19)	51	1327	2.56	0.45					
(20)	42	889	3.13	0.58					
B10 (13)	30	294	3.29	0.67	B20 (3)	17	661	2.15	0.53
(14)	67	448	4.84	0.80	(4)	38	1233	2.63	0.50
B14 (9)	36	597	3.01	0.58	B22 (1)	39	1084	2.89	0.55
(10)	61	1185	3.92	0.66	(2)	34	1216	2.36	0.46
B16 (8)	52	1599	2.82	0.49	C1 (24)	92	2250	4.55	0.70
B18 (5)	36	968	2.66	0.52	C2 (25)	53	980	3.89	0.68
(6)	41	1227	2.52	0.47	C3 (26)	25	259	2.32	0.50
Harbour fine sand community									
B6 (17)	53	654	3.82	0.67	C4 (27)	31	312	3.50	0.71
(18)	55	861	3.58	0.62	C5 (28)	49	596	3.75	0.67
B8 (15)	17	164	2.69	0.66	C6 (29)	35	402	3.36	0.65
(16)	21	122	3.14	0.71	C7 (30)	41	511	3.42	0.64
B 12 (11)	34	275	3.65	0.72	C8 (31)	36	462	3.04	0.59
(12)	23	309	3.09	0.68	C9 (32)	45	532	4.06	0.74
B16 (7)	40	468	3.54	0.67	C10 (33)	60	1184	4.17	0.71
					C11 (34)	48	1029	3.80	0.68
Harbour stable shell-sand community									
B2 (21)	62	3876	2.95	0.50	A6 (70)	84	1516	4.29	0.67
(22)	52	1875	3.43	0.60	(71)	96	2001	4.14	0.63
A2 (75)	69	1213	4.31	0.71	A8 (68)	38	310	3.13	0.60
(76)	49	458	4.64	0.83	(69)	22	100	3.08	0.69
A10a (45)	57	616	4.45	0.76					
(46)	40	637	2.95	0.55	A10a (49)	88	1664	4.62	0.71
(47)	72	1278	3.46	0.56	(50)	75	1011	4.25	0.68
(48)	84	1110	4.63	0.72	(51)	114	2588	4.93	0.72
Harbour unstable sand community									
B0 (23)	31	76	4.21	0.85	A10b (52)	12	205	1.92	0.54
A0 (108)	12	51	2.85	0.80	(53)	10	234	2.13	0.64
(109)	2	9	0.76	0.76	(54)	9	263	2.21	0.70
A4 (72)	16	135	2.53	0.63	(55)	11	362	1.80	0.52
(73)	19	166	2.54	0.60	(56)	9	99	2.21	0.70
(74)	12	120	2.23	0.62	(57)	13	51	2.97	0.80
					(58)	11	31	2.90	0.84
Shallow offshore fine sand community									
W1 (39)	19	483	0.87	0.20	W4 (35)	37	100	3.99	0.77
(40)	18	200	1.79	0.43	(36)	21	119	3.29	0.75
(39^1)	18	50	3.78	0.90	(37)	21	65	3.97	0.90
(40^1)	17	52	3.71	0.91	(38)	36	206	3.92	0.76
W2 (41)	40	231	4.29	0.81	W5 (110)	24	308	1.75	0.38
(42)	33	160	4.21	0.83	(111)	10	137	1.82	0.55
W3 (43)	36	265	3.85	0.74	(110^1)	23	78	3.70	0.82
(44)	24	125	3.33	0.73	(111^1)	9	47	2.61	0.75

Notes
(1) Diversity was not calculated for samples from station A10c, in which only counts for annelids and molluscs were available.
(2) The data for samples 39^1 and 40^1 are the same as for samples 39 and 40, apart from the deletion of *Zethalia zelandica* from the analysis.
(e) The data from samples 110^1 and 111^1 are the same as for samples 110 and 111, apart from the deletion of *Antisolarium egenum* from the analysis.

example, the mean number of individuals in samples with high dominance diversity, from stations W2, W3, and W4, was 156, compared with a mean of 282 individuals in samples with low dominance diversity, from stations W1 and W5. The higher number of individuals from the latter group of samples was associated with the presence of two species of gastropod, *Zethalia zelandica* at station W1 and *Antisolarium egenum* at station W5, at densities of 450--2165 individuals/m^2. If d_r is recomputed for the samples from stations W1 and W5 without taking these species into account, it is apparent that their low dominance diversity was largely due to the presence of a single abundant species at each station (Table 9).

COMPARISON WITH OTHER SHALLOW-WATER SOFT-BOTTOM COMMUNITIES

New Zealand

Two communities have previously been described from the Otago Harbour. Ralph and Yaldwyn (1956) described a sandbank community characterised by *Chione stutchburyi* and *Abarenicola affinis* and a channel community characterised by *Maoricolpus roseus, Harmothoe praeclara* and *Ophiomyxa brevirima,* calling these an *Austrovenus* association (*Austrovenus* = *Chione*) and a *Maoricolpus* association respectively. The *Austrovenus* association is roughly equivalent to the harbour fine sand community of the present study, but is more narrowly defined. *Chione* is not necessarily present in the harbour fine sand community and amphipods may be abundant (up to $>500/m^2$). The *Maoricolpus* association may be equated with the harbour mud community as earlier defined. However, *Maoricolpus* is not necessarily present in or confined to samples from the harbour mud community, but is found in a variety of environments, particularly where there is a firm sediment with at least moderate current speeds, and with a variety of other species.

Shallow-water environments similar to Otago Harbour and Blueskin Bay have been described by a number of authors, including Powell (1937), Grace (1966), Morton and Miller (1968), Batham (1969) and Knight (1974). The communities described by Grace, Powell, and Morton and Miller, were from relatively-sheltered areas in the north of the North Island, 1000–1150 km north of Otago Harbour, at 36–37°S. Knight examined communities in Lyttelton Harbour, at 43°S, while Batham studied a sheltered bay at Stewart Is, about 150 km south of Otago Harbour, at 47°S.

Morton and Miller (1968) considered faunal distributions in a sheltered area near Whangarei Heads. They described a mosaic of small communities, relating their distribution to differences in depth, sediment type and water movement. Many of the major species also occurred in similar localities in Otago Harbour and Blueskin Bay, including *Chione stutchburyi, Paphirus largillierti, Tawera spissa, Gari stangeri, Amphidesma australe, Myadora striata* and many others. Grace (1966) described seven or eight soft-bottom communities from the entrance of the Whangateau Harbour, but gave little information about the composition of the communities and no detailed sediment data. However, three characterising species occur in similar habitats in Otago Harbour. These are *Chione stutchburyi, Gari stangeri* and *Tawera spissa.* The more detailed study by Powell (1937) in the Manukau and Auckland Harbours distinguished five major groupings or 'formations' which were subdivided into 'associations'. Little emphasis was placed on anything other than the larger mollusc and echinoderm species and only a broad classification of sediment characteristics was made. The Otago Harbour mud, fine sand and unstable sand communities and the offshore fine sand community do not appear to have any close equivalent in Powell's formations. The Otago Harbour stable shell-sand community has characteristics in common with associations of both the *Tawera-Glycimeris* formation and the *Maoricolpus* formation, with a number of species listed as dominants by Powell being present. These include *Tawera spissa* from the *Tawera-Glycimeris* formation, and *Maoricoplus roseus, Dosina zelandica* and *Paphirus largillierti* from the *Maoricolpus* formation.

Knight's (1974) work in the Lyttelton Harbour used Fager's recurrent groups analysis and discriminant analysis on samples collected by a variety of equipment. Three communities were recognised, together with a group of 'continuum species' whose distribution was discussed in terms of environmental gradients. Two of the communities were considered to have parallels in the Otago Harbour, the *Hemiplax-Virgularia* and the *Chione* communities being related to the *Maoricolpus* and the *Austrovenus* associations of Ralph and Yaldwyn (1956). In the terminology of the present study, the three Lyttelton Harbour communities are probably parallel developments of the Otago Harbour mud and fine sand communities, but a close comparison is difficult. *Virgularia gracillima* was not found in the Otago Harbour survey, and the distribution of *Hemiplax hirtipes* was most closely related to the amount of shell and macroscopic algae present, in both the harbour mud community and the harbour fine sand community. *Chione stutchburyi* was locally very abundant in the harbour fine sand community, but the overall species composition of samples from the community was not markedly altered in these areas and their classification as a separate community was not warranted. The third Lyttelton Harbour community was characterised by *Zeacolpus vittatus* and *Pectinaria australis*; both genera are present in Otago Harbour, with *Zeacolpus symmetricus* occurring mainly in the harbour mud community and *Pectinaria australis* mainly in the harbour fine sand community.

The study by Batham (1969), in Glory Cove, Stewart Island, was made on a sandy mud bottom with a fairly uniform species composition. A general feature of the samples was the presence of the foliaceous red alga *Lenormandia chauvinii*, also common in the mud community of the Otago Harbour. There is also some degree of similarity to samples from the harbour stable shell-sand community, with the presence of species such as *Terenochiton inquinatus, Maoricolpus roseus, Paphirus largillierti*, and *Tawera spissa*. However, in Glory Cove there were large numbers of various species of echinoderms not found in Otago Harbour.

Other New Zealand benthic studies that have been carried out were mostly in environments differing substantially from Otago Harbour and Blueskin Bay in depth or substrate characteristics (Fleming 1950, 1952, Dell 1951, Hurley 1959, 1964, Estcourt 1967, 1968, and McKnight 1968, 1969a). McKnight (1969b) reviewed the work on New Zealand subtidal marine communities, and recognised a total of 17 communities, classified mainly on the basis of dominant echinoderms and molluscs. The *Maoricolpus* association of Ralph and Yaldwyn (1956) was regarded as being probably tidal scour material, and the presence of *Nucula hartvigiana* and *Cyclomactra ovata* at one site in Otago Harbour was used to suggest that an *'Amphiura'* community may be present. *Cyclomactra* was not found in the present survey, although *Nucula nitidula* was common in the harbour stable shell-sand community; several amphiurids were locally common in this community, but were not consistently present.

A factor complicating the comparison of Otago Harbour communities with other benthic communities in New Zealand waters is the selectivity of the collecting methods used. Dredges have been used in most cases, with the occasional use of grabs (Estcourt 1967, 1968). During the course of this study, the operation of a naturalists dredge, a small Hayward orange-peel grab and a 0.1 m^2 Smith-McIntyre grab were observed on several occasions and their efficiency assessed on different substrates. All instruments were inefficient on compacted sediments, and failed to give a quantitative indication of the subsurface infauna in all but silt or clay substrates; in addition, many of the smaller crustacean species were lost.

In Otago Harbour, the use of a dredge or grab would probably have resulted in several stations being separated from others in the same community, and several stations from different communities would probably have been classified together. *Maoricolpus roseus* was occasionally abundant (up to 2440/m^2) in samples from both the harbour mud and harbour stable shell-sand communities, often where a quantity of shell was present in the sediment. Superficial sampling of such an area would give the appearance of a fauna largely comprising *Maoricolpus,* or lead to its being classified as tidal-scour material. Hermit crabs may be locally common in a compact shell-sand substrate (e.g., stations A2, A7, A10a), and these areas would give the appearance of being dominated by hermit crabs. If experience in Otago Harbour can be taken as a guide, the use of less-selective sampling techniques will probably modify the current classification of benthic communities from New Zealand waters.

Parallel communities

In a review of soft-bottom continental shelf benthic communities, Thorson (1957) used the concept of parallel communities and isocommunities (Thorson 1951, 1955) to group communities according to the similarity of their characteristic species. In this way a framework has been provided into which other workers have been able to place their results. For example, Longhurst (1958) working in the Gulf of Guinea, was able to classify five of the six communities as local representatives of parallel communities first described in the northern Atlantic, the sixth community apparently paralleling similar communities in other warm sea areas. A more flexible system of classification is used by Pérès (1961), in which shelf and shallow-water benthic communities are initially classified by depth (infralittoral, circalittoral), with a secondary classification by biotope. Less emphasis is placed on quantitative differences in community composition than by Thorson, but the community groupings achieved by Thorson and Pérès are largely compatible.

New Zealand communities were considered by Thorson under the following headings:

1. *Tellina lilacina* community (a parallel *Tellina* community), an intertidal sandflat community described by Oliver (1923) at Cheltenham Beach, Auckland, as a *Dosinia-Tellina* association. (*T. lilacina* is a mis-spelling for *T. liliana,* now *Macomona liliana.*)
2. *Amphiura rosea* community (a parallel *Amphiura* community), comprising a community described from the Auckland Harbour by Powell (1937) and from Queen Charlotte Sound by Dell (1951), as an *Echinocardium* formation, and from western Southland fiords as a 'soft mud substratum community' by Fleming (1950).
3. *Maoricolpus roseus* community (an isocommunity of the *Turritella* and *Cerithium* communities), comprising the *Maoricolpus* formation described by Powell (1937) from the Auckland and Manukau Harbours, and an assemblage from a 'sandy mud and muddy sand substratum', by Fleming (1950) in the western Southland fiords.
4. Communities without known parallels, including the *Arachnoides placenta* community, described as an *Arachnoides* formation by Powell (1937) from the Manukau Harbour. (*A. placenta* = *Fellaster zelandiae*.)

Thorson's review omits a number of other communities described by Oliver (1923), Powell (1937) and Fleming (1952). The use of *Echinocardium* by New Zealand workers as a preferred characterising species for Thorson's *Amphiura rosea* community was discussed by Hurley (1964), who pointed out that *A. rosea* is replaced by *A. norae* in the south of New Zealand, in communities showing obvious affinities. Estcourt (1967) described an association from the Marlborough Sounds, characterised by *Asychis theodori, A. trifilosa, Echinocardium cordatum* and *Amphiura rosea,* which he considered to have a close resemblance to the northern hemisphere *Maldane sarsi-Ophiura sarsi* community of Thorson (1957). Stations described by Dell (1951) as an *Echinocardium* formation were placed by Estcourt in his *Asychis-Echinocardium-Amphiura* association.

Of the five communities described from Otago Harbour and Blueskin Bay, only the harbour fine sand community may easily be related to Thorson's classification, as an isocommunity to the *Macoma* community. The characterising genera of the *Macoma* community include *Macoma, Arenicola* and *Cardium,* these being replaced in the Otago Harbour fine sand community by *Macomona, Abarenicola* and the venerid *Chione stutchburyi.* Several species of Veneridae are common in parts of the harbour stable shell-sand community, suggesting an isocommunity to Thorson's *Venus* communities. The commonest of these are *Paphirus largillierti* and *Tawera spissa,* but there is a general paucity of other genera even closely related to those considered by Thorson to characterise a *Venus* community (*Spisula, Tellina, Thracia, Natica, Astropecten, Ophelia* and *Echinocardium*). The presence of the turritellid *Maoricolpus roseus* in abundance would suggest that a *Maoricolpus* community may occur in Otago Harbour, but the use of *M. roseus* as a characterising species would be inconsistent with the lack of constancy in accompanying species. At one station of the harbour stable shell-sand community, station B2, a considerable number of small filter-feeding crustaceans was present (more than 6000 individuals/m^2), presenting a situation analogous to an 'amphipod community' (Thorson 1957), but there are no grounds for considering this station essentially different from the other stations of the harbour stable shell-sand community.

To some extent the lack of close parallels to communities described by Thorson may be due to the use of a community classification based on local environmental discontinuities rather than the use of systematic or ecological equivalents of the characteristic species chosen by Thorson. However, a feature of Otago Harbour and Blueskin Bay is the variety of environmental influences operating, and it is probably inappropriate to expect accordance with a classification based on the relatively uniform level-bottom areas with which Thorson was primarily concerned.

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APPENDIX 1: Station List.

Station	Sample No.	Depth (m)	Date	Comments
Transect A (all samples 0.2 m^2, unless otherwise indicated)				
A0	108, 109	12.6	12.ii.66	Bottom level, medium sand with some shell. Visibility 5–6 m, surface temp. 15.1°, low tide.
A2	75, 76	11.8	4.vii.65	Bottom very uneven (ridges up to 1 m high). Sand with a considerable amount of whole and broken shell. Visibility 5 m, surface temp. 7.4°, low tide.
A4	72, 73, 74	10.6	26.vi.65	Clean sandy bottom. Visibility 4 m, surface temp. 8.4°, high tide.
A6	70, 71	13.0	20.vi.65	0.1 m^2 samples. Bottom firm, coarse shell overlying a shell-sand mixture. Visibility 4–5 m, surface temp. 7.4°, low tide.
A8	68, 69	10.6	13.v.65	Bottom shelly with parallel ridges probably due to dredging. *Pyura pachydermatina* in moderate nos (about 1/m^2), often with *Maurea punctulata* on the stems. Surface temp. 9.8°, high tide.
A10a	45	11.6	30.iv.65	Bottom fine sand, with *Pyura pachydermatina* (about 1/m^2). Firm mud 20–40 cm below the surface, sometimes exposed. Surface temp. 10.4°, high tide.
"	46	10.9	6.v.65	Bottom similar to 45. Surface temp. 10.3°, low tide.
"	47	10.4	30.v.65	Bottom similar to 45. surface temp. 8.0°, low tide.
"	48	10.2	4.vi.65	Bottom similar to 45. Visibility 3 m, low tide.
"	49, 50	10.6	15.vii.65	Bottom similar to 45. Visibility 5 m, low tide.
"	51	12.1	4.x.65	Bottom similar to 45. Surface temp. 9.4°, visibility 4–5 m, high tide.
A10b	52, 53	3.0	6.v.65	Bottom sloping, fine-medium sand with no shell. Surface temp. 10.4°, low tide, depth estimated.
A10b	54, 55	3.1	6.vi.65	Bottom similar to 52, 53. Surface temp. 8.5°, low tide.
A10b	56, 57	3.1	13.vii.65	Bottom similar to 52, 53, except a mobile (10 cm) sand ridge present. Surface temp. 7.7°, visibility 5 m, high tide.
"	58	5.3	9.ix.65	Bottom similar to 52, 53. Surface temp. 8.5°, visibility 6 m, high tide.
A10c	59, 60	-0.1	8.v.65	Bottom level, fine sand with broken shell. Algae present in moderate quantities. Surface temp. 10.3°, high tide.
"	61, 62	0.0	7.vi.65	Bottom similar to 59, 60, little algae in 61, more in 62. Surface temp. 8.5°, visibility 3 m, high tide.
"	63, 64	0.1	14.vii.65	Bottom similar to 59, 60. Surface temp. 7.8°, visibility 4–5 m, high tide.
"	65	-0.9	25.viii.65	Bottom similar to 59, 60. Surface temp. 8.6°, visibility 5 m, high tide.
"	66	-0.5	28.viii.65	Bottom similar to 59, 60. Surface temp. 8.5°, high tide.
"	67	0.0	9.ix.65	Bottom similar to 59, 60. Surface temp. 9.6°, visibility 5–6 m, high tide.
Transect B (all samples 0.2 m^2)				
B0	23	6.5	17.iii.66	Bottom clean sand with some large shells and well-rounded rocks up to 25 cm in diameter. Some green algae (*Ulva*) on rocks and embedded shells. Surface temp. 14.5°, high tide.
B2	21, 22	3.2	1.vii.65	Bottom clean sand. Temperature, bottom and surface 8.5°, visibility 2.5 m, high tide.
B4	19, 20	3.5	23.vi.65	Bottom silty, grading to a firm black sand, little shell, much plant debris, especially in 19. Surface temp. 7.3°, visibility 7–8 m, low tide.
B6	17, 18	0.3	10.vi.65	Bottom sandy with little algae. Surface temp. 8.5°, visibility 3 m, high tide.
B8	15, 16	0.6	12.vi.65	Bottom sandy, with a hard-packed layer of *Chione* and *Ostrea* shell 10–15 cm down. Surface temp. 6.6°, visibility <1 m, high tide.
B10	14	5.0	18.vi.65	Bottom fairly soft, black sand, little algae. Surface temp. 6.8°, visibility 4–5 m, low tide.
"	13	4.1	13.vi.65	Bottom similar to 14. Surface temp. 6.4°, high tide.
B12	11, 12	0.9	17.vi.65	Bottom firm sand. Surface temp. 7.0°, visibility 3 m, high tide.
B14	9, 10	2.1	17.vii.65	Bottom muddy sand. Surface temp. 5.7°, visibility 1.5 m, low tide.
B16	7, 8	2.1	10.viii.65	Sample 7 – bottom fine sand with little algae. Sample 8 – dense algae with siltier sediment. Surface temp. 5.9°, visibility 1.5 m, tide at mid-flood.
B18	5, 6	1.8	13.viii.65	Bottom soft muddy sand, with some algae. Surface temp. 6.5°, visibility 1.5 m, high tide.
B20	3, 4	2.1	16.viii.65	Bottom soft, muddy, some algae. Surface temp. 6.3°, low tide.
B22	1, 2	2.6	23.ii.66	Bottom soft, muddy, some algae. Surface temp. 16.7°, visibility 1.5 m, low tide.
Transect C (all samples 0.2 m^2)				
C1	24	2.4	2.i.67	Rock chips and shell mixed with muddy sand, some algae. Surface temp. 16.5°, visibility 1.5 m, tide at mid-ebb.
C2	25	2.9	7.i.67	Bottom soft mud, numerous live *Maoricolpus* with apices embedded. Surface temp. 13.6°, visibility 0.5 m, tide at mid-flood.
C3	26	2.4	10.i.67	Bottom fairly firm muddy sand. Surface temp. 14.7°, visibility 2.5 m, low tide.

APPENDIX 1—*continued.*

Station	Sample No.	Depth (m)	Date	Comments
C4	27	2.4	7.i.67	Bottom firm sand. Surface temp. 13.6°, visibility 0.5 m, tide at mid-flood.
C5	28	1.7	10.i.67	Bottom similar to 27. Surface temp. 14.7°, visibility 2.5 m, low tide.
C6	29	0.4	11.i.67	Bottom similar to 27. Surface temp. 14.9°, visibility 1.5–2 m, low tide.
C7	30	0.5	11.i.67	Bottom similar to 27. Surface temp. 14.9°, visibility 1.5–2 m, low tide.
C8	31	0.2	12.i.67	Bottom firm sand, some shell. Surface temp. 14.4°, visibility 5–6 m, low tide.
C9	32	0.0	12.i.67	Bottom similar to 31. Surface temp. 14.4°, visibility 5–6 m, low tide.
C10	33	-0.3	18.i.67	Bottom firm sand with obvious entire and broken *Chione* shell. Surface temp. 18.5°, visibility 4.5 m, high tide.
C11	34	-0.5	18.i.67	Bottom similar to 33. Surface temp. 18.5°, visibility 4.5 m, high tide.
Series W (all samples 0.2 m^2)				
W1	39, 40	8.0	10.xi.66	Bottom fine sand, numerous *Zethalia* on the surface. Moderate bottom swell, no current. Visibility 0.5 m.
W2	41, 42	19.0	12.xii.66	Bottom fine sand, rippled. Bottom swell amplitude 1 m, no current. Bottom temp. 12.4°, visibility 2–2.5 m.
W3	43, 44	28.5	17.xi.66	Bottom fine sand. Light bottom swell, no current. Visibility 2–3 m.
W4	35–38	13.1	1.xi.66	Bottom fine sand with some shell. Bottom swell moderate, no current. Visibility 1–1.5 m.
W5	110, 111	19.0	23.ii.67	Bottom slightly muddy sand. No bottom swell, very slight current. Visibility 7–8 m.

APPENDIX 2: Systematic list of species collected from Otago Harbour and Blueskin Bay. Major revision of some taxonomy has been made since the completion of this study in 1969, and the nomenclature used here will need to be checked against that used by later authors.

Phylum PROTOZOA
Class Rhizopoda
Gromia oviformis Dujardin

Phylum PORIFERA
Class Calcarea
Leuconia ?aspersa
Class Demospongiae
sponge 2

Phylum COELENTERATA
Class Hydrozoa
Family Campanulariidae
Obelia probably *geniculata* (Linnaeus)
Family Sertulariidae
Amphisbetia fasciculata (Kirchenpauer)
Amphisbetia trispinosa (Coughtrey)
Symplectoscyphus johnstoni (Gray)
Family Plumulariidae
Plumularia wattsi Bale
Family Tubulariidae
Tubularia larynx Ellis & Solander
Class Anthozoa
Family Actiniidae
Anthopleura aureoradiata Stuckey
Family Edwardsiidae
Edwardsia tricolor Stuckey
Family Haloclavidae
Peachia carnea Hutton

Phylum ASCHELMINTHES
Class Nematoda
nematode 1
nematode 2
nematode 3
Plylum Nemertinea
nemertine 1
nemertine 2
nemertine 5

Phylum ANNELIDA
Class Polychaeta
Family Ampharetidae
Ampharete kerguelensis McIntosh
Phyllamphicteis foliata (Haswell)
Family Amphictenidae
Pectinaria australis Ehlers
Family Arabellidae
Drilonereis sp.1
Family Arenicolidae
Abarenicola affinis (Ashworth)
Family Capitellidae
Capitella capitata (Fabricius)
capitellid 1
Capitellides sp.1
cf. *Capitomastus* sp.1
Heteromastus filiformis (Claparède)
Notomastus zeylanicus Willey
Notomastus sp.2
Family Chrysopetalidae
Paleanotus chrysolepis Schmarda
Family Cirratulidae
Caulleriella sp.1
Chaetozone sp.1
Cirratulus sp.1
Cirriformia filigera (delle Chiaje)
Tharyx sp.1
Timarete anchylochaeta (Schmarda)
Family Dorvilleidae
Dorvillea incerta (Schmarda)
Family Eunicidae
Eunice sp.3
Family Flabelligeridae
Diplocirrus sp.1
Flabelligera bicolor (Schmarda)
Family Glyceridae
Glycera americana Leidy
Glycera capitata Oersted
Glycera lamelliformis McIntosh
Glycera lamellipodia Knox
Hemipodus simplex (Grube)
Family Goniadidae
Glycinde dorsalis (Ehlers)
Goniada grahami Benham
Goniada sp.1
Goniada sp.2
Family Hesionidae
Podarke angustifrons (Grube)
Family Lumbrineridae
Lumbrineris sphaerocephala (Schmarda)
Lumbrineris sp.1
Lumbrineris sp.2
Lumbrineris sp.3
Family Magelonidae
Magelona ?papillicornis Müller
Family Maldanidae
Asychis theodori Augener
Euclymene sp.1
Macroclymenella stewartensis Augener
Nichomache plimmertonensis Augener
Nichomache sp.2
Praxillella sp.1
Family Nephtyidae
Aglaophamus macroura (Schmarda)
Aglaophamus virginis (Kinberg)
Aglaophamus sp.1
Family Nereidae
Neanthes cricognatha Ehlers
Nereis falcaria Willey
Perinereis nuntia vallata (Savigny)
Platynereis australis (Schmarda)
Family Opheliidae
Armandia maculata (Webster)
cf. *Ophelia* sp.1
Travisia olens Ehlers
Family Orbiniidae
Haploscoloplos cylindrifer (Ehlers)
Naineris laevigata (Grube)
Orbinia papillosa (Ehlers)
Scoloplos ohlini (Ehlers)
Scoloplos sp.1
Family Oweniidae
Owenia fusiformis delle Chiaje
Family Paraonidae
Aricidea sp.1
Paraonis sp.1
Family Phyllodocidae
Eteone platycephala Augener
Eulalia sp.1
Eulalia sp.2
phyllodocids, unidentified
Family Polynoidae
Harmothoe praeclara (Haswell)
Lepidasthenia n.sp.1
Lepidonotus sp.1
Family Sabellidae
Branchiomma curta (Ehlers)
Branchiomma serratibranchis (Grube)
Euchone cf. *pallida* Ehlers
Euchone sp.1
Euchone sp.2
Family Scalibregmidae
Scalibregma inflatum Rathke
Family Serpulidae
Serpula ?vermicularis Linnaeus
cf. *Spirobranchus* sp.1
Spirorbis spp.
Family Sigalionidae
Sigalion ovigerum Monro
Sigalion sp.1
Sthenelais sp.1
Family Sphaerodoridae
Sphaerodorum sp.2

Family Spionidae
Aonides n.sp.1
Boccardia n.sp.1
cf. *Boccardia* n.g., n.sp.1
cf. *Boccardia* n.g., n.sp.4
cf. *Boccardia* n.g., n.sp.5
Nerine antipoda (Augener)
Nerine sp.1
Nerine sp.2
Prionospio aucklandica Augener
Prionospio n.sp.1
Prionospio n.sp.2
Prionospio n.sp.4
Rhynchospio glutea (Ehlers)
Spio ?aequalis Ehlers
Spio cf. *filicornis* (Müller)
Spiophanes bombyx (Claparède)
Family Syllidae
Autolytus chathamensis Knox
Autolytus monoceros (Ehlers)
Eusyllis sp.1
Exogone heterosetosa McIntosh
Langerhansia probably *cerina* Grube
Odontosyllis polycera Schmarda
Odontosyllis sp.1
Pionosyllis sp.1
Pionosyllis sp.2
Sphaerosyllis perspicax Ehlers
Sphaerosyllis sp.2
syllids, unidentified
Syllis sp.1
Typosyllis sp.1
Family Terrebellidae
Lanice conchilega (Pallas)
Lysilla sp.1
Nicolea maxima Augener
Phisidia sp.1
Polycirrus sp.1
Proclea sp.1
Streblosoma sp.1
Class Oligochaeta
Family Tubificidae
tubificid 1
tubificid 2

Phylum ARTHROPODA
Subphylum Pycnogonida
Family Ammotheidae
Achelia dohrni
Achelia sp.1
Achelia sp.2
Achelia sp.3
Family Pallenidae
Callipallene sp.1
Subphylum Mandibulata
Class Crustacea
Subclass Ostracoda
Family Asteropidae
Asterope grisea Brady
Synasterope quadrata (Brady)
Family Cypridinidae
Azygocypridina imperator (Brady)
Cycloleberis zealandica (Baird)
Euphilomedes agilis (Thomson)
Muelleriella hispida (Brady)
Scleroconcha sculpta (Brady)
Family Cytheridae
Loxoconcha punctata Thomson
Xestoleberis compressa Brady
Subclass Copepoda
Family Caligidae
Caligus buechlerae Hewitt
Family Corycaeidae
corycaeid 1
Subclass Malacostraca
Order Nebaliacea
Nebalia longicornis Thomson
Order Stomatopoda
Family Lysiosquillidae
Heterosquilla spinosa (Wood-Mason)

Order Mysidacea
Family Mysidae
cf. *Heteromysis* sp.1
Siriella sp.1
cf. *Siriella* sp.1
Order Cumacea
Family Bodotriidae
Cyclaspis argus Zimmer
Cyclaspis elegans Calman
Cyclaspis levis Thomson
Cyclaspis triplicata Calman
Family Diastylidae
Colurostylis lemurum Calman
Colurostylis pseudocuma Calman
Diastylopsis thileniusi (Zimmer)
Gynodiastylis carinata Calman
Gynodiastylis laevis Calman
Family Leuconidae
Leucon sp.1
Order Tanaidacea
Family Paratanaidae
Paratanais tenuis Thomson
Family Tanaidae
Tanais novaezelandiae Thomson
Order Amphipoda
Family Acanthonotozomatidae
Panoplea spinosa Thomson
Family Ampeliscidae
Ampelisca acinaces Stebbing
Family Amphilochidae
Amphilochus filidactylus Hurley
Gitanopsis pusilloides Shoemaker
Gitanopsis squamosa (Thomson)
Neocyproidea peninsulae Hurley
Family Aoridae
Aora typica Krøyer
Lembos kergueleni (Stebbing)
Family Atylidae
Nototropis cf. *minokoi* (Walker)
Family Calliopiidae
cf. *Harpinioides* sp.1
Family Caprellidae
Caprella aequilibra Say
Caprellina longicallis (Nicolet)
Family Corophiidae
Corophium acherusicum Costa
Corophium sextonae Crawford
Family Dexaminidae
Paradexamine pacifica (Thomson)
Polycheria ?tenuipes Haswell
Family Eusiridae
Eusirus antarcticus Thomson
Family Gammaridae
Maera subcarinata (Haswell)
Maera sp.1
Melita sp.1
Parapherussa crassipes (Haswell)
Family Haustoriidae
Haustorius sp.1
Platyischnopus neozelanicus Chilton
Urothoe sp.1
Urothoides sp.1
Family Jassidae
Jassa sp.1
Parajassa sp.1
Family Leucothoidae
Leucothoe trailli Thomson
Family Liljeborgiidae
Lil'jeborgia akaroika Hurley
Lil'jeborgia hansoni Hurley
Family Lysianassidae
Acontiostoma marionis Stebbing
Aristias sp.1
Hippomedon n.sp.1
lysianassid 3
lysianassid 4
lysianassid 5
Parambasia rossi Stephenson
Parambasia sp.1
Parawaldeckia thomsoni (Stebbing)

Parawaldeckia n.sp.1
Parawaldeckia n.sp.2
Tryphosa cf. *kergueleni* (Miers)
Family Oedicerotidae
Bathymedon sp.1
Monoculodes sp.1
oedicerotid 1
Family Photidae
Eurystheus dentifer (Haswell)
Eurystheus longimanus (Chilton)
Eurystheus sp.1
Haplocheira barbimana (Thomson)
Photis brevicaudata Stebbing
Protomedeia sp.1
Family Phoxocephalidae
Heterophoxus sp.1
Heterophoxus sp.2
Heterophoxus sp.3
Phoxocephalus regium Barnard
Pontharpinia australis (Barnard)
Pontharpinia sp.1
Proharpinia hurleyi Barnard
Family Podoceridae
Podocerus cristatus (Thomson)
Family Pontogeneiidae
pontogeneiid 1
Family Prophliantidae
Ceina egregia (Chilton)
Family Stenothoidae
Stenothoe sp.1
Family Talitridae
Allorchestes novizealandiae Dana
Order Isopoda
Family Anthuridae
Anthelura sp.1
Paranthura flagellata (Chilton)
Family Astacillidae
Astacilla falclandica (Tatersall)
Astacilla tuberculata (Thomson)
Family Eurydicidae
Cirolana hirtipes Milne-Edwards
Cirolana pellucida Tatersall
Family Ianiridae
Ianira neglecta Chilton
Family Idotheidae
Glyptonotus sp.1
Macrochiridotea uncinata Hurley & Murray
Family Jaeropsidae
Jaeropsis palliseri Hurley
Family Munnidae
Haliacris neozelanica (Chilton)
Family Sphaeromatidae
Cilicaea canaliculata (Thomson)
Isocladus armatus (Milne-Edwards)
sphaeromatid 1
Family ?Trichoniscidae
?*Trichoniscus* sp.1
Order Decapoda
Family Callianassidae
Callianassa filholi Milne-Edwards
Family Cancridae
Cancer novaezealandiae (Jacquinot)
Family Crangonidae
Pontophilus australis (Thomson)
Pontophilus pilosoides Stephensen
Family Goneplacidae
Ommatocarcinus macgillivrayi White
Family Hymenosomatidae
Halicarcinus cooki Filhol
Hombronia depressa (Jacquinot & Lucas)
Family Majidae
Leptomithrax longimanus Miers
Notomithrax peroni (Milne-Edwards)
Family Ocypodidae
Hemiplax hirtipes (Jacquinot)
Family Paguridae
Pagurus cooki
Pagurus spinulimanus (Miers)
Pagurus n.sp. (aff. *cookii*)
Pagurus spinulimanus (Miers)
Pagurus n.sp. (aff. *cooki*)
Pagurus n.sp. (aff. *thomsoni*)
Pagurus n.sp. (aff. *traversi*)
Pagurus n.sp. 1
Family Palaemonidae
Periclimenes batei Holthuis
Family Porcellanidae
Petrolisthes novaezelandiae Filhol
Family Portunidae
Nectocarcinus antarcticus (Jacquinot)
Phylum MOLLUSCA
Class Amphineura
Family Chitonidae
Amaurochiton glaucus (Gray)
Anthochiton canaliculatus (Quoy & Gaimard)
Family Cryptoconchidae
Acanthochiton zelandicus amplificatus Iredale & Hull
Notoplax mariae (Webster)
Family Ischnochitonidae
Ischnochiton circumvallatus (Reeve)
Ischnochiton maorianus Iredale
Ischnochiton sp.1
Family Lepidopleuridae
Terenochiton otagoensis Iredale & Hull
Family Lepidochitonidae
Paricoplax cf. *platessa* (Gould)
Class Gastropoda
Family Acmaeidae
Notoacmea helmsi (Smith)
Family Buccinulidae
Buccinulum littorinoides (Reeve)
Buccinulum pertinax (von Martens)
Family Calyptraeidae
Sigapatella novaezelandiae Lesson
Zegalerus tenuis (Gray)
Family Cerithiidae
Zeacumantus subcarinatus (Kiener)
Family Columbellidae
Paxula paxillus (Murdoch)
Family Cominellidae
Cominella glandiformis (Reeve)
Family Eatoniellidae
Eatoniella dilatata (Powell)
Eatoniella kerguelensis chiltoni (Smith)
Eatoniella limbata (Hutton)
Eatoniella pullmitra Ponder
Family Fissurellidae
Incisura lytteltonensis (Smith)
Family Liotridae
Liotella polypleura (Hedley)
Family Mathildidae
Mathildona sp.1
Family Mitridae
Austromitra rubiginosa (Hutton)
Family Muricidae
Axymene pumila (Suter)
Xymene plebejus (Hutton)
Xymenella pusilla (Suter)
Family Naticidae
Tanea zelandica (Quoy & Gaimard)
Family Philinidae
?*Philine* sp.1
Family Pyramidellidae
Agatha geogiana (Hutton)
Chemnitzea zealandica (Hutton)
Chemnitzea sp.1
Chemnitzea sp.3
Chemnitzea sp.4
Eulimella sp.1
Gumina dolichostoma (Suter)
Linopyrga rugata (Hutton)
Odostomia cryptodon Suter
Odostomia cf. *indicata* Suter
Odostomia cf. *vestalis* Murdoch
Family Rissoellidae
Rissoella rissoaformis (Powell)
Family Rissoidae
Eastea rekohuana Powell
Powellisetia subtenuis (Powell)
rissoid n.sp.1

Rufodardanula exaltatus (Powell)
Scrobs hedleyi (Suter)
Subonoba cf. *foveauxiana* (Suter)
Family Scissurellidae
Scissurona rosea (Hedley)
Family Trochidae
Micrelenchus caelatus (Hutton)
Micrelenchus huttoni (Smith)
Micrelenchus sp.1
Thoristella chathamensis dunedinensis (Suter)
Thoristella sp.2
Zediloma subrostrata (Gray)
Family Turridae
Neoguraleus finlayi Powell
Neoguraleus lyallensis (Murdoch)
Neoguraleus sinclairi (Gillies)
Neoguraleus cf. *sinclairi* (Gillies)
Family Turritellidae
Maoricolpus roseus (Quoy & Gaimard)
Zeacolpus symmetricus (Hutton)
Family Umboniidae
Antisolarium egenum (Gould)
Zethalia zelandica (A. Adams)
Class Bivalvia
Family Amphidesmatidae
Amphidesma australe (Gmelin)
Amphidesma forsterianum Finlay
Family ?Crassatellidae
?*Cuna* sp.1
Family Cyamiidae
Cyamiomactra problematica Bernard
Cyamiomactra n.sp.1
Family Gaimardiidae
Neogaimardia forsteriana (Finlay)
Neogaimardia minutissima (Iredale)
Family Galeommatidae
Scintillona zelandica (Odhner)
Family Leptonidae
Arthritica bifurca (Webster)
Lasaea maoria Powell
Mylitella vivens Finlay
Family Mactridae
Longimactra elongata (Quoy & Gaimard)
Maorimactra ordinaria (Smith)
Resania lanceolata Gray
Family Montacutidae
Mysella unidentata Odhner
Neolepton antipodum (Finlay)
Notolepton sanguineum (Hutton)
Family Myochamidae
Myadora boltoni Smith
Myadora striata Quoy & Gaimard
Family Mytilidae
Aulacomya maoriana (Iredale)
Gregariella barbata (Reeve)
mytilids, small, unidentified
Mytilus edulis aoteanus Powell
Ryenella impacta (Hermann)
Family Nuculidae
Nucula dunedinensis Finlay
Nucula nitidula A. Adams
Family Ostreidae
Ostrea lutaria Hutton
Family Sanguinolariidae
Gari stangeri (Gray)
Soletellina siliqua Reeve
Family Semelidae
Leptomya retiaria (Hutton)
Family Solemyidae
Solemya parkinsoni Smith
Family Tellinidae
Macomona liliana (Iredale)
Zearcopagia disculus (Deshayes)
Family Thraciidae
Thracia vitrea (Hutton)
Family Veneridae
Chione stutchburyi (Gray)
Dosina zelandica (Gray)
Paphirus largillierti (Philippi)
Tawera spissa (Deshayes)
Phylum BRYOZOA
bryozoan 1
Caberea zelandica (Gray)
Celleporina granum (Hincks)
Flustrella binderi (Busk)
Membranipora membranacea (Linnaeus)
Phylum PHORONIDA
Phoronopsis sp.1
Phylum ECHINODERMATA
Class Asteroidea
Family Asteriidae
Allostichaster insignis (Farquhar)
Coscinasterias calamaris (Gray)
Family Asterinidae
Patiriella regularis (Verrill)
Class Holothuroidea
Family Caudinidae
Paracaudina chilensis (Müller)
Family Chiridotidae
Kolostoneura novaezelandiae (Dendy & Hindle)
Trochodota dendyi Mortensen
Trochodota dunedinensis (Parker)
Family Cucumariidae
Heterothyone ocnoides (Dendy)
Class Ophiuroidea
Family Amphiuridae
Amphiura amokurae Mortensen
Axiognathus squamatus (delle Chiaje)
Monamphiura aster (Farquhar)
Monamphiura spinipes (Mortensen)
Family Ophiodermatidae
Pectinura gracilis Mortensen
Family Ophiomyxidae
Ophiomyxa brevirima H. L. Clark
Phylum HEMICHORDATA
Class Ascidiacea
Family Ascidiidae
Ascidiella aspersa (Müller)
Family Botryllidae
Botrylloides leachi (Savigny)
Family Molgulidae
?*Molgula sluiteri* (Michaelsen)
Phylum CHORDATA
Subphylum Vertebrata
Class Pisces
Family Blenniidae
Tripterygium varium (Forster)
Family Gobiesocidae
Trachelochismus pinnulatus (Forster)
Family Pleuronectidae
Peltorhamphus novaezeelandiae (Günther)
Family Syngnathidae
Syngnathus blainvillianus Eydoux & Gervais

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