Rocky Shore Ecology of a Southern New Zealand Fiord

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Abstract

Doubtful Sound, a long, narrow, mountain-girt fiord on the west coast of the South Island of New Zealand, has a rainfall of approximately 200in per annum. This gives inshore surface salinities of less than one-third the salinity of outside seawater around much of the sound, in places being below 1%0. There is a steep salinity gradient between the fresher surface water and the saltier water a few feet below. This apparently depresses the level to which various shore animals ascend. Shaded inner-sound shores are largely algal-dominated, with few molluscs except the abundant brackish-water snail Potamopyrgus antipodum. On more open shores, Elminius modestus is important. Verrucaria maura is conspicuous at high tide level, though submerged at springs. Zonation is often striking. Outer sound shores, where not overshadowed, are more similar to eastern South Island rocky shores. Doubtful Sound is compared with Otago Harbour, where salinities are only slightly depressed, and where molluscs are more in evidence, and algae less so, on intertidal rocks.

INTRODUCTION

Two days spent on the inner part of Doubtful Sound during February, 1957, showed me that shores here were strikingly different from those I have studied in Otago. Dominant species are frequently different, and zonation is commonly much more marked than on any other New Zealand shores I have seen. In view of these features, two subsequent field trips have been made to Doubtful Sound, each of five days' duration.

METHODS

Doubtful Sound lacks road access at the time of writing, land access being by a 10-mile tramping track from Lake Manapouri, over Wilmot Pass. This restricted the amount of equipment carried in, and of specimens carried out. A road is now being built, however, in connexion with the huge hydro-electric scheme that will divert water from Lakes Manapouri and Te Anau into Doubtful Sound. Absence of tracks around the largely precipitous shores of the sound meant that shore sampling was carried out from launch and dinghy. Station letters from A to P were given to spots sampled at from half to low tide, for a period of \$\frac{1}{2}\$

hour to 1 hour or more. Briefer stops, or stops when the tide was above half, were made at several other places. Much of the shore was observed from the travelling launch, the region thus covered (Text-fig. 1) being the length of Malaspina Sound, around Bauza Island and the Shelter Islands, Hall Arm and Crooked Arm. Black-and-white and coloured photographs were taken extensively. Salinities were measured roughly with a Twaddell hydrometer during trip 2; somewhat more accurately during trip 3 with a Baird and Tatlock 12in shot-poised hydrometer, range 1.000 to 1.030, water temperatures being taken at the same time. Sub-surface water samples were taken during trip 2 by diving with a corked plastic cylinder, filled and re-corked at an estimated depth (M. Rudwick); and during trip 3 by sending down on a line a weighted half-litre glass measuring cylinder, air-filled and with its opening downwards on its descent, which was jerked upright and allowed to fill at a measured depth, and then rapidly brought to the surface.

Nomenclature of most algae follows Naylor (1954), of barnacles, Moore (1944), of molluscs, Powell (1961), and of flowering plants, Allen (1961). Name changes since my earlier rocky shore papers (Batham, 1956, 1958) are: Mytilus planulatus becomes Mytilus edulis aoteanus; Melarhaphe becomes Melarhapha; Pomatoceros coeruleus becomes P. cariniferus, and Asterina becomes Patiriella.

PHYSICAL ENVIRONMENT

The mountainous west coast of the southern part of the South Island, New Zealand, is deeply dissected by a number of long, narrow fiords. Of these, Doubtful Sound is about 22 miles long, and in most parts approximately 1 mile wide (Text-fig. 1). Three narrow side-arms run off it to the south-west; and to the N.E., inland of Secretary Island, it forms a continuous waterway with Thompson Sound and Bradshaw Sound. Offshore from the fiordland coast there is virtually no continental shelf, and within Doubtful Sound itself the often precipitous mountain-sides (Plate 1, figs. 1, 3) run steeply into deep water. Depths in most parts of the sound are over 40 fathoms and in several places over 100 fathoms. No obvious sill occurs near the entrance, except for a rock coming within about 5 fathoms of the surface WNW of the outer end of Bauza Island (H.M.S. "Acheron" Survey, 1851; unpublished report of survey of Doubtful Sound by G. L. Haskins, R.N.Z.N., 1961). Thus the rocky shoreline is almost without sandy beaches; exceptions being at the heads of Deep Cove and Crooked Arm. Local portions of the shore are pebbly (head of Hall Arm), or with stones or boulders where creeks enter. But most of it is continuous, rather hard rock, consisting of high-grade schists and gneisses.

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Rainfall

Prevailing moisture-laden winds coming eastwards across the Tasman Sea cause heavy precipitation along the mountain backbone of the west of the South Island. Rainfall in inches, measured usually daily by staff at the hostel at the head of Doubtful Sound, was 198.17 for the year of 1956, 192.40 for a six-month period (year not recorded), 246.46 for a full-year period (year not recorded), 176.74 for 1961, approximately 155 for 1962. This gives an average rainfall of 232in per annum, or of 0.64in per day. In certain individual years, some months

would have less than half the rainfall of others, but over the period recorded no months were regularly "dry" ones. Sometimes a week or slightly more passes without rain. In 1956, the greatest rainfall recorded in 24 hours was 7.43in (March 9), and in another year 11.01in was recorded for November 19. Precipitation on the area feeding Doubtful Sound is mostly rain, only a small proportion being snow. This extremely heavy rainfall, resulting in high humidities and great dilution of surface waters, is the most striking environmental feature of Doubtful Sound, when comparing it with most other New Zealand shores.

Winds

These were not recorded. Judging from the 12 days I spent at Doubtful Sound, and from the appearance of shore vegetation, it seems that, whereas at times strong winds funnel along the fiord, for the greater part of the time the inner sound and the side-arms are relatively calm. At the sides and seaward end of Bauza Island strong to gale force west to NW winds are probably frequent. The outer faces of the Shelter Islands show a high lichen level, topped with windshorn coastal scrub. But from the inner end of Bauza Island inwards the shores commonly showed branches of dense forest trees hanging over them (Plate 1, fig. 3), except on exposed promontories or where cliffs were too steep for forest to get a grip.

Salinities

Surface salinities recorded ranged from 0%o at the head of the Sound to 31%o at the side of Bauza Island, at Station G (Text-fig. 1, Table II). In a given part of the sound, water close inshore (where seepage, waterfalls and streams were frequent) at times gave considerably lower salinity readings than in the centre of the sound—e.g., 10%o and 11%o inshore at Station D (fine day), and 30%o nearby in the centre of the sound (fine day). However, a surface reading at the latter spot on the third of three days of rain gave 14%o. Readings on the shore of Elizabeth Island were higher (24%o, 25%o) than at Station D nearer the sound mouth, presumably because from a small island there is not the run-off of rainwater that is usually occurring round the sides of the sound.

On calm days on the inner sound one could see, a few feet below the surface, an obvious discontinuity layer, where leaves drifted. This suggested making comparisons of surface with sub-surface salinities at a given spot. Checks at Stations B and D (Table I) show that, in relatively calm water, there is a steep salinity gradient from nearly fresh surface water to relatively salty water a few feet down. In terms of shore organisms and changing tides, this means that species at high tide would, when immersed, usually be in relatively fresh water, whereas those at low tide would be subject to greater extremes, but would be in relatively salty water much of the time. Strong winds doubtless mix surface with subsurface waters. However, as the inner parts of the sound are usually fairly calm, this salinity layering, with fresher water above, is probably the usual condition.

Humidity

This was not recorded; but filmy ferns thrive in the open just above high tide level at Station H, and tree-ferns show luxuriant crowns in the open canopy near the shore along Deep Cove and Hall Arm (Plate 1, fig. 2). These biological indicators suggest that the air is usually virtually saturated in the innermost part of the sound.

Tides

Tidal rise and fall at springs in Deep Cove is approximately 7ft. High tide turned at Deep Cove at 10.30 a.m. on 25/1/60, when the predicted time of high tide at Bluff was 11.10 a.m.

Wave Action

In the absence of wind, wave action is absent in the inner threequarters of the sound, just detectable at the inner tip of Bauza Island, strong and continuous at the west end of Bauza Island and the Shelter Islands.

Surface Sea Temperatures

The mean of 8 inshore day-time temperatures around Doubtful Sound during February 25–29, 1960, was 15.9° C. (range 15.0–17.1), and that of 7 from February 23–27, 1963 was 14.1° C (range 12.0–16.0). These means are close to, but slightly lower than, the mean 9 a.m. surface sea temperatures taken from the Portobello Marine Station wharf, Otago Harbour, on the same dates (means 16.1 and 14.9° C). Doubtful Sound winter sea temperatures were not recorded.

BIOLOGICAL DATA

The distribution of the ecologically-important or significant shore species of Doubtful Sound is summarised in Table II. The Stations are ordered in increasing magnitude of surface salinity, from left to right; except that, as salinities were not recorded during the three brief shore stops A, J, and F, these are placed in their presumed salinity sequence. "Shaded" refers to shores mostly or continuously in the shade, due either to their south- or SW-facing aspect, or because branches of forest trees hang over them. "Exposed" refers to shores exposed to brighter light (sunlight on the relatively rare occasions when skies are clear) for the greater part of a summer's day. Presumably the average humidity is lower on the latter.

Station sites (lettered) are shown on map, Text-fig. 1. Surface salinities range from lowest, at left, to highest, at right. Those read roughly with a Twaddell 4 hydrometer are in brackets.

Species Abundance.—xx, dominant or abundant; x, present; (x) sparse, but found on searching; blank, not observed; o, not observed, despite deliberate checking.

This table attempts to include all ecologically important macroscopic rocky shore animals present, except for amphipods (generally abundant), and isopods other than Ligia. Algae present included several species of Enteromorpha and ulvoid species, and also a filamentous brown at several low salinity stations; also additional algal species at low tide. Timing of shore stops did not permit sampling actually at low spring tide, except at Stations H, K. O and E.

Group I.—Fresh to brackish or brackish species

Group II.—Widely euryhaline species.

Group III.—Algae patchily present but stunted at low salinities.

Group IV.—Species present but at depressed tidal level at lower salinities.

Group V.—Species only at outer part of Sound—either marine stenohaline, or because they require considerable water movement, or both.

Group VI.—Species dependent on continuous water movement.

Field observations show that the shores of the sound can be reasonably subdivided into (1) inner sound shores, from about the opening of Crooked Arm inwards, including Crooked and Hall Arms; and (2) outer sound shores, from Station O seawards.

1. Inner Sound

A shaded shore of the inner sound, with greatly reduced surface salinites (down to 0%0), typically shows a continuous plant covering. Stations B and K are examples. The high tide black zone consists of the lichen Verrucaria maura, forming a glistening, continuous horizontal band, looking almost as if a dark stripe had been painted on the rock. This black zone can scarcely be described as a supralittoral or splash zone, as on 3 different days I saw it completely submerged during moderate spring tides. The water level then sharply cut off the lower margin of the overlapping forest, with branches of Nothofagus menziesii, Neopanax colensoi, and Griselinia littoralis, leaves of Astelia nervosa and fronds of Blechnum procerum actually dipping into the sea. When air-exposed, the Verrucaria showed an abundance of Ligia novaezealandiae scuttling over its surface.

Below the black zone, the upper midlittoral shows several algae competing for dominance. At high tide level, the fine red alga Bostrychia vaga, commonly forms a continuous covering. At or below half tide level, the curious, crisp, mosslike, dark green Cladophoropsis lyallii often dominates. This alga in places forms a cover several cm thick. In it live crabs (Hemigrapsus crenulatus and a small hymenosomid*), an abundance of amphipods and small molluses. The latter, in the inner sound, are the tiny, fresh- to brackish-water snail, Potamopyrgus anti-podum, present in vast numbers. At the outer tip of Elizabeth Island (Station M, salinity 25%0, Potamopyrgus in small numbers overlaps Lasaea in the Cladophoropsis. Further seawards, Lasaea hinemoa† replaces the snail in this alga, occurring in great abundance.

Amongst, below and upon the Cladophoropsis, several other algae are usually present. Greens include Enteromorpha process of subundulata and Letterstedtia ulvoidea. Rivularia australis and stunted Adenocystis utricularis are frequently scattered on the Cladophoropsis. At Station K, Cladophoropsis had smothered a sprinkling of Elminius modestus, possibly indicating a seasonal succession.

Stunted Hormosira banksii is dominant in the lower midlittoral in parts of the sound, absent in others, the factors controlling this not being evident. Actually at low tide level (where average salinities would be higher than further up), Mytilus edulis aoteanus is patchily abundant. Modiolus neozelanicus and Elminius modestus are usually present on these shaded faces, but are chiefly confined to crevices and not obvious at a glance.

An inner sound exposed shore (exposed both to sun and to wind-waves) is represented by Station N, on a small promontory about $\frac{1}{4}$ mile from the head of the sound. As on various other promontories and more light-exposed shores round the

sound, there occurred above the black zone a dense supralittoral covering of the lichen Pertusaria graphica, looking as if the rock had been painted white. Amongst and just above it were scattered other lichens—Caloplaca sublobulata, Rinodina thiomela, Buellia littoralis, and a species of Parmelia. These and other lichens here covered a height of about 3 feet between the top of the Verrucaria zone and the slightly wind-shorn forest (with Astelia nervosa, Earina autumnalis, Cardiomanes reniforme, Metrosideros umbellata, totara, small Phyllocladus alpinus, tree Coriaria and stunted Nothofagus menziesii at its shore periphery). The black Verrucaria maura zone was well developed, but less regular than along more wind-sheltered parts of the fiord.

A clear balanoid zone was shown in the upper and middle midlittoral, the species involved here and round most of Doubtful Sound being the euryhaline Elminius modestus. Across this balanoid zone at high tide neap level Apophloea lyallii formed an irregular, dark band; below which Lichina pygmaea var. intermedia was patchily abundant. Across the lower midlittoral, Hormosira banksii formed a dense zone; below which a fine Enteramorpha covered the rocks, with scattered Mytilus edulis aoteanus and Gigartina decipiens.

The midlittoral dominants of nearby shaded shores, Bostrychia vaga and Cladophoropsis, were present here also, but inconspicuous, in crevices. Also in crevices in this low salinity station (8%0) were Potamopyrgus antipodum in abundance, scattered Notoacmea helmsi and Zediloma arida, Membranipora cf. lacroixii, a nereid, Hemigrapsus crenulatus and the small hymenosomid.

At first glance, this relatively-exposed inner sound shore, despite its low salinity, looks not unlike many N.Z. shores—with Verrucaria above, a balanoid zone broken by Apophloea and Lichina, and Hormosira below. But the following characteristic N.Z. intertidal species were absent: chitons, Cellana and siphonarian limpets, high tide littorinids, Risellopsis, Melagraphia aethiops, Petrolisthes elongatus, Elminius plicatus and Chamaesipho columna, and Bostrychia arbuscula.

Portions of the inner sound intermediate between the shaded and the open shores just described are shown in Plate 2.

Fig. 4, a semi-shaded shore near the head of Hall arm, is not as completely plant-dominated as more deeply shaded shores, showing a balancid band in the upper midlittoral. At high tide, *Verrucaria maura* forms a dense and striking black zone. Immediately beneath it, the *Elminius modestus* band (whitish) shows scattered patches of *Bostrychia vaga* (pale brown). The mid-tide band is a mixture of *Enteromorpha* (pale green) and *Cladophoropsis lyallii* (dark green). A zone of *Hormosira banksii* is continuous across the lower midlittoral. The tide was not fully out. Zonation is well shown.

In Fig. 5, zonation is even more striking on a vertical shore just landwards of Elizabeth Island. Where, as here, a hillside is too steep to carry trees with overhanging branches, the supralittoral white lichen zone and the high tide black zone are both conspicuous. The species were presumably *Pertusaria graphica* and *Verrucaria maura*, sampling at this spot being impracticable. The midlittoral is presumably of *E. modestus* mixed with algae. Such marked zoning characterises many of the more wind-sheltered parts of the inner fiord.

In Fig. 6, a large boulder near the head of Deep Cove shows shaded and open faces side by side. The shaded face to the left shows a narrow *Verrucaria* zone below the white *Pertusaria graphica*; a broad, fawn band of *Bostrychia vaga* across the upper midlittoral; *Lichina pygmaea* var. *intermedia* (dark) across the

mid-midlittoral; Enteromorpha just below, and dark green Cladophoropsis lyallii dominating the lower midlittoral. The right-hand face, more exposed to light and to wind-waves, shows a broader, glistening Verrucaria maura zone, with a sprinkling of Elminius modestus just below it. At half tide, Apophloea lyallii (dark red) cuts across this, whilst further down are Enteromorpha and a filamentous brown Below low tide level at the base of the boulder are Mytilus edulis aoteanus, these as well as the boulder itself carrying extensive colonies of the brackish-water hydroid Cordylophora lacustris. On two different days, surface salinity readings were 0%0, and the water did not taste detectably salty.

On travelling seawards from Deep Cove, one meets additional marine species on the shore at the seaward end of Elizabeth Island (Station M). Here, Sypharochiton pelliserpentis* was not infrequent in the lowest part of the intertidal, though it did not extend up in its usual manner. Also submerged at low tide on this shore (but not further in) were patches of encrusting coralline algae, the greater part of which was dead (i.e., white). The presence of these at first sight appeared anomalous as far up the sound as this, when absent from the well-sampled Station D. However, whereas D was on a mountain face with much freshwater seepage, and surface salinities of 10%0, 11%0 M on a small island with but slight seepage showed inshore salinities, at different places around it, of 25%0 and 24%0. M. was an open exposed, primarily balanoid shore (E. modestus), with Apophloea and Hormosira. Crevices showed the shade algae, patches of Cladophoropsis here showing Potamopyrgus (sparse) mixed with Lasaea hinemoa (abundant). Above a 2ft high Verrucaria band, Pertusaria graphica was conspicuous.

Station D was in most respects a typical shaded, inner sound, algal-covered shore, though with some additional marine species (e.g., small Patiriella regularis and Aulacomya maoriana at low tide). Special interest at this point in the sound centred round a rock Dr Rudwick brought up from 2-3 fathoms, which carried the brachiopods Terebratella inconspicua and T. sanguinea. T. inconspicua is patchily abundant in Otago Harbour up to low tide neap level, but was nowhere met intertidally at Doubtful Sound. Brachiopods are relatively stenohaline (Table I). Terebratella inconspicua, like Mytilus edulis aoteanus, Pomatoceros cariniferus and Sypharochiton pelliserpentis, does not come as far up the shore in inner Doubtful Sound as in more highly saline Otago Harbour. One suspects the steep vertical salinity gradient is restricting these (and probably other animals) to lower than their usual tidal levels, whereby they would be exposed to low salinity water for only short periods.

2. Outer Sound

Station O, on a small island in Shelter Cove, was an east-facing relatively sunexposed shore, though sheltered from wind. Surface salinity readings (during rain) were 24%0 and 27%0. Suddenly one had come to a relatively "normal" marine southern New Zealand shore. Potamopyrgus antipodum had dropped out. The Verrucaria maura zone was irregular, and not like a painted stripe. The dominant balanoid was still E. modestus, though with Chamaesipho columna scattered amongst it, and Tetraclita purpurascens abundant under stones. Along

the upper midlittoral, Apophloea lyallii was joined by tufts of Gelidium (probably Gelidium caulacanthemum and G. pseudocaulacanthemum). Bostrychia vaga still occurred, but B. arbuscula now entered. Pachymenia lusoria, relatively sparse and stunted where it appeared in the inner sound, was here well grown, and formed a fringe above the Hormosira zone. Hormosira likewise was no longer stunted (e.g., a measured plant here was 59cms long, its larger bladders 20 x 13 mms). Below it was a band of pink paint corallines (healthy and abundant), tufts of Corallina officinalis, and miscellaneous other reds. A Cystophora (probably C. retroflexa) was glimpsed sublittorally, but there was no sign of Macrocystis or Durvillea. Petrolisthes elongatus, under stones, were smaller and less abundant than in Otago Harbour. Surprisingly, 2 small specimens of Pollicipes spinosus were found in a crevice, although I could not observe at O any hint of the wave surge of the open coast.

Two species not familiar to me on Otago shores, occurring here and also at Station F, were the crab *Heterozius rotundifrons* and a low, encrusting, red alcyonarian, the latter abundant in low tide pools and crevices.

Other species noted at Station O were Codium dichotomum, Scytothamnus australis, ?Haliclona (mauve), Spirorbis sp., Pomatoceros cariniferus (patchily abundant), Acanthochiton zelandicus, Melagraphia aethiops, small Zediloma sp., Aulacomya maoriana, encrusting bryozoans, Coscinasterias calamaria and Cnemidocarpa coerulea. Had more than 65 minutes been available at this stop, in more favourable weather, doubtless many more species would have been noted.

Stations E and F, at the inner end of Secretary Island, provided a surprising contrast with each other. E, a shaded shore in the shelter of Blanket Bay, at first glance is a typical inner-sound shaded shore, with B. vaga, Cladophoropsis, Hormosira and other algae virtually covering the shore below the Verrucaria zone. Closer searching revealed some additional molluscs-Melarhapha cincta on the B. vaga, one Siphonaria zelandica, occasional small Sypharochiton pelliserpentis; as well as scattered Notoacmea helmsi and Modiolus neozelanicus and an abundance of Lasaea hinemoa. However, it is definitely an algal rather than a mollusc or balanoid shore, with E. modestus only in scattered patches. Station F, nearby but sunexposed, is a balanoid shore (E. modestus), with Apophloea lyallii at high tide, and a Hormosira zone across the lower midlittoral. Two Cellana species were present, but in small numbers. Low tide browns included Xiphophora chondrophylla var. maxima and Cystophora scalaris, whilst Scytothamnus australis occurred midlittorally. Petrolisthes elongatus was abundant under stones. At high tide, a few small Melarhapha oliveri joined an abundance of M. cincta. Above, the strongly developed black zone of V. maura thrived not only on the rock, but also—unusual for this species—on overhanging branches of Dracophyllum longifolium and Olearia oporina; rocks above and among the Verrucaria carrying dense Pertusaria graphica, scattered Caloplaca sublobulata and Rinodina thiomela.

Station P was a brief landing on the inner tip of Bauza Island, when the tide was above half. This *E. modestus* shore was chiefly noteworthy for carrying a number of well-grown *Cellana strigilis*—the only Doubtful Sound shore I was on where a *Cellana* species was in evidence. Surge of open surf was just detectable here. The *V. maura* zone was wavy.

G, on the Gut side of Bauza Island, was the most seaward landing I made. Very tattered *Macrocystis pyrifera* and 2 plants of *Durvillea antarctica* (neither of which had been seen attached further up the sound) were not unexpected on

this surging, current-swept shore. A few Elminius plicatus (half of them empty) were scattered amongst E. modestus. (Chamaesipho columna was almost certainly here, but not noted during the hurried stop.) Amongst dense Apophloea lyalli, Bostrychia arbuscula was patchily abundant.

The seaward tip of Bauza Island and the Shelter Islands are submitted to breaking surf as well as wind-waves. Landing was not practicable. However, the launch went close enough in for me to see a virtually continuous Durvillea antarctica zone in the lower midlittoral. The balanoids above this are predicted to be Elminius plicatus and Chamaesipho columna, probably without Elminius modestus. A darkish high-tide band was probably Apophloea lyallii and Bostrychia arbuscula. The supralittoral black zone was irregular, broad and not sharply defined—about 5ft high on outer Bauza, 10–15ft or more on outer Shelter Islands. Terrestrial vegetation (forest) was 20ft or more above the Durvillea on outer Bauza, and somewhat wind-shorn; on the Shelters, the shrub line was higher, and very wind-shorn.

One feature conspicuous along parts of the sound shore was a dark mussel band in the upper midlittoral, cutting across more or less vertical balanoid faces. The mussel involved is almost certainly *Modiolus neozelanicus*, although no samples were taken. The sites where it formed a band were ones where current rip was doubtless strong, such as where Malaspina Sound turns into Crooked Arm.

COMPARISON OF DOUBTFUL SOUND AND OTAGO HARBOUR ROCKY SHORES

Doubtful Sound resembles Otago Harbour (Batham, 1956 and unpublished observations) in that both are long, narrow, landlocked fiords at similar latitudes in southern New Zealand, with similar summer surface water temperatures. Environmentally they differ chiefly in that Doubtful Sound (at any rate at its head) receives nearly 8 times the annual rainfall that Otago Harbour does, and is surrounded by steeper, higher mountains, giving greater run-off. Consequently, inshore surface salinities of inner Doubtful Sound are typically less than one-third of normal seawater, and in parts below 1%0. Otago Harbour, by contrast, has surface salinities usually between 32.5 and 34.6%0 half way along it, and only slightly lower near the head*. Other, probably less significant, differences are that normal Doubtful Sound humidities are obviously much higher than around Otago Harbour; and Doubtful Sound is much deeper, which probably results in more stable sea temperatures, predicted to be higher in winter than Otago Harbour ones. Hours of sunshine on Otago Harbour shores are doubtless much higher. Probably average water movement from wind-waves is greater in Otago Harbour, though continuous wave action occurs further up Doubtful Sound than up Otago Harbour.

The greater part of Doubtful Sound shores, away from the entrance, shows in shade an algae-dominated cover, in more open conditions an *Elminius modestus*-algae shore. Among abundant to dominant algal species occurring round Doubtful Sound are *Cladophoropsis lyallii* and *Bostrychia vaga*, neither of which has been found by the writer on Otago Harbour shores. Larger midlittoral molluscs occur-

ring and often abundant round Otago Harbour shores, such as Sypharochiton pelliserpentis, Melagraphia aethiops and Cellana ornata, only appear at Doubtful Sound where salinities are above about 20%0; the Doubtful Sound lower-salinity shores showing only 3 small molluscs (Potamopyrgus antipodum, Notoacmea helmsi, and at less depressed salinities Lasaea hinemoa). Some continuously shaded Otago Harbour shores show a predominantly plant covering (though with molluscs), but it is typically of pink paint corallines and Bostrychia arbuscula and B. mixta. The only abundant shore plants shared by the two regions are Verrucaria maura, Lichina pygmaea var. intermedia, Hormosira banksii and Enteromorpha spp. Enteromorpha may seasonally dominate short stretches of Otago Harbour shore where water seepage occurs and molluscs are very sparse, such localised patches being more similar to many Doubtful shores than is most of Otago Harbour.

The absence of the normally-abundant N.Z. midlittoral molluscs along most Doubtful Sound shores is presumably correlated with the considerably reduced salinity. Krijgsman and Brown (1960) record the anaesthetising effect of lowered salinity on various marine molluscs. Many algae, on the other hand, tolerate a wide range of salinities. These facts, combined with high air humidities when the tide is out, probably explain why inner Doubtful shores are largely plant-covered, whereas Otago Harbour shores are mostly mollusc-dominated.

Somewhat anomalous points are the virtual absence of *Modiolus neozelanicus* and *Apophloea lyallii* in nearly all of Otago Harbour, when these thrive on the Otago outer coast and to the head of Doubtful Sound. Doubtful Sound shows that factors other than lack of continuous wave-action restrict their spread in Otago Harbour. The sparseness of *Elminius modestus* in Otago Harbour is also not readily explained, considering its abundance in Doubtful Sound, and on some warmer N.Z. and colder English shores (Crisp, 1958).

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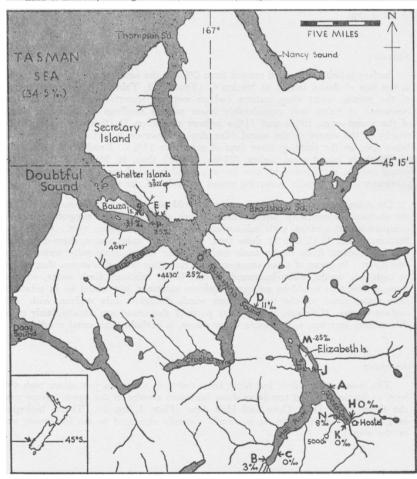
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- * Close to Halicarcinus cooki, with trifid rostrum and 2 pairs of lateral spines on the carapace, but more delicate; not the freshwater hymenosomid H. lacustris.
- † The intertidal specimens of Lasaea at Doubtful Sound were about half with the typical deep pink shell of Lasaea hinemoa, whereas the rest resembles this in form, but have creamy-yellow shells. W. Ponder, who is revising N.Z. Lasaea species, regards this as "either new or a peculiar variety of L. hinemoa".
- * All specimens checked from Doubtful Sound showed the second plate dark, as does the Tasmanian S. maugeanus Iredale and May.
- * Daily sampling from Marine Station wharf, January-December, 1963; 2 samples near head of harbour, 24 August 1962. Titrations by D. J. Slinn.



Text-fig. 1.—Map of Doubtful Sound region of Fiordland, S.W. of South Island, New Zealand, site shown by arrow on inset (after N.Z. M.S. 122 Fiordland Map, 1956, with further streams and lakes added by A. Cookson). Shore stations are lettered A to P, and some surface salinities are shown.

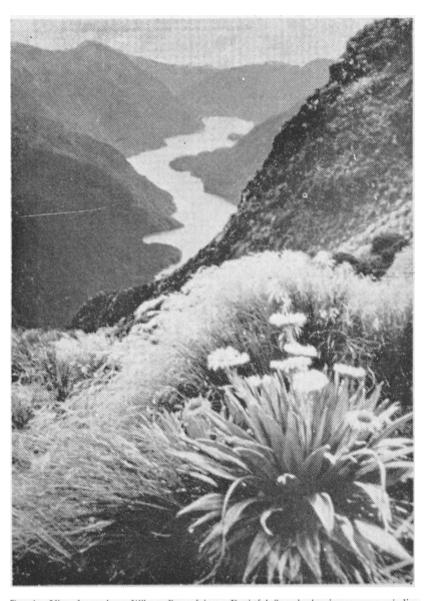


Fig. 1.—View from above Wilmot Pass of inner Doubtful Sound, showing narrow, winding, mountain-girt fiord.

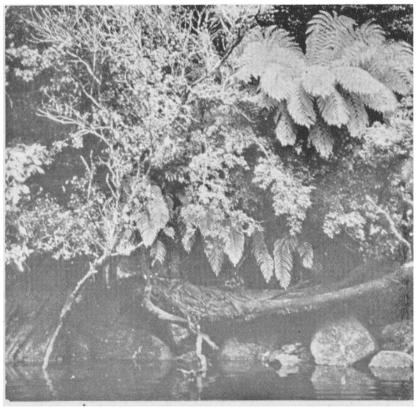


Fig. 2.—Shore at head of Hall Arm Luxuriant crown of tree-fern Dicksonia in canopy just above high tide mark indicates high humidity.

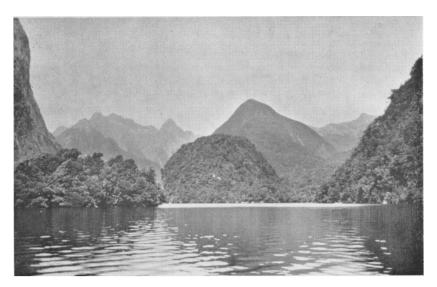


Fig. 3.—Opening of Hall Arm from Malaspina Sound, showing forest to water level and steepness of mountain sides running into fiord.



Fig. 4.—Semi-shaded shore at head of Hall Arm, near Station B. Shore plant-dominated and markedly zoned. Description, p. 222.



Fig. 5.—Open, vertical, inner sound shore. Striking zonation is shown by Verrucaria (black) and by white lichen above (presumably Pertusaria graphica).



Fig. 6.—Boulder at head of Deep Cove. Right face more exposed both to light and to wind-waves. Description, p. 222.

(Readings in brackets were from Twaddell 4 hydrometer; 1963 readings were with a B. and T. 12in hydrometer, 1.000–1.030. Density readings were corrected for temperature.)

	Stati (Head of	on B Hall Arm)	Station D (Halfway along main sound)					
Depth	Date 25/1/60	Date 23/2/63	Date 25/1/60	Date 27/2/63				
Surface	(3%0)	4%0	(12%0)	6% o 7% o				
3ft		22% o 17% o		7%0				
6ft		25% o 25% o		8%0				
9ft		27%0		16%0				
10ft	(23%0)	27% o 28% o	(17%0)					
12ft			(22%0)	22% o 21% o				

Table I.—SURFACE AND SUB-SURFACE SALINITIES, TWO STATIONS, INNER DOUBTFUL SOUND.

STATION		Н	K	C	В	N	A	D	J	L	M	0	P	E	F	G
Surface salinity per mil		0 (0)	0	0	3	8		(12) 6		24	25	24 27	25	(30)		(31
	Exposed/shaded	ES	S	E	S	E		S	S	S	E	E	S	S	E	E
I	Potamopyrgus antipodum Cordylophora lacustris	x xx	xx			xx				0	(x)	0	0	0		
П	Verrucaria maura Lichina pygmaea v. intermedia Cladophoropsis byallii Enteromorpha spp. Letterstedia ulvoidea Adenocystis utricularis Rivularia australis Bostrychia vaga Apophloea byallii Gigartina decipiens Notoacmea helmsi Zediloma arida Modiolus neozelanicus Elminius modestus Ligia novaezealandiae Hemigrapsus crenulatus Hymenosomid	xx xx xx xx x x (x) x xx	xx xx xx 0 x xx x x x x x x x x	xx xx	xx xx xx xx xx xx xx xx	x xx x x x x x x x x x x x x x x x x x	x (x) x x x x (x) xx	XX XX X X X X X X X X X X X X	x xx x x	xx xx 0 x xx xx xx 0 0	x (x)	(x) x x xx xx xx xx xx	x (x) x x x x x x	XX	x xx	xx xx xx
III	Hormosira banksii Pachymenia lusoria	0	0	x	0 x	xx 0		x (x)	xx x	x	xx	xx xx	x	xx xx	xx	
IV	Pomatoceros cariniferns Mytilus edulis aoteanus	x	0	x		0 (x)		XX	168			xx x		xx	(x)	
V	Lasaea hinemoa Sypharochiton pelliserpentis Petrolitishes elongalus red alcyonarian Siphonaria selandica Melarhapha cincta Melarhapha cincta Gellana strigilis Cellana ornata Bostrychia arbuscula Chamaesipho columna Elminius plicatus	0	0		10	0 0 0 0 0 0 0 0 0 0				0	x x x	xx xx xx x x 0 0 x x x 0	xx x xx (x)	x, x x x x 0 0	x xx xx x x xx	XX
VI	Durvillea antarctica	1		-	-											2

Table II.—MAIN DOUBTFUL ROCKY SHORE SPECIES IN RELATION TO SALINITY.