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Atlas of Marine-fouling Bryozoa of New Zealand Ports and Harbours

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ABSTRACT

Forty species of native and exotic marine bryozoans are currently recognised as foulers of vessels and submerged artificial surfaces in New Zealand ports and harbours. Some 42% of species mentioned in a 1965 OECD catalogue of main marine-fouling organisms of European waters now occur in New Zealand and more may yet come to be recorded, based on past trends — exotic bryozoans have been coming into New Zealand at least since the 1890s, including nine species not recorded in the OECD catalogue. The most ubiquitous fouling bryozoans in New Zealand, occurring at a significant number of the ports and smaller harbours, are seven well-known subcosmopolitan species — in order of their chronological introductions these are *Cryptosula pallasiana, Bugula neritina, Bugula flabellata, Tricellaria occidentalis, Bugula stolonifera, Conopeum seurati,* and *Watersipora subtorquata.* Most have been recorded for the first time only since the late 1940s. Only 11 endemic species have been encountered as foulers in ports and harbours and these are minor components of little nuisance value.

Keywords: Marine Bryozoa, New Zealand, ports, harbours, larvae, introduced species, *Cryptosula, Bugula, Tricellaria, Conopeum, Watersipora,* settlement season, key to species, control

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New records of marine-fouling species for New Zealand include (after adjustment for synonymies) *Aeverrillia armata, Buskia socialis, Electra tenella, Bugula simplex,* and *Schizoporella errata.*

The report discusses the biology of bryozoan larvae at the time of settlement and metamorphosis, the most critical and susceptible phase in marine fouling, as well as the invasive strategies of marine-fouling species. Descriptions and illustrations are provided for each of the 40 species as well as a key to identification and information on reproduction and settlement season where these are known. Suggestions are also given on ameliorating the problem of marine-bryozoan fouling.

INTRODUCTION

What are Bryozoans?

Bryozoans (sea mats, lace corals, moss animals) comprise a phylum of mostly marine invertebrates. While neither the technical nor even the common names are familiar to most people, bryozoans themselves will almost certainly have been encountered by anyone fossicking under boulders on a seashore or by owners of pleasure craft or fishing boats who clean their hulls regularly.

Bryozoans are colonial animals which form coloured encrustations or tufts which superficially resemble other forms of sedentary marine life. The encrusting species form thin, flat, circular or irregular patches (hence, sea mats) that are mostly hard to the

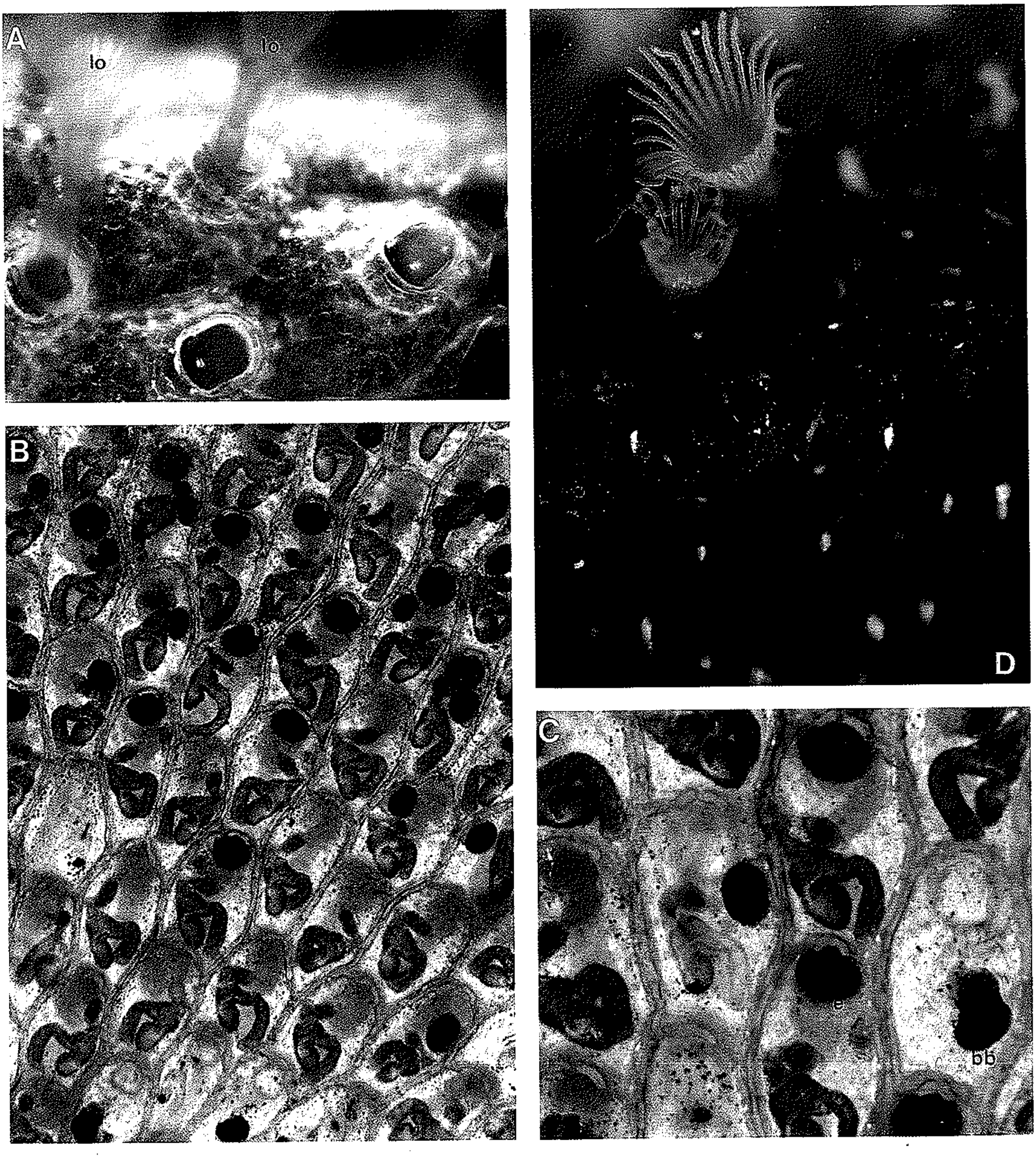

Plate 1. A–C, *Cryptosula pallasiana*, showing, A, zooids near the growing edge of a colony, with two emergent lophophores, x 80; B, underside of part of a colony growing on glass, showing retracted polypides — the stomachs are brownish-orange, the dark objects are developing embryos, x 25; C, part of same colony enlarged, showing a closer view of the digestive tracts of several zooids, one newly developed at middle left; four zooids have developing embryos (e) and one has the regression product of a polypide, viz. a brown body (bb), x 55. D, *Watersipora subtorquata*, showing one fully expanded lophophore, one in the process of expanding, and two others, adjacent to each other, just beginning to emerge, x 40.

touch. If the patches should produce erect folds they can give the impression of small corals (and if perforated, then 'lace corals'). The tufted or bushy species can resemble hydroids or small seaweeds (hence, moss animals, which is what the Greek-derived technical name Bryozoa means). However they may appear, all bryozoans have in common that they are colonies of little box-like or tube-like units (zooids), each of which comprises a body wall (the box or tube) and a polypide — made up of a simple U-shaped digestive tract (Plate 1B, C) and an apparatus of tentacles (a lophophore) (Plate 1A, D) that typically has a funnel shape when expanded into the water to feed. The tentacles are densely covered on their inner faces with cilia, which beat in such a way as to generate a current of water toward the mouth at the bottom of the funnel. Food consists of small plankton or non-living organic particles.

Individual zooids range from about 0.3 to 1.5 mm long, depending on the species, in the majority of bryozoans. Extended lophophores range from about 0.3 to just over a millimetre long and, again depending on the species, each may have from eight to slightly more than 30 tentacles, so that the largest lophophores can be seen by the unaided eye.

Colony sizes vary also. Whereas the smallest bryozoan species are interstitial forms living on or between sand grains, with only one to several feeding zooids, some other species, including marine foulers, form very large colonies — stringy gelatinous tresses a metre long, dense coralline masses, or brittle crusts the size of a cabbage head fastened to pilings. Some uncalcified species may grow this big in one or a few seasons, depending on water temperature and food supply, but generally the larger calcified species take several years to attain such a size. Small tufted species may be annuals or perennials. These generally attain a height of two to several centimetres. Most encrusting species form more-or-less circular patches 1–5 cm across.

Bryozoan colonies begin life when the larva that develops from a fertilised egg attaches to a substratum (rock, piling, seaweed, boat hull, etc.) and there metamorphoses into the first zooid of a colony, the ancestrula. The ancestrula buds off one or more daughter zooids, which in turn bud other daughter zooids, and so the colony grows, either upwards in the case of bushy or tufted colonies, or radially outwards in the case of circular encrusting colonies. In the latter case, the underside of the colony is usually firmly adherent to the substratum and it is difficult to remove the colony for examination without damaging it.

Bryozoans as Marine-fouling Organisms

Any underwater surface becomes covered by microscopic or macroscopic organisms. When such organisms affect the performance or functioning of man-made structures they are referred to as 'fouling'. Fouled structures can include intake pipes for industrial or power plants in marine and fresh waters, oil rigs, buoys, moorings, current meters, and hulls and other surfaces of boats, ships, and submarines. The cost of increased fuel consumption because of the frictional resistance imposed on a ship's passage through water is well appreciated (e.g., Woods Hole Oceanographic Institution 1952; Ryland 1970, pp 74–76; Houghton 1970) and is one of the major reasons why antifouling paints have been developed to deter settlement. Even a slime layer of only 1 mm thickness can cause an 80% increase in skin friction and a 15% loss in ship speed compared with values obtained for a clean hull (Lewthwaite *et al.* 1985).

Bryozoans are one of the six groups of invertebrates documented in a series of catalogues of main marine-fouling organisms (Ryland 1965), the others being barnacles (Southward & Crisp 1963), serpulid polychaete tube-worms (Nelson-Smith 1967), sea squirts and related forms (Millar 1969) (for the Organisation for Economic Cooperation and Development (OECD), sponges (Sarà 1974) (for the Centre de Recherches et d'Études Océanographiques), and hydroids (Morri & Boero 1986) (for the Office d'Études Marines et Atmosphériques (ODEMA)). So far, more than 4000 species of marine bryozoans have been described, but many more are known to exist in the world's oceans. Although very common in the intertidal zone, bryozoans are generally more abundant below diving depths so that the greatest species diversity is between 50 and 250 m depth. Beyond 250 m, bryozoan species diversity may still be quite high at 1000 m but declines noticeably beyond 1500 m. Only a handful of species is known beyond 6000 m depth (Hayward 1981; d'Hondt & Schopf 1984; Gordon 1987).

Of the many hundreds of species that may be encountered intertidally and which would seem, therefore, to be potential foulers of shallow-water structures, most, in fact, do not figure in marine-fouling surveys of ports and harbours [Soule & Soule (1977) listed nearly 130 species worldwide]. The reasons for this may be sought in larval and adult tolerances. The larva, in particular, is a critical stage in fouling. Bryozoan larvae tend to show habitat preferences based on reactions to light, water movement, substrate texture and colour, and the physical/chemical properties of the surface (e.g., Lynch 1947, 1949a, 1959a, b, 1960, 1961; Mawatari 1951a; Mawatari & Kobayashi 1954; Crisp & Ryland 1960; Ryland 1960a, 1962, 1967, 1977; Eiben 1976; Maki *et al.* 1989; Roberts *et al.* 1991). It would seem, by inference, that marine-fouling bryozoan species are less substrate specific than most, as larvae. In fact, this appears not to be the case, and, outside of marine-fouling situations, larvae of such species do not have a competitive advantage over less-generalist species. Indeed, in the case of the most abundant, subcosmopolitan, marine-fouling bryozoans, while they may thrive in the particular conditions of ports and harbours, they are rarely found outside of such settings. In general, it can be said of the major marine-fouling bryozoans that the mature colonies are more tolerant of the wider ranges of temperature, salinity, turbidity, and pollution that prevail in ports and harbours than open-coastal species. In cleaner or deeper water, however, a majority of bryozoan species probably have potential as foulers (*see*, for example, data in Mawatari & Mawatari (1986), and Appendix 3 in this report).

Most work on the critical phase of larval settlement and metamorphosis in bryozoans has been carried out on fouling species. The larvae of the majority of these are whitish, yellowish, orange, pink, or red subspherical or yo-yo-shaped bodies (called coronate larvae) less than 0.5 mm in diameter. They are yolky and non-feeding with a short free-swimming period (minutes to hours, rather than days). Upon release from the brooding structures of parent zooids, larvae of most fouling species are strongly photopositive, but this response abates or becomes reversed (Ryland 1960a, 1977). This change appears to be metabolically determined because the duration of the initial taxis is dependent on temperature and is independent of quantity of illumination (Ryland 1962, 1977). Little is known about the biology of this phototaxis or about its relationship to the onset of the second phase of larval behaviour, in which larvae begin apparent substrate exploration. Having swum by their cilia and/or become carried by water movements relatively short distances (several centimetres to several metres), they are influenced by light, flow, and features of the substrate to settle, generally in shaded situations although there is much variation in larval behaviour (*see* summaries in Ryland 1976a, b, 1977). Typically, larvae swim in circles of decreasing circumference over the substratum surface, appearing to 'test' it with long bundles of cilia — the effective strokes of these cilia pass first over the substrate and then through a heavily ciliated groove on the anterior surface of the larva (Woollacott 1984). In this exploration phase, larvae frequently attach temporarily to the substrate, evidently through the production of a mucous secretion that also aids ciliary gliding during this phase (Reed & Cloney 1982; Reed & Woollacott 1982), but they may break this bond and continue 'testing' the surface at new sites. The ability to disengage from the substrate and continue exploring indicates a high capacity for discrimination in the selection of a suitable substratum.

A few species have non-yolky triangular larvae (called cyphonautes larvae) which feed in the plankton, evidently for a maximum duration of some weeks (Soule & Soule 1977). In these species, eggs and larvae are not brooded — the eggs are released directly into the sea to metamorphose there. Fertilisation occurs at the time of egg release (so far as has been ascertained), either during transfer of eggs into brooding structures or as eggs are released into the water, depending on the species. Cyphonautes larvae have a similar pre-settlement behavioural repertoire to coronate larvae (Stricker 1988; Stricker *et al.* 1988).

The nature of the substrate surface is of prime importance. The most recent work has shown that wettability, an indication of the degree of surface hydrophilicity, is paramount in influencing larval settlement. Wettability is the tendency for a substrate to induce spreading of a liquid on its surface, and is an expression of the critical surface energy or tension of the substrate. Of artificial substrata, for example, wax and polystyrene may be described as non-wettable and glass wettable. Oyster shell is also highly wettable. In general, larvae of fouling bryozoans avoid wettable surfaces (Eiben 1976; Loeb 1977; Mihm *et al.* 1981; Woollacott 1984; Rittschof & Costlow 1987, 1989a,b; Roberts *et al.* 1991; Gerhart *et al.*, in press). This avoidance, however, can be countered by the presence of a film of suitably attractive bacteria, whether or not wettability is affected (Mihm *et al.* 1981; Brancato & Woollacott 1982; Maki *et al.* 1989). This is a complicating factor in devising non-toxic (e.g., heavy-metal-free) antifouling paint surfaces. Some bryozoan larvae do not require a bacterial film for settlement, and, inasmuch as larvae can settle within minutes of release from parent colonies, a clean surface can be settled by bryozoans as fast as, or faster than, bacteria (Roberts *et al.* 1991). On the other hand, some species among the superfamily Buguloidea regularly contain symbiotic bacteria in the larval pallial sinus (e.g., in *Bugula neritina* and *B. simplex*, but not in *B. stolonifera* or *Tricellaria occidentalis*) and these bacteria are released as a cloud over the substrate at the onset of metamorphosis. This association depends on species and is independent of location, season, or year (Woollacott 1981). Possibly the bacteria condition the substrate in a way that affects the larvae of the same or other bryozoan species or of other marine organisms (Woollacott 1984). Experiments by Kirchman and Mitchell (1984) and Colon-Urban *et al.* (1991) have implicated lectins (sugar-binding proteins) — larval settlement may occur via lectins that bind to polysaccharides produced by the bacteria.

Bryozoans cause damage not only through direct effects, but also through indirect effects, frequently as organisms critical to the ecological development of fouling communities (Woollacott 1984). Bushy bryozoans, which can densely cover ships' hulls like a sward, provide the greatest impedance to passage through water. Two-dimensional encrusters, especially species of *Watersipora* in which established colonies [but not larvae (Wisely 1962; Wisely & Blick 1967)] are fairly resistant to copper-based paint formulations (Weiss 1947; Wisely 1958; Ryland 1967), can provide a substratum upon which more three-dimensional foulers can settle (Wood & Allen 1958). Another problem is that sulphate-reducing bacteria occurring under encrusting bryozoans can accelerate metal corrosion (Srivastava & Karande 1986).

Marine-fouling bryozoans do not only affect structures. Some, like *Bowerbankia gracilis*, can be a problem in aquaculture, settling on cultivated species (such as oysters) (Soule & Soule 1977), and alien bryozoans can sometimes thrive in new settings, away from natural controls like predators, or former physical conditions, thereby disrupting or otherwise affecting the indigenous marine ecology. Morton and Miller (1968, p. 389) noted the dominance of a shipping-introduced bryozoan at Westmere Reef in Waitemata Harbour, Auckland — "In late spring, summer and autumn, the low tidal rocks are blackened in more protected places with ... *Watersipora cucullata* [sic; = *W. arcuata* Banta, 1969a — see later] a thriving newcomer to New Zealand harbours, first noticed at Auckland about 1957 ... Below the *Elminius* [acorn barnacle] level but above the settling silt, *Watersipora* often provides the total cover, displacing or smothering the tubeworms and other sessile animals by simply growing over them. It spreads rapidly after settlement : from small ... patches it grows in a month to a continuous sheet [over] any lower midlittoral surfaces relatively free of silt, whether rock, iron or wood." Dromgoole and Foster (1983), Willan (1987), and Read and Gordon (1991) have documented the impact of other types of invasive marine organisms on New Zealand marine ecology. *Watersipora arcuata* almost certainly entered New Zealand on ships' hulls (Banta 1969b) but other sources have been documented or inferred for introductions of other marine organisms in New Zealand. These include wet fishing nets (Powell 1976), drilling platforms (Powell 1976; Foster & Willan 1979), and dunnage (Foster & Dromgoole 1983). Ballast water is also a major vector for marine introductions — Hutchings *et al.* (1987), Williams *et al.* (1988), and Jones (1991) have documented a wide range of organisms that were transported by this means in Australia-bound shipping; bryozoans were not listed among them but Carlton (1985) has shown that species with cyphonautes larvae could certainly be transported in ballast water. A draft policy on regulation or control of ballast-water introductions is currently being formulated for New Zealand (Kopp 1991).

The New Zealand Marine-fouling Bryozoan Fauna

Since 1950, a number of exotic marine-fouling bryozoan species have been documented for New Zealand (e.g., Ralph & Hurley 1952; Macken 1958; Skerman 1958, 1959, 1960a, b; Harger 1964; Gordon 1967, 1986, 1989; Morton & Miller 1968; Banta 1969a, b). Skerman (1958, 1960b) also noted the occurrence of some indigenous species as foulers. Since 1967, one of us (DPG) has been informally collecting marine-fouling bryozoans during vacation travel within New Zealand, noting occasional new arrivals of exotic species. Inasmuch as no deliberate documentation had been made of fouling bryozoans at New Zealand ports and harbours since the work of Skerman, the present authors undertook to visit all major ports and a variety of smaller berthages, from the Bay of Islands to Bluff (Fig. 1). The visits were carried out during July and August 1988, with supplementary visits to some ports by the first author since then.

It is a subjective judgment as to what constitutes a fouling species. Merely to occur at a shipping port is not regarded here as reason enough for inclusion and even the occurrence of a species on a wharf piling (as with some indigenous species) does not automatically mean the species has nuisance value. After some consideration, 40 species are listed in this report as marine fouling (Table 1). Most of these were documented as occurring on the hulls of fishing or pleasure craft as well as on other substrata. A few species, occurring only on pilings, or, in two instances, on the New Zealand green-lipped mussel (*Perna canaliculus*) attached to pilings, are included, either because they are exotic species or because they were reasonably conspicuous.

Table 1
The species of marine-fouling Bryozoa (sea mats, moss animals, lace corals) occurring at New Zealand ports and harbours and some other locations, based on the literature and recent surveys.

SPECIES \ PORT	Opua	Whangarei	Marsden Point	Auckland	Onehunga	Tauranga	Gisborne	New Plymouth	Napier	Wellington	Tarakohe	Pelorus Sound	Picton	Nelson	Lyttelton	Timaru	Oamaru	Moeraki	Dunedin	Bluff	Other Localities
Aeverrillia armata				x																	
Alcyonidium sp.				x								x									
Amathia distans				x																	
Anguinella palmata				x										x							
Arachnopusia unicornis												x			x				x		x [g]
Beania plurispinosa			x	x		x		x	x					x			x				
Beania sp.			x											x							
Bowerbankia gracilis				x	x				x								x				x [j]
Bowerbankia imbricata				x										x							
Bugula flabellata	x		x	x		x			x	x		x	x	x	x		x	x	x	x	x [i]
Bugula neritina	x	x	x	x		x		x	x	x	x	x	x	x	x	x			x		x [c,i]
Bugula simplex															x						
Bugula stolonifera	x			x				x	x		x	x		x	x	x				x	x [e]
Buskia nitens				x													x				
Buskia socialis																					x [e]
Caberea rostrata				x																x	
Caberea zelandica				x											x						
Calloporina angustipora																			x		
Celleporella bathamae																			x	x	
Celleporina proximalis												x							x		
Chaperia granulosa							x		x								x			x	
Chaperiopsis cervicornis																		x	x	x	
Chiastosella watersi																	x				
Conopeum seurati	x	x	x	x	x		x		x					x	x						
Crassimarginatella fossa			x															x		x	
Cryptosula pallasiana			x	x			x	x	x	x	x		x	x	x	x	x	x	x	x	x [d,h,j]
Electra pilosa												x	x								
Electra tenella							x		x												x [b]
Escharoides angela							x								x						
Hippadenella cf. *margaritifera*																				x	
Parasmittina delicatula			x																		
Rhynchozoon larreyi				x																	x [c]
Schizoporella errata	x			x																	
Schizosmittina cinctipora																			x		
Scruparia ambigua			x	x		x			x		x			x						x	x [e]
Tricellaria occidentalis		x		x		x	x		x		x	x		x	x						x [h]
Tubulipora sp.															x						
Watersipora arcuata	x	x	x	x		x		x	x					x							x [a,c,f]
Watersipora subtorquata	x		x	x		x	x	x	x	x	x	x	x	x	x	x			x		
Zoobotryon verticillatum				x	x																

a Bay of Islands
b Pakiri Beach, drift on *Atrina*
c Leigh Cove
d Whangateau Harbour
e North Cove, Kawau Island
f Mahurangi Estuary
g Maui-A oil platform
h Aotea Lagoon
i *Mikhail Lermontov*
j Oban, Stewart Island

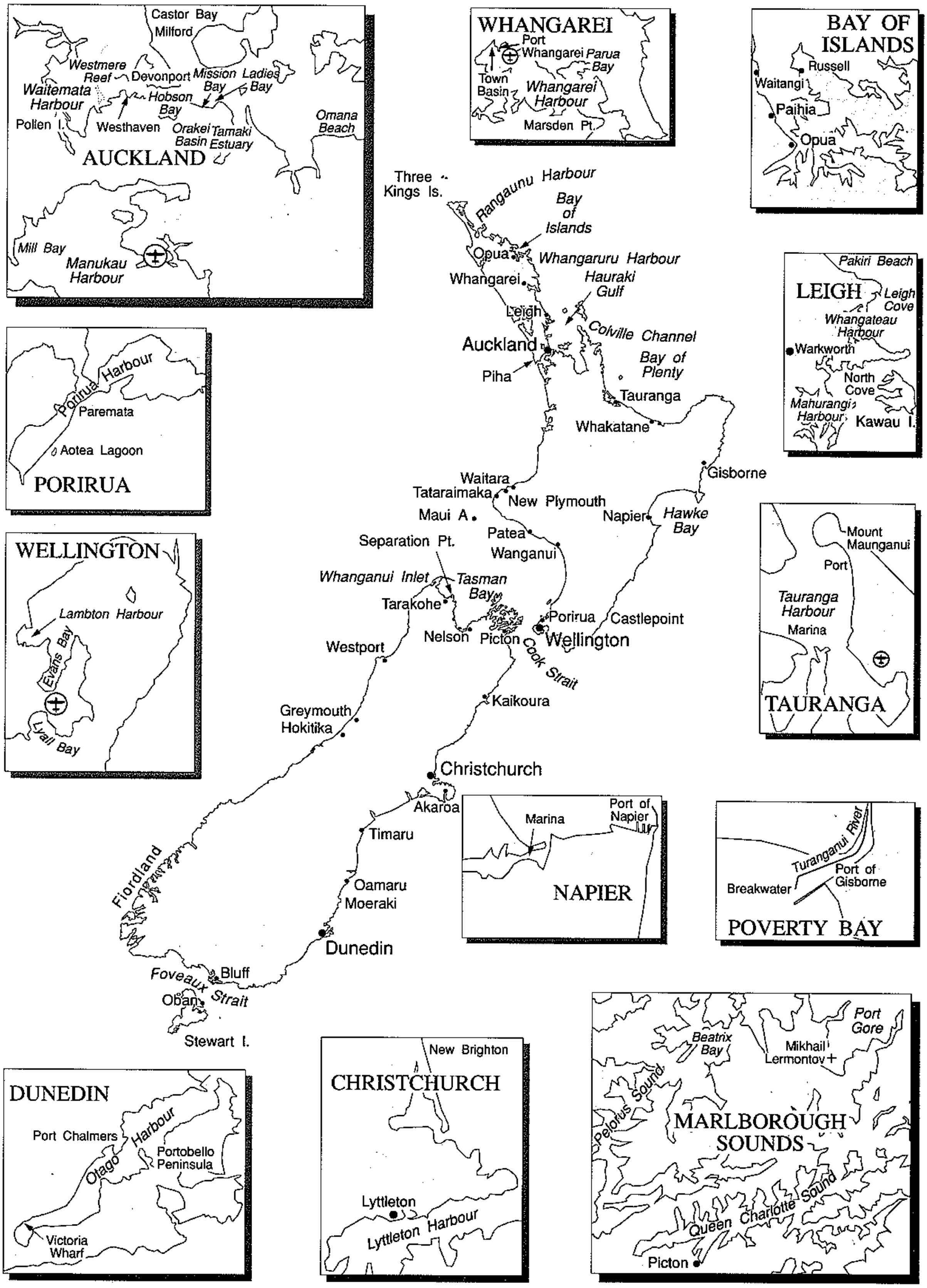

Fig. 1.
Location diagrams for all the New Zealand localities mentioned in the text. The inset diagrams are not to the same scale.

FIELD KEY TO THE SPECIES

The following key is based on characters of mature live colonies and those features that can be detected in the field with a x 10 hand-lens. For most species the key will also be helpful for dried or preserved colonies. A glossary of the technical terms used in the key and the following species descriptions is given in Appendix 2.

1.	Colony forming a crust or patch; or runner-like with no erect or branching portions	2
	Colony erect or pendent, bushy with no encrusting portion; or with small erect branches from a ramifying portion that is never crust-like	28
2.	Colony forming a crust or patch of zooids, flat or with mounded or nodular portions, never runner-like	3
	Colony comprising thin runners or stolons from which zooids arise, which, even when dense, never form a true crust	39
3.	Colony whitish to semitransparent, or with a slight yellowish cast	4
	Colony otherwise coloured	13
4.	Distal ends of zooids erect, tubular, sometimes united in series, with a circular orifice lacking an operculum	*Tubulipora*
	Zooids more box-like, or, if irregularly disposed and semi-erect, with an operculate orifice	5
5.	Zooids completely lacking thin spines or spine-like processes (tubercles may be present)	6
	At least some zooids with thin spines or spine-like processes	7
6.	Zooids completely membranous and uncalcified, more or less transparent	*Alcyonidium* sp.
	Zooids otherwise	11
7.	Zooids with most or all of the frontal wall membranous	8
	Zooids with at least one third of the frontal wall calcified	*Electra pilosa*
8.	Zooids with at least some lateral spines	9
	Zooids with only a short pair of distal spines or these lacking	*Conopeum seurati*
9.	Almost all zooids with 6–8 pairs of lateral spines; a pair of tubercles proximally; no ovicells	*Electra tenella*
	Some zooids with a few short lateral spines; many zooids lacking them	10
10.	Zooids whitish, the lateral rim narrow; no ovicells	*Conopeum seurati*
	Zooids whitish or with a yellowish cast owing to larvae in ovicells; lateral rim broad	*Crassimarginatella fossa*
11.	Zooidal frontal shield imperforate, often transparent	*Celleporella bathamae*
	Zooidal frontal shield with pores	12
12.	Zooids regularly disposed; frontal shield evenly perforated	*Cryptosula pallasiana*
	Zooids mostly irregularly disposed; frontal shield with marginal pores only	*Celleporina proximalis*
13.	Colony beige, fawn, or pale brown	14
	Colony otherwise coloured	17
14.	Colony firmly attached to substratum; zooids with a cryptocyst and oral spines	15
	Colony loosely attached to substratum; cryptocyst lacking; spines oral and lateral	16

15. Spines simple, unbranched; ovicells lacking *Chaperia granulosa*
Spines antler-like; ovicells present *Chaperiopsis cervicornis*

16. Spines interdigitating across the frontal membrane; tubular connections between zooids seen only in basal view *Beania plurispinosa*
Spines not interdigitating; tubular connections seen easily in frontal view *Beania* sp.

17. Colony orange 18
Colony otherwise coloured 24

18. Zooidal frontal shield with few relatively large foramina; a long spine emerging from one side of the orifice *Arachnopusia unicornis*
Zooids not as above 19

19. Zooidal frontal shield evenly perforated with numerous pores 20
Zooidal frontal shield centrally imperforate; pores lateral only 22

20. Orifice relatively large, bell-shaped; no ovicells or avicularia *Cryptosula pallasiana*
Orifice smaller, not bell-shaped; ovicells and avicularia present 21

21. Avicularia with pointed mandibles; sinus roundly V-shaped *Schizoporella errata*
Avicularia with rounded mandible, spatulate, often lacking; sinus narrowly U-shaped *Schizosmittina cinctipora*

22. Orifice with spines distally and a spout-like prominence proximally *Escharoides angela*
Orifice lacking oral spines; a rounded tubercle proximally *Hippadenella* cf.*margaritifera*

23. Colony black to greyish-black with vermilion growing edges 24
Colony pinkish, red, or purplish 25

24. Zooidal orifice with convex proximal rim *Watersipora arcuata*
Zooidal orifice with proximal sinus *Watersipora subtorquata*

25. Colony pinkish 26
Colony reddish-purple *Chiastosella watersi*

26. Colony deep pink; zooids everywhere regular in shape *Calloporina angustipora*
Colony paler or redder; zooids irregularly disposed in colony centre 27

27. Colony whitish-pink to reddish-pink; zooids porcellanous; avicularia with pointed mandibles *Rhynchozoon larreyi*
Colony pale pinkish-orange; zooids not porcellanous; avicularia with rounded mandibles *Parasmittina delicatula*

28. Colony calcified, the branches biserial to multiserial 29
Colony calcified or uncalcified; the branches not as above 35

29. Backs of branches with vibracular bristles that lash when disturbed 30
Branches not as above 31

30. Zooidal scutum small; a giant avicularium at branch bifurcations *Caberea rostrata*
Zooidal scutum large; giant avicularia lacking *Caberea zelandica*

31. Branches biserial 32
Branches multiserial 33

32. Colony purplish-brown to burgundy in colour — *Bugula neritina*
Colony pale in colour — 34

33. Avicularia occurring on both marginal and inner zooids — *Bugula flabellata*
Avicularia occurring on marginal zooids only — *Bugula simplex*

34. Zooids with scuta, perforate ovicells, and sessile lateral avicularia — *Tricellaria occidentalis*
Zooids lacking scuta; with imperforate ovicells and moveable bird's-head avicularia — *Bugula stolonifera*

35. Colony lightly calcified, with runner-like chains of zooids attached to the substratum from which short uniserial branches arise — *Scruparia ambigua*
Colony uncalcified; zooids arranged otherwise — 36

36. Colony bushy, erect or pendent — 37
Colony with adherent runner-like stolons, with or without short erect branches — 39

37. Colony large, like stringy gelatinous noodles, the main axes about 1 mm diameter, with zooids arranged all around — *Zoobotryon verticillatum*
Colony smaller, zooids arranged otherwise — 38

38. Zooids beige, opaque, externally merging with branch axes — *Anguinella palmata*
Zooids semitransparent, arranged in short spirals on branches — *Amathia distans*

39. Zooids borne regularly in opposite pairs on the creeping stolon — *Aeverrillia armata*
Zooids not borne so regularly — 40

40. Zooids more or less longitudinally symmetrical, with no lateral processes — 41
Zooids longitudinally asymmetrical, with small lateral processes — 42

41. Stolon thinner than zooids; embryos pink; tentacles 8 — *Bowerbankia gracilis*
Stolon often as thick as zooids; embryos yellow; tentacles 10 — *Bowerbankia imbricata*

42. Zooids generally dense, on adherent and erect stolons — *Buskia socialis*
Zooids generally sparse, on creeping stolons only — *Buskia nitens*

DESCRIPTIONS OF THE SPECIES

Alcyonidium sp.
(Fig. 2, A)

Colony form: Encrusting patches, uncalcified.
Size: Up to 4 cm diameter.
Description: Smooth, thin circular crusts on stones, shell, or wood; pale greyish-brown in colour to semitransparent. Zooids more or less rectangular in shape, about 0.35–0.55 mm long and 0.22–0.39 mm wide, the frontal surface flat to slightly convex. The orificial region forming a slight bulge towards the distal end of the zooid. Tentacles 16–18.
Settlement season: Late summer (February) in Pelorus Sound.
Distribution: Hobson Bay, Auckland, on shells under the changing sheds, December 1977, intertidal; Beatrix Bay, Pelorus Sound, on fibrous-cement panels, February 1988, 20 m depth.
Remarks: The bryozoan genus *Alcyonidium* is widely distributed around the world but was not definitely known to occur in New Zealand (apart from misidentifications) until the record of midtidal understone colonies at Portobello, Otago Harbour (Ryland 1975) of an unidentified species known from at least 1955. Other records of mainland *Alcyonidium* species are given by Gordon (1986). The genus is now known to be widely distributed around New Zealand but how many species there are is a mystery — they look more or less identical to British and European species, but, because *Alcyonidium* species can be genetically distinct while looking similar (Hayward 1985), and because the New Zealand occurrences are mostly in

non-fouling situations, it is not certain if they are the same. Ryland (1965) did not list *Alcyonidium* among the British and European fouling bryozoans.

The references to *Alcyonidium* and the related genus *Flustrellidra* in Morton and Miller (1968, p. 412 *et seq.*, fig. 152) were given in the context of a general discussion about the bryozoan order Ctenostomida and were not meant to imply that these genera had been found in Auckland Harbour (M.C. Miller, pers. comm. 1991).

Anguinella palmata van Beneden, 1845â
(Plate 5, A)

Colony form: Erect tufts, uncalcified.
Size: Up to 6.0 cm (in New Zealand).
Description: Erect or pendent tufts, comprising a main axis with numerous branches of tubular zooids that are slightly incurved toward the axis. Colour pale beige. Zooids opaque, up to 1.0–1.5 mm long, merging without external differentiation into the branch axes, the internal details not visible. Tentacles 10.
Settlement season: Not reported in the literature.
Distribution: Devonport Wharf (Morton & Miller 1968); Omana Beach and Ladies Bay (Waitemata Harbour) and Port of Nelson (Gordon 1986). Also southern Britain, eastern coasts of the North Sea, Senegal, Ghana, Zaire, Atlantic coast of America from Massachusetts to Florida, Brazil, and New South Wales (Prenant & Bobin 1956; Winston 1982a; Cook 1985; Hayward 1985; Ryland & Hayward 1991). The type locality is Ostende, Belgium.
Remarks: The New Zealand distribution in two shipping harbours points to an introduction via maritime transport. Allen (1953) reported the occurrence of *A. palmata* in New South Wales in 1953. It was first recorded in New Zealand by R.J. Harger (unpublished notes, University of Auckland, ?1960) (see Gordon 1967).

According to Prenant and Bobin (1956) colonies can reach 20 cm in length. Although not presently known from wharf pilings, the species appears to be naturalised intertidally at the eastern end of Auckland Harbour.

Aeverrillia armata (Verrill, 1873)
(Fig. 2, B)

Colony form: Encrusting, ramifying, uncalcified.
Size: A few centimetres long.
Description: Zooids occur in pairs, arising at regular intervals on either side of segmented, ramifying, thread-like, stolons; each zooid with a tiny kenozooidal segment between it and the stolon. Feeding zooids transparent to yellowish, about 0.55–0.60 mm tall and 0.175 mm wide, the body wall somewhat flattened and thinner on the side facing the stolon; at each of the 4 corners of the distal ends of zooids is a short prominence bearing a bristle (spine). A pleated collar is visible around the emergent lophophore of 8 tentacles. The gut of each zooid shows clearly through the body wall, revealing a stomach gizzard of 4 conical 'teeth'.
Settlement season: No information.
Distribution: Devonport, Auckland Harbour, on wharf piles (Morton & Miller 1968). Also Atlantic coast of America from Maine to Brazil, excluding tropical waters (Winston 1982a). The type locality is Vineyard Sound, Massachusetts.
Remarks: Morton and Miller (1968) first recorded *A. armata* in New Zealand, on wharf piles at Devonport, Auckland. Their illustration (1968, p. 413, fig. 152) is labelled *Buskia* (to which *Aeverrillia* species were once referred) and is clearly recognisable as *A. armata.* J.E. Morton made the illustration from actual material (pers. comm.) taken from pilings at the most shaded part of Devonport wharf. The above description, however, is based on those in Rogick and Croasdale (1949) and Maturo (1957). A search by D.P. Gordon in 1977 and by both authors in 1988 failed to locate the species at Devonport wharf, so the record of Morton and Miller (1968) remains the only one to date. A few zooids of a species of *Aeverrillia* were encountered in the Leigh marine reserve in 1968, however (DPG, pers. obs.).

According to Maturo (1957), *A. armata* may be found in salinities from 12 psu (equivalent to parts per thousand) to full oceanic conditions. It occurs on a variety of substrata, including red and brown seaweeds (Rogick & Croasdale 1949) and hydroids (Osburn & Veth 1922). In southern New England free branches attain 2.5 cm long. The ecologically similar species *Aeverrillia setigera* (Hincks) has a wider distribution around the world, occurring naturally in northern and eastern Queensland waters (see Rogick 1945) though apparently not yet in New Zealand.

Amathia distans Busk, 1886
(Fig. 2, C; Plate 5, B)

Colony form: Erect to suberect, branching.
Size: Branches attain 4–5 cm in length.
Description: Colony a pale brownish-transparent, rampant over the substratum, with many free branches. These consist of jointed stolonal axes about 0.117–0.198 mm diameter with paired clusters of zooids

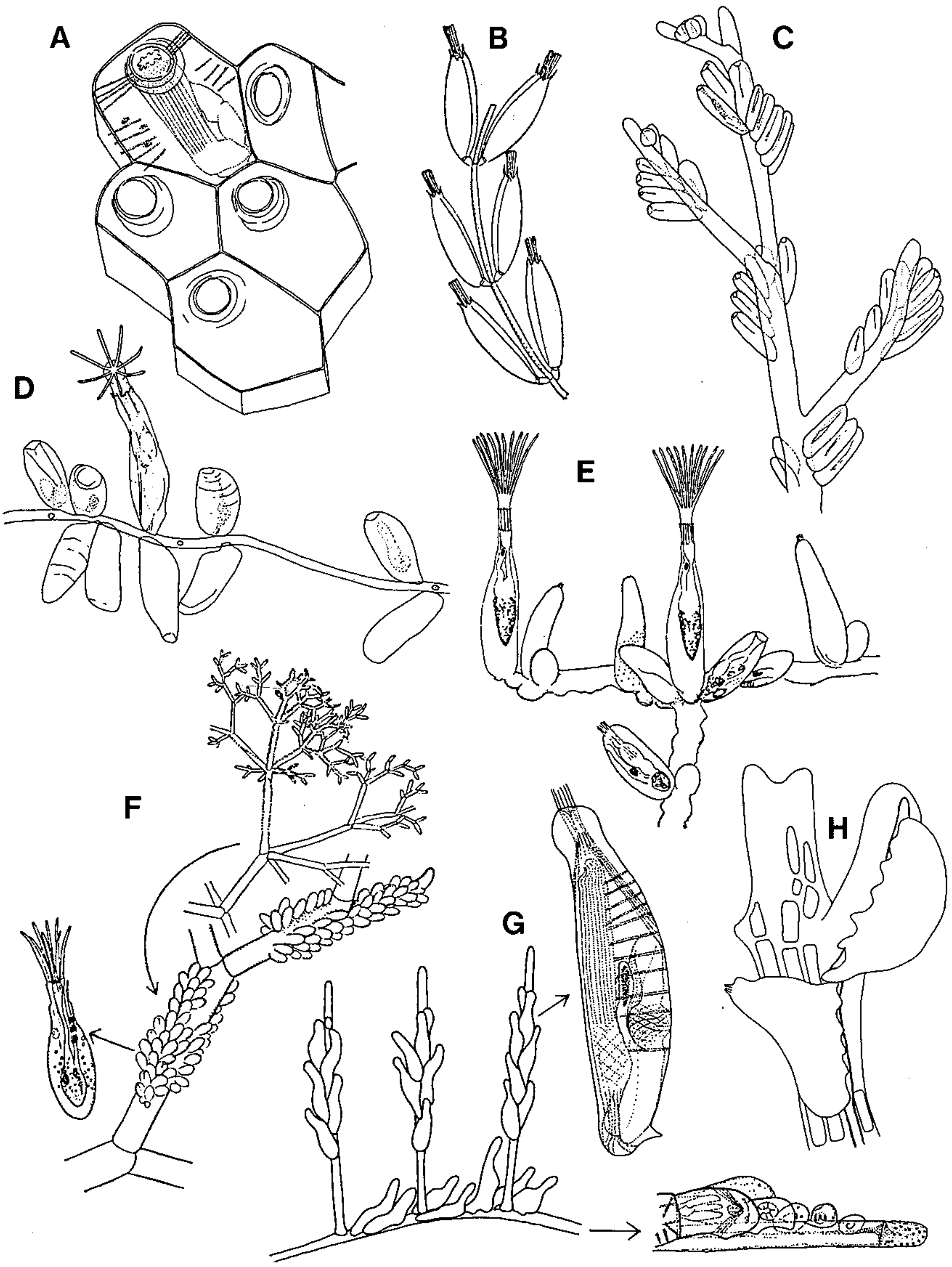

Fig. 2. A, *Alcyonidium* sp., x 60. B, *Aeverrillia armata,* x 30. C, *Amathia distans,* x 25. D, *Bowerbankia gracilis,* x 33. E, *Bowerbankia imbricata,* x 33. F, *Zoobotryon verticillatum,* x 1, x 3, x 24. G, *Buskia socialis,* x 17, x 93, x 93. H. *Buskia nitens,* x 70. (B, D–F after or modified from Morton and Miller (1968)).

arranged spirally around the axis for the full length of the internodes or more often just in the distal parts near bifurcations. Retracted zooids 0.43–0.51 mm long and 0.15–0.18 mm wide, with up to 17 pairs in a cluster. Distal ends of branches may attach to the substratum.
Settlement season: No information.
Distribution: Omana Beach, Auckland Harbour, on rocks and shells; intertidal. Also widely distributed throughout the world, occurring in France, the Mediterranean and Red Seas (Prenant & Bobin 1956), the Atlantic coast of America from North Carolina to Brazil (Maturo 1957; Winston 1982a), South Atlantic (Busk 1886), Victoria, Australia, Java (Harmer 1915), Japan (Mawatari & Mawatari 1986), Puget Sound, Washington (O'Donoghue & O'Donoghue 1925), and Southern California (Osburn & Soule 1953). The type locality is off Salvador (Bahía), Brazil.
Remarks: *Amathia distans* was first noted in New Zealand by R.E. Harger and recorded on cards in the marine reference collection at Auckland University in ?1960. It was subsequently reported on by Gordon (1967) and Morton & Miller (1968, fig. 152, as *A. biseriata*). Like *Anguinella palmata* it appears to have become naturalised intertidally in some of the eastern parts of Auckland Harbour where it occurs in varied situations. It settles on the stems of another stoloniferous ctenostome bryozoan, *Zoobotryon verticillatum*, the brown alga *Sargassum sinclairii*, or, more usually, under sandstone boulders, on oyster valves and polychaete worm-tubes. On shores like Omana Beach, *A. distans* is tolerant of very turbid conditions. It can be settled on by a variety of other organisms, including suctorians, diatoms and other microalgae, and the entoproct *Barentsia gracilis*.

Morton and Miller (1968, fig. 152) illustrated one of the characteristic features of *A. distans* — the zooids of the left-hand branch of a bifurcation spiral anticlockwise up the branch and those of the right-hand branch clockwise. This characteristic was described in the type material by Chimonides (1987, p. 338).

Bowerbankia gracilis Leidy, 1855
(Fig. 2, D)

Colony form: Encrusting, ramifying, uncalcified.
Size: Several centimetres long.
Description: Zooids borne in clusters of different ages and sizes at irregular intervals along segmented thread-like stolons. Stolons typically narrower than the extended zooids. Zooids more or less transparent, 0.47–0.62 mm long when retracted, 0.73–1.04 mm long when extended. Stomach gizzard present. Lophophore tentacles 8. Embryos relatively large, occurring in body cavity, pink.
Settlement season: Summer, at the Leigh marine reserve.
Distribution: Goat Island Bay, Leigh, Waitemata Harbour, Onehunga, Port of Napier, Oaonui, Tataraimaka (North Taranaki), Totaranui, Oban (Stewart Island) (Gordon 1986). Also widely distributed around the world — Europe, Britain, Greenland, eastern United States, Washington State to Mexico, South Africa, India, Japan (as *B. caudata* [Mawatari & Mawatari 1986]), South Australia (*see* Bobin & Prenant 1954; Prenant & Bobin 1956; Brock 1982; Winston 1982a; Hayward 1985). The type locality is Point Judith, Rhode Island.
Remarks: Morton and Miller (1968, fig. 152) first illustrated New Zealand specimens of this species, though not referring to the species name. In their figure a zooid is shown with eight tentacles, typical of *gracilis*, although in part of the drawing the diameter of the stolon is shown proportionally larger than is normal for the species. Ryland (1975) and Gordon (1986) reported colonies from Goat Island Bay (Leigh marine reserve), some distance from berthages, and the species would appear to be thoroughly naturalised in New Zealand. When densely spreading colonies are encountered, as under sandstone boulders on the echinoderm reef-flat in the Leigh marine reserve, they appear as a characteristic fine grey 'fur' just visible to the naked eye. Larval settlement and metamorphosis in *B. gracilis* have been described by Reed (1978) and Reed and Cloney (1982) and some aspects of the ecology of the species are given by Occhipinti Ambrogi (1985).

Bowerbankia imbricata (Adams, 1798)
(Fig. 2, E)

Colony form: Encrusting, ramifying, uncalcified.
Size: Several centimetres long.
Description: As for *B. gracilis* but the stolons approximately the diameter of extended zooids. Zooids 0.46–0.81 mm long and about 0.23 mm wide when contracted. Tentacles 10. Embryo yellow.
Settlement season: Summer, at the Leigh marine reserve.
Distribution: Goat Island Bay, Leigh, Whangateau Harbour, Auckland Harbour, Port Nelson, on rocks, shells, wood, barnacles, ascidians, other bryozoans, and algae (Gordon 1986). Also Europe, Britain, Argentina, Atlantic and Pacific coasts of North America, Japan, Alaska, Indonesia (*see* Bobin & Prenant 1954; Prenant & Bobin 1956; Hayward 1985; Mawatari & Mawatari 1986; Ryland & Hayward 1991). The

type locality is Milford Haven, south Wales.

Remarks: As noted by Gordon (1986), *B. imbricata* was illustrated and erroneously identified by Gordon (1967) as *Nolella pusilla*, from Auckland Harbour. Ryland (1975) also recorded *B. imbricata* from Goat Island Bay, Leigh marine reserve. Both *B. imbricata* and *B. gracilis* were included in Ryland's (1965) OECD catalogue of main marine fouling organisms. Their distribution in New Zealand mostly in shipping harbours is consistent with the likelihood of having been introduced through maritime transport, although both now appear completely naturalised.

Zoobotryon verticillatum (della Chiaje, 1828)
(Fig. 2, F)

Colony form: Pendent, branching.
Size: To 50 cm long.
Description: Colony like thin, stringy, gelatinous noodles up to 1 m long; repeatedly branching, the internodes about 27 mm or less in length and about 1-2 mm in thickness. Branching dichotomous to verticillate, with as many as 4 branches arising from a node. Zooids about 0.5–1.00 mm long, arranged in several series along each stolon segment, but deciduous in winter so that only the rampant basal parts of colonies and some stolonal branches survive. Tentacles 8. Stomach gizzard present. Embryos whitish.
Settlement season: Summer.
Distribution: Waitemata Harbour (Pollen Island), Manukau Harbour (Mill Bay, Karore Bank, Onehunga Wharf). Also tropicopolitan to warm-temperate seas — Mediterranean, West Africa, Caribbean, Brazil, California, Hawaii, Japan, India, New Caledonia, Australia (*see* Prenant & Bobin 1956; Brock 1982; Winston 1982a; Cook 1985; Mawatari & Mawatari 1986). The type locality is Naples, Italy.
Remarks: The species was first noted in New Zealand by R.E. Harger and recorded on cards in the marine reference collection of Auckland University, ?1960, and subsequently recorded by Gordon (1967) and Morton and Miller (1968) as *Zoobotryon pellucidum* Ehrenberg, a junior synonym of *Z. verticillatum*. The most recent record is of small colonies at Onehunga Wharf in February 1987 (DPG, pers. obs.). It appears to have become naturalised in both Auckland harbours.

Buskia nitens Alder, 1856
(Fig. 2, H; Plate 2, A)

Colony form: Encrusting, ramifying, uncalcified.
Size: Up to about 1 cm.
Description: Colony inconspicuous; comprising thin ramifying stolons bearing small, transparent zooids about 0.30–0.40 mm long and 0.20 mm wide, close together or widely separated. Each zooid somewhat recumbent on the stolon, with only the anterior end raised, the lateral margins often crenulated with little projections. Tentacles 8. Stomach gizzard present.
Settlement season: No information for New Zealand; late summer to late autumn in Britain (Hayward 1985).
Distribution: Castor Bay, Auckland, and Oamaru, on filamentous red algae, hydroids, and mussel shells. Also widely distributed — Europe, Britain, Caribbean, Brazil, Alaska to Mexico, Japan, Malaysia, Tanzania (Harmer 1915; Osburn & Soule 1953; Mawatari & Mawatari 1986). The type locality is off Northumberland, England.
Remarks: This inconspicuous species is scarcely detectable with the naked eye. Hayward (1985) mentions that zooids are more easily seen when containing their yellow embryos. First noticed in New Zealand, and reported in the same year, by Gordon (1967), it has been discovered only once since then, by the present authors, on mussel (*Perna canaliculus*) shells at Oamaru Wharf in August 1988.

Buskia socialis Hincks, 1887
(Fig. 2, G)

Colony form: Erect, or encrusting with erect branches, uncalcified.
Size: Up to 3.2 cm long.
Description: Zooids colourless, borne in 2 series along the encrusting and erect stolons; the proximal ends of the zooids recumbent on the stolon and the anterior ends somewhat raised. Stolon about 1.13 mm diameter. Zooids around 0.60–0.79 mm long and 0.15–0.17 mm wide when partially retracted. The lateral edges at the proximal end are typically produced into one or a few projections adjacent to the stolon. Stomach gizzard present.
Settlement season: No information available.
Distribution: Mediterranean and Adriatic Seas, Red Sea, Brazil. The type locality is the Adriatic coast.
Remarks: This may be the first record of this species from the western Pacific. It was discovered on live shells of the green-lipped mussel *Perna canaliculus* in 3 m of water at North Cove, Kawau Island, Hauraki Gulf, 11 May 1977, by Mr Gary Venus. Ocean-going pleasure craft frequent this coast but it is not known if this was the source of the introduction. Brock's (1985) illustration of putative *Bowerbankia imbricata* from Adelaide appears to be of *Buskia socialis*. According to Prenant and Bobin (1956) the species has eight tentacles.

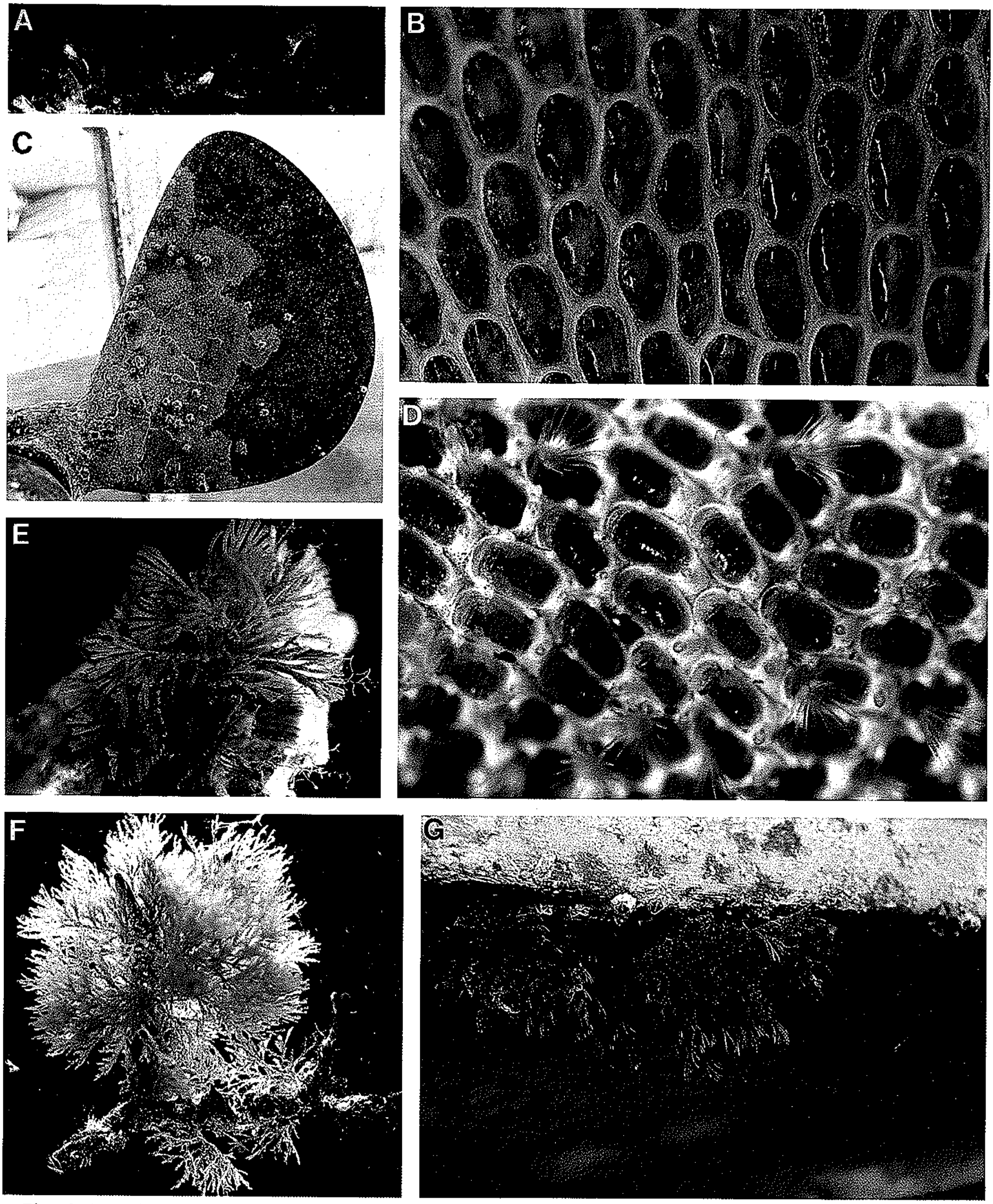

Plate 2. A, *Buskia nitens:* three zooids on a valve of *Perna canaliculus,* x 30. B, *Conopeum seurati,* x 38. C, *Conopeum seurati:* several dried colonies on a propellor blade, x 0.2. D, *Electra pilosa,* in breeding condition, with testicular tissue seen around the edges of the membranous area; several lophophores are emergent, x 40. E, *Caberea zelandica,* x 2. F, *Tricellaria occidentalis,* x 2. G, *Bugula neritina:* dried colonies on the keel of a fishing boat, x 0.5.

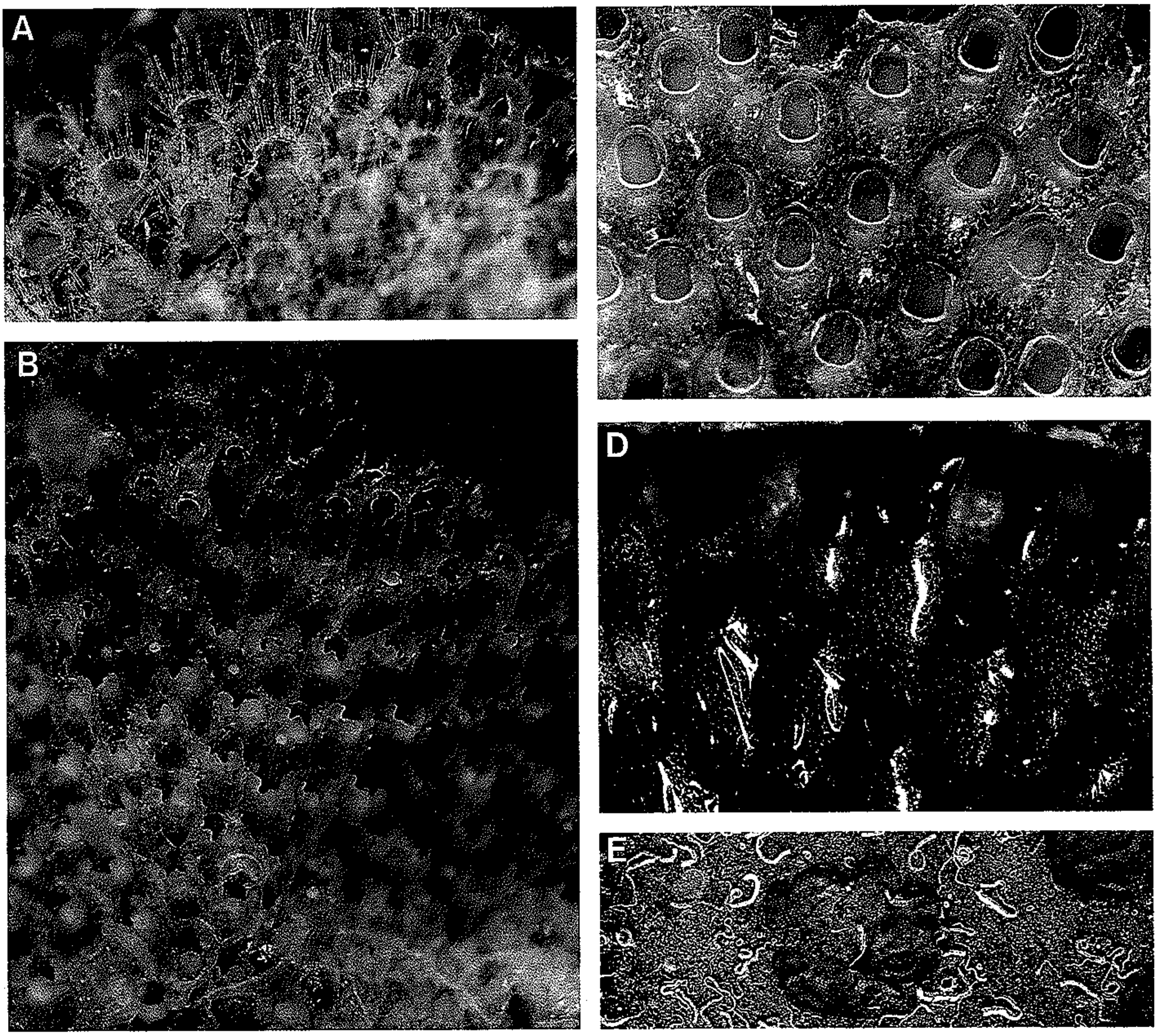

Plate 3. A, *Beania plurispinosa*, x 37. B, *Rhynchozoon larreyi*, x 18 (the photo shows it as semitransparent — it is normally pinkish and opaque). C, *Cryptosula pallasiana* containing mature embryos, x 29. D, *Watersipora subtorquata:* zooids at the growing edge of a colony, x 40. E, *Watersipora subtorquata:* dried colony on a boat hull, x 1.

Scruparia ambigua (d'Orbigny, 1841)
(Plate 5, C, D)

Colony form: Encrusting, ramifying, with erect branches; weakly calcified.
Size: Up to about 1 cm high.
Description: Colony delicate, with erect uniserial chains of transparent zooids from encrusting uniserial zooids. Zooids more or less club-shaped, with a membranous area in the expanded part, about 0.30–0.50 mm long overall, each arising from the frontal side of a parent zooid just proximal to the membranous area. Brood chambers somewhat oval, borne on the ends of zooids, the whole arrangement looking somewhat like an icecream cone, the brood chamber with a median line dividing it into 2 halves. No spines or avicularia. Tentacles 10.
Settlement season: Evidently summer (Ryland & Hayward 1977).
Distribution: Evidently widely distributed around New Zealand, having been recorded from Leigh, Piha, Waitemata Harbour, Manukau Harbour, Mount Maunganui, Gisborne, Castlepoint, Wellington, Nelson, Separation Point, Kaikoura, Milford and Breaksea Sounds, Portobello, Oban (Gordon 1986). Also widely distributed around the world except in polar waters (Prenant & Bobin 1966; Ryland & Hayward 1977; Ryland & Hayward 1991). The type locality is the Falkland Islands.
Remarks: Although inconspicuous, *S. ambigua* is often commonly encountered, growing as it does on bushy fouling bryozoans, hydroids, and leafy brown algae. It can also occur on shell and glass.

Conopeum seurati (Canu, 1928)
(Plate 2, B, C; Plate 4, A)

Colony form: Encrusting, sheet-like, calcareous.
Size: Up to 8 cm diameter.
Description: Thinly encrusting pale brownish-white sheets of zooids, with some overgrowth in the centre of large colonies. Zooids 0.38–0.66 mm long and 0.17–0.45 mm wide, elongate-oval in shape, with most of the frontal surface membranous; skeletal rim granular; often a pair of short spines distally and, more rarely, 3–5 pairs of slender spines laterally. No avicularia or ovicells. Larva planktonic. Tentacles 15–16.
Settlement season: No information locally; from early summer to mid-autumn in Britain (Ryland & Hayward 1977).
Distribution: Opua, Whangaruru, Whangarei (Town Basin), Marsden Point, Whangateau Harbour, Waitemata Harbour, Orakei Basin, Tamaki Estuary, Onehunga, Gisborne, Napier, Patea, Whanganui Inlet, Nelson, and Lyttelton on stones, shells, pilings, pontoons, boat bottoms, and plastic litter (Gordon 1896; Read & Gordon 1991). Also the Sea of Azov, the Caspian Sea and estuarine habitats in Britain, North Africa, northern Mediterranean, ?Florida (Bobin & Prenant 1962; Ryland 1967; Ryland & Hayward 1977; Winston 1982a). The type locality is the estuary of Oued Bezirk, Tunisia.
Remarks: In Britain, this species can produce semi-erect colonies on *Ruppia* and other plants, whereas, in New Zealand, only encrusting colonies are known so far. Colonies are also known from enclosed waters in Eastern Europe where there is no regular outlet to an estuary or the sea (Zevina & Kuznetsova 1965) — as a consequence, the species is tolerant of extreme ranges of salinity and temperature, including freezing and drying out.

This exotic species was first recorded in New Zealand by Gordon (1986) but it is reported by Read and Gordon (1991) as having been first noted in 1969, in the Tamaki Estuary, Auckland, on sandstone rocks near the Otahuhu power station which came into operation at that time. The species evidently was in New Zealand prior to then, however — a dated collection of shells of the mytilid bivalve *Xenostrobus securis* in the collection of conchologist O.J. Marston bore several colonies of *C. seurati*. They were taken from a culvert near an old wharf at Kaihoka, on the northern arm of Whanganui Inlet, northwest South Island, in January 1963. This is a rather remote locality, which indicates that *C. seurati* must have already existed at a more-frequented port or harbour elsewhere, possibly Nelson, although it was first discovered there only in 1985. It is very tolerant of both quiet, turbid, estuarine waters (as in the Whangarei Town Basin and Nelson marina) and waters of near-oceanic salinity and strong current speeds (as at Marsden Point). The broadest colonies encountered by us occurred on the propeller blades of a yacht (Opua, Bay of Islands). Some aspects of the ecology of *C. seurati* are given by Occhipinti Ambrogi (1985).

Electra pilosa (Linnaeus, 1761)
(Plate 2, D; Plate 4, B)

Colony form: Encrusting, calcareous.
Size: Up to several centimetres long.
Description: Colony whitish, forming circular, linear, or lobate patches depending on the roughness or smoothness of the substratum. Zooids 0.39–0.62 mm long and 0.15–0.28 mm wide, elongate-oval or rectangular, with a membranous area covering 50–70% of the frontal surface; this area bordered by a narrow

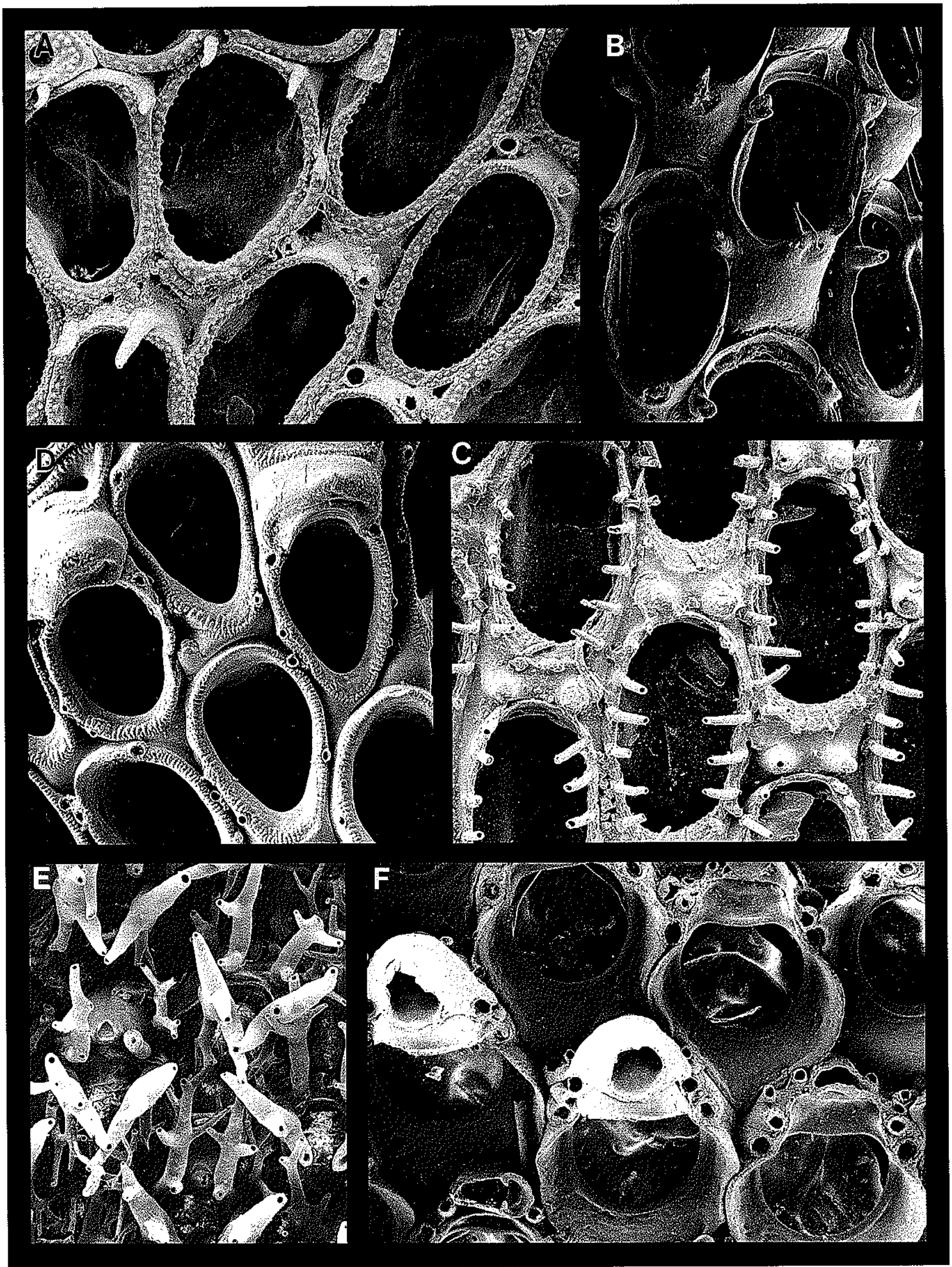

Plate 4. Encrusting Bryozoa: A, *Conopeum seurati*, x 94. B, *Electra pilosa*, x 99. C, *Electra tenella*, x 88. D, *Crassimarginatella fossa*, x 86. E, F, *Chaperiopsis cervicornis*, with spines intact, x 82, with spines removed, x 114.

calcareous rim which typically bears 1–2 short chitinous spines on each side; the remaining frontal surface calcified, perforated, often bearing a long curved spine from a median prominence. Tentacles generally 11–12 in New Zealand colonies. No avicularia or ovicells. Larva planktonic.
Distribution: Widely distributed around both coasts of New Zealand, mostly on red and brown seaweeds; occasional in marine-fouling situations, as on the hulls of pleasure craft at Picton (August 1988) and on a fibrous-cement experimental panel at 10 m depth, Beatrix Bay, Pelorus Sound (February 1988). One of the commonest species of marine Bryozoa, it has been reported from almost all the world's seas. The type locality on the Swedish coast is unknown.
Settlement season: Late summer in Pelorus Sound. Late summer and autumn in Britain (Ryland & Hayward 1977).
Remarks: *Electra pilosa* is a very variable species, in terms of both colonial and zooidal morphology (*see* Norman 1894; Prenant & Bobin 1968; Ryland & Hayward 1977; Gordon 1986).

Electra tenella (Hincks, 1880)
(Plate 4, C)

Colony form: Encrusting, sheet-like, calcareous.
Size: To several centimetres diameter.
Description: Encrusting brownish-white sheets of zooids; these more or less elongate-rectangular, 0.37–0.75 mm long and 0.11–0.34 mm wide, the membranous frontal wall occupying almost all the frontal area; bordered by a minutely granular lateral rim and with a pair of tubercles proximally. Larva planktonic.
Settlement season: Not reported.
Distribution: Pakiri Beach on dead *Atrina* shells. Also the Atlantic coast of Florida, Puerto Rico, and Brazil (Winston 1982a, b), and Japan (Mawatari & Mawatari 1986). The type locality on the Atlantic coast of Florida is unknown.
Remarks: This is the first record of this exotic species in New Zealand. It was first seen by one of us (DPG) in 1977 on drift *Atrina* shells at Pakiri Beach, Northland. It has also recently been encountered on plastic debris in the Hauraki Gulf (Mr Leigh Stevens, pers. comm., August 1991). According to Winston (1982b) it is commonly found on drift plastic debris in Florida, but it has only once been reported as a fouling species (Weiss 1948).

Crassimarginatella fossa Uttley, 1951
(Plate 4, D)

Colony form: Encrusting, sheet-like, calcareous.
Size: To several centimetres diameter.
Description: Colony whitish-yellow, especially tending to yellowish in the breeding season. Zooids 0.37–0.63 mm long and 0.24–0.34 mm wide, elongate-oval, generally narrowing proximally. Membranous frontal wall occupying most of the frontal area, bordered by granular margins and with a smooth calcified shield proximally, bearing a tubercle. Occasional large avicularia between the zooids. Ovicell a broad recumbent chamber at the distal end of each brooding zooid, with a crescentic furrow along the middle.
Settlement season: No data available.
Distribution: Marsden Point, Colville Channel, Tasman Bay, New Brighton, Timaru, Moeraki, Fiordland (Gordon 1986). The type locality is the Colville Channel, between Great Barrier Island and the Coromandel Peninsula.
Remarks: Normally found on rocks and shells, this endemic New Zealand species occurs in a marginally marine-fouling situation on wharf piles at Marsden Point, at the entrance to Whangarei Harbour. It was also encountered on the hull of a fishing boat at Moeraki.

This species is very similar to *C. papulifera*, common at Goat Island Bay, Leigh, which has only a narrow, slit-like furrow to the ovicell.

Chaperia granulosa Gordon, 1986
(Plate 7, A)

Colony form: Encrusting, calcareous.
Size: To 1–2 cm diameter.
Description: Relatively small, pale-brownish, circular colonies. Zooids 0.51–1.18 mm long and 0.47–0.85 mm wide, with an extensive granular-surfaced calcareous shelf (cryptocyst) under the membranous frontal wall, proximal to the broad operculum. A row of 6–9 spines, jointed at the base, around the distal border of each zooid; a mid-distal pair smallest, often at a lower level and at an angle to the others; the longest spines attaining 0.66 mm in length. A pair of calcareous ridges below the sides of the orifice under the operculum. Lophophore tentacles 14. No avicularia or ovicells, the yolky orange-yellow larva brooded within the parent zooid.
Settlement season: Late spring to late summer.
Distribution: Goat Island Bay, Leigh, Auckland Harbour, Marlborough Sounds, Fiordland, western Foveaux Strait, on stones and shells from 0–507 m depth. The type locality is Stephens Hole, off D'Urville Island, Cook Strait.

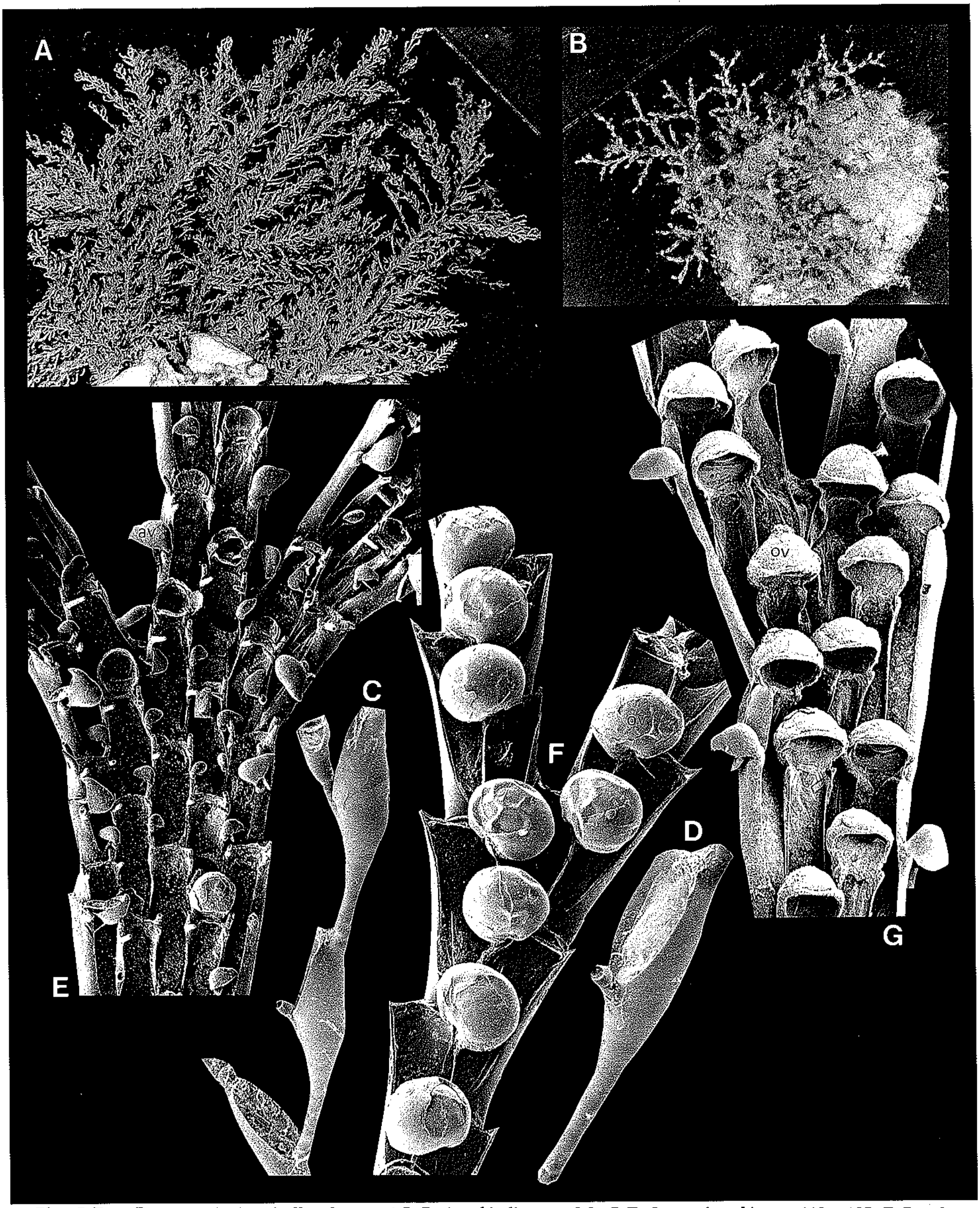

Plate 5. Erect Bryozoa:. A, *Anguinella palmata*, x 1.5. B, *Amathia distans*, x 2.3. C, D, *Scruparia ambigua*, x 113, x 185. E, *Bugula flabellata*, x 30. F, *Bugula neritina*, x 43. G, *Bugula simplex*, x 55. (av = avicularium; ov = ovicell)

Remarks: *Chaperia granulosa* occurs on shells, rocks, and pilings at the ports of Gisborne, Napier, Oamaru, and Bluff and was found on the hull of a fishing boat at Bluff. Larvae can also settle on glass, iron, stainless steel, and tin (Gordon 1968). Gordon (1986) has discussed the taxonomic relationships of this endemic species with the similar, algal-dwelling, *C. acanthina* (Lamouroux) with which it was previously confused.

Chaperiopsis cervicornis (Busk, 1854)
(Plate 4, E, F)

Colony form: Encrusting, calcareous.
Size: 1–2 cm diameter.
Description: Pale-brownish colonies, visibly spinose. Zooids 0.39-0.51 mm long and 0.24-0.37 mm wide, with raised lateral margins, and an extensive smooth-surfaced calcareous shelf (cryptocyst) under the membranous frontal wall proximal to the operculum. A pair of calcareous ridges below the sides of the orifice under the operculum. A row of 8 antler-like spines around the distal rim of the orifice, with a transversely set mid-distal avicularium between the bases of the most distal spines on many zooids. Lophophore tentacles 14–15. Ovicell hood-like, with a chamber at its apex.
Settlement season: Not known.
Distribution: Widely distributed throughout New Zealand from the Three Kings Islands to Foveaux Strait, on rocks, shells, and algae from the intertidal to 220 m depth. The type locality is in Bass Strait, near Tasmania.
Remarks: The slender antler-like spines are very characteristic of this species, which has been found in fouling situations such as on wharf piles, and once on the hull of a fishing boat at Bluff. Larvae can also settle on rock, shell, algae, ascidians, and rubber (Gordon 1968).

Bugula flabellata (Thompson *in* Gray, 1848)
(Plate 5, E)

Colony form: Erect, bushy.
Size: To 4 cm high.
Description: Flexible bushy colonies, erect or pendent; buff-coloured when alive, greyish-buff when dry. Branches 3–6 zooids wide, the zooids 0.64–0.86 mm long and about 0.21 mm wide; each distal zooidal corner with a pair of spines except for the outer corners of marginal zooids where there are three, of which one is sometimes quite long. Membranous frontal wall extending to proximal end of zooid. Avicularia on small stalks, bird's-head-like, able to rock back and forth, graded in size from large marginal ones to small avicularia on the middle zooids of a branch, each attached to its parent zooid about midlaterally. Lophophore tentacles 14. Ovicell more or less globular with a straight proximal rim. Larva yellow. Ancestrula upright, with 9 marginal spines and basal rootlets.
Settlement season: September to May in Auckland Harbour (Skerman 1959).
Distribution: Known from most New Zealand ports from Opua to Bluff, though not yet encountered at Whangarei, Onehunga, Gisborne, New Plymouth, Tarakohe, or Timaru. Dr C.H. Hay collected specimens from the fishing wharf at Akaroa on 24 December 1988, an area not sampled by us. Also probably widely distributed in warm and temperate waters of both hemispheres (Prenant & Bobin 1966; Ryland 1967; Ryland & Hayward 1977; Mawatari & Mawatari 1986). The type locality is Cork, Ireland.
Remarks: This is one of the most commonly encountered fouling bryozoans at New Zealand ports (Harger 1964; Gordon 1967, 1986; Morton & Miller 1968). It was first definitely recorded in New Zealand by Macken (1958) in Wellington Harbour, but it is possible that the *'Bugula* sp.' of Ralph and Hurley (1952), encountered in the summer of 1949-50 in Wellington Harbour, and *'Bugula* sp. nov. cf. *B. flabellata'*, recorded at Lyttelton in November 1954 (Skerman 1958) were also this species. It has also been reported from the Maui-A oil platform off the South Taranaki coast, from near the sea surface to 35 m depth (Foster 1982), and on the sunken Russian cruise liner *Mikhail Lermontov* in Gore Bay, Marlborough Sounds, where it occurs with *B. neritina* and epizoic *Scruparia ambigua*, mostly on projections like railings, davits, mast, and radar, with proportionally fewer colonies on the hull. The ship sank on 16 February 1986 — both *Bugula* species were common on 10 December 1986 and were still present on 21 February 1990 (as determined from specimens collected by Dr C.H. Hay)

Reproduction in relation to life history in *B. flabellata* has been described by Dyrynda and Ryland (1982).

Bugula neritina (Linnaeus, 1758)
(Plate 2, G; Plate 5, F)

Colony form: Erect, bushy.
Size: To 9.8 cm high.
Description: Flexible bushy colonies, purplish-brown, the branches biserial. Zooids 0.66–1.07 mm long and 0.28–0.34 mm wide, alternating, the outer distal corner pointed but lacking definite spines. Membranous

Plate 6. Erect Bryozoa: A, *Bugula stolonifera*, x 53 (avicularia were shed during specimen preparation; their attachment points are visible as holes on zooidal margins). B, C, *Caberea rostrata*, x 83, x 83. D, E, *Caberea zelandica*, x 140, x 102. F, *Tricellaria occidentalis*, x 79. (av = avicularium; ov = ovicell; sc = scutum; vi = vibracular chamber)

frontal wall extending more or less to the proximal end of the zooid. Tentacles 18–24. No avicularia, Ovicell large, white, globular, attached at the inner distal corner of the zooid. Larva brownish. Ancestrula upright, lacking spines or rootlets.
Settlement season: Between September and June in Auckland Harbour, peaking December to March, and between December and May at Lyttelton, peaking January and February, i.e., when the sea temperature exceeds 15 °C (Skerman 1958, 1959).
Distribution: Known from most New Zealand ports from Opua to Dunedin, though not yet encountered at Onehunga, Gisborne, or Oamaru. Also nearly cosmopolitan except in cold polar and subarctic/ subantarctic regions (Prenant & Bobin 1966; Ryland & Hayward 1977; Mawatari & Mawatari 1986). The type locality in the Mediterranean Sea is unknown.
Remarks: Like *B. flabellata,* this is one of the more commonly encountered marine-fouling bryozoans at New Zealand ports, especially on boat hulls (Harger 1964; Gordon 1967, 1986; Morton & Miller 1968). It was first recorded in New Zealand by Hutton (1873) but the given locality was Lyall Bay, on the Wellington south coast, not the harbour, and Lyall Bay is the type locality for *Bugula prismatica* (Gray, 1843) which is similarly purplish-coloured with conspicuous white ovicells (*see* Gordon 1986). Also, a number of Hutton's (1873) records of other British or European bryozoans in New Zealand waters have been found to be in error, so the record of *B. neritina* at Lyall Bay in the 1870s, while not impossible, is doubtful. The first reliable record is that of Ralph and Hurley (1952), based on colonies first encountered in May 1949 in Wellington Harbour, where it still occurs, but it has never been seen or reported at Lyall Bay since Hutton's (1873) record.

Bugula neritina has been the subject of a number of overseas toxicity experiments using heavy metals and/or heavy-metal-based paint formulations (e.g., Miller 1946; Wisely 1963; Wisely & Blick 1967; Benson & Moncrieff 1976) — in general, mercury is more toxic to larvae than copper and copper more than zinc. A number of other studies have been of larval-settlement behaviour and growth of colonies (e.g., McDougall 1943; Lynch 1947, 1949; Mawatari 1951; Woods Hole Oceanographic Institution 1952; Skerman 1958; Wisely 1959; Kawahara 1960a, b, 1961, 1962, 1963, 1965; Kawahara & Iizima 1960; Ryland 1960; Harger 1964; Woollacott & Zimmer 1971; Mihm *et al.* 1981; Reed & Woollacott 1982; Kirchman & Mitchell 1984; Keough 1986, 1989a,b; Keough & Chernoff 1987; Kitamura & Hirayama 1987a, b; Mitchell & Maki 1988; Rittschof & Costlow 1987, 1989a, b; Rittschof *et al.* 1988; Maki *et al.* 1989; Roberts *et al.* 1991), showing larval responses to filmed and unfilmed surfaces, that larvae can delay settling for 36 hours (although most settle within two hours), and that colonies can attain 7 cm height in just two months. In Auckland Harbour, larvae can settle on shell, wood, algae, sponges, and glass (Gordon 1968). The species can also settle and grow well on ferro-cement.

Although *B. neritina* is best known as a marine-fouling organism, it has coincidentally achieved prominence as a source of a novel biochemical, bryostatin, which has proven efficacious against leukaemia (Ireland *et al.* 1988).

Bugula simplex Hincks, 1886
(Plate 5, G)

Colony form: Erect, bushy.
Size: Around 1.5 cm high.
Description: Flexible bushy colonies, buff-coloured, the branches 2–6-serial, narrowest at their origin, and up to 1.09 mm wide. Zooids 0.56–0.94 mm long and 0.13–0.19 mm wide, alternating, lacking projecting spines. Membranous frontal wall extending to the proximal end of the zooid. A pedunculate bird's-head avicularium on the outer lateral rim of marginal zooids only, about 0.25 mm long. Ovicell somewhat hemispherical in shape.
Settlement season: Not known locally; midsummer to late autumn in Britain (Ryland & Hayward 1977).
Distribution: Lyttelton. Also the Mediterranean, Britain, eastern seaboard of the United States from Maine to Florida, South Australia (Ryland 1958; Prenant & Bobin 1966; Ryland & Hayward 1977; Brock 1982; Ryland & Hayward 1991). The type locality is the Adriatic coast.
Remarks: This is the first record of this species from New Zealand and possibly the southern hemisphere. It superficially resembles small colonies of *Bugula flabellata* in the field and was initially taken by us to be that species. We encountered *B. simplex* only at the boatyard at Lyttelton, on 16 August 1988. It accords well with northern hemisphere specimens except that the avicularia in our material are a little longer, and the distolateral corners of the spines are not developed.

The effect of microbial films on larval settlement in *B. simplex* has been described by Brancato and Woollacott (1982).

Bugula stolonifera Ryland, 1960
(Plate 6, A)

Colony form: Erect, bushy.
Size: Around 3–4 cm high.
Description: Flexible bushy colonies, greyish, the

branches biserial. Zooids 0.47–0.77 mm long and about 0.19 mm wide, alternating, the outer distal corner with a pair of short spines, the inner corner with a single spine. Membranous frontal wall extending to the proximal end of the zooid. A pedunculate bird's-head avicularium generally on the outer margin of each zooid, variable, approximately the width of a zooid in length, not exceeding 0.24 mm. Ovicell nearly hemispherical, the proximal rim straight with a sinuous calcareous band around it.
Settlement season: Early summer to mid-autumn in Britain (Ryland & Hayward 1977).
Distribution: Opua, North Cove of Kawau Island, Waitemata Harbour, New Plymouth, Napier, Tarakohe, Pelorus Sound, Nelson, Lyttelton, Timaru, and Bluff. Also found in the Mediterranean Sea, Adriatic Sea, southern Britain, Ireland, Ghana, Massachusetts to Florida, Gulf of Mexico, Brazil, Panama Canal; South Australia (Powell 1971; Ryland & Hayward 1977; Brock 1982; Winston 1982a; Cook 1985; Ryland & Hayward 1991). The type locality is at Swansea, South Wales.
Remarks: This exotic species was first noted in New Zealand by Harger (1964), based on colonies found settling on experimental panels in Auckland Harbour. Panels immersed on 15 May 1962 were dominated by *B. stolonifera* by 19 June, with as many as 15–20 colonies per square centimetre. It was subsequently reported on by Gordon (1967, 1986) and Morton and Miller (1968). In the past three decades it has spread far beyond Auckland and is now found at most ports throughout the country. It seems never to be as dense or as widespread on substrata as the other two fouling *Bugula* species, however. Larvae can settle on wood and ferro-cement.

The effect of microbial films on larval settlement in *B. stolonifera* has been described by Brancato and Woollacott (1982), and some aspects of the ecology of the species are given by Occhipint Ambrogi (1985).

Beania plurispinosa Uttley & Bullivant, 1972
(Plate 3, A; Plate 7, B)

Colony form: Loosely encrusting.
Size: To several centimetres diameter.
Description: Colony buff-coloured, lightly calcified, and not firmly fixed to the substratum, so that colonies can be peeled off. Zooids excessively spinose, 0.63–0.75 mm long, 0.27–0.33 mm wide, prostrate proximally, suberect and overlapping somewhat distally; each zooid connected to its 6 neighbours by 6 tubes (seen from underneath); the lateral zooidal margins constricted just proximal to the orifice. Distal rim supporting about 9 spines in a semicircular row distal to the constriction, with 2 additional rows of more slender spines beneath; 8 slender, overlapping, spines on each lateral margin proximal to the constriction, and up to 30 spines scattered over the basal surface. Ovicells occur as egg-shaped concavities in the basal wall distal to the constriction. From the basal wall of some of the zooids is a stalked rootlet with a grappling-hook-like attachment. Rare avicularia can sometimes be seen in basal view. Lophophore tentacles 19–20. Embryos and larvae orange-yellow.
Settlement season: August till March (Leigh) (Gordon 1970).
Distribution: Throughout the New Zealand region, from the intertidal to 220 m depth, from Raoul Island (Kermadec Ridge) to Foveaux Strait; also Port Jackson, New South Wales (Gordon 1984, 1986). The type locality is off Cape Pattison, Chatham Island.
Remarks: This common native species can often be found on wharf pilings (as at Marsden Point, Auckland, Mount Maunganui, New Plymouth, Napier, Nelson, and Oamaru) although it has not yet been encountered on boat hulls. Larvae can settle on rock, shell, algae, ascidians, other bryozoans, and rubber (Gordon 1968, as *B. hirtissima*).

Beania sp.
(Plate 7, C)

Colony form: Loosely encrusting.
Size: Up to 1–2 cm across.
Description: Colony buff-coloured, lightly calcified, not firmly fixed to the substratum. Zooids 0.45–0.75 mm long and 0.13–0.38 mm wide, not overlapping, mutually connected by 6 tubes to neighbours, the gaps between zooids often visible frontally. Two pairs of short spines distally, and 4–5 pairs of short, non-overlapping, lateral spines. No ovicells or avicularia. Lophophore tentacles 18.
Settlement season: Not recorded.
Distribution: Marsden Point, Waitemata Harbour, and Nelson.
Remarks: This undescribed species may occur on wharf piles, along with *B. plurispinosa*, and on leafy brown seaweeds.

Caberea rostrata Busk, 1884
(Plate 6, B, C)

Colony form: Erect, bushy.
Size: To 2–3 cm high.
Description: Colony orange, the branches spread out in fan-like fashion, biserial, nonjointed. Zooids 0.37–0.50 mm long and 0.17–0.20 mm wide; both the

proximally calcified part of the zooid and the calcareous shelf (cryptocyst) under the membranous frontal wall are smooth. A short, flattened, spine-like structure (scutum) projects from the inner lateral margin of each zooid over part of the membranous wall. A short spine, jointed at the base, occurs on either side of the orifice. Midfrontal avicularia small, each adjacent to the attachment of the scutum; a giant avicularium, about as large as a feeding zooid, projects outwards below each branch bifurcation, the tip pointed and upturned. Ovicells flattened. Dorsal side of branches with diverging series of elongate chambers (vibracula), from each of which arises a long, serrated bristle; these lash backwards and forwards in unison when the colony is disturbed. Embryos red, fading to orange upon maturation.
Settlement season: Not recorded.
Distribution: Widely distributed in the New Zealand region from the Kermadec Ridge and Three Kings Islands to Fiordland from low tide to 274 m depth. Also found at Tristan da Cunha in the South Atlantic. The type locality is the Challenger Plateau, west of Cape Farewell (*see* Busk 1884; Hastings 1943; Gordon 1984, 1986).
Remarks: This native species may occur on submerged experimental panels, as at Auckland (Harger 1964) or on the hulls of fishing boats, as at Bluff (pers. obs.). It is referred to in Morton and Miller (1968) as *Caberea transversa*, a species of Harmer (1923) from Indonesia, which differs in having, among other things, much larger scutal spines and no giant avicularia.

Caberea zelandica (Gray, 1843)
(Plate 2, E; Plate 6, D, E)

Colony form: Erect, bushy.
Size: To 3 cm high.
Description: As for *C. rostrata* but stouter, the zooids 0.30–0.36 mm long and about 0.24 mm wide, the cryptocyst granular. Scutum larger than in *C. rostrata*, more like a protective shield, the proximal part broad, rounded to a point, the distal part small, triangular. A short pair of basally jointed spines either side of the orifice (one of each pair lacking in ovicelled zooids). Small midfrontal avicularia present. No giant avicularia. Tentacles 12. Ovicells flattened. Vibracular chambers relatively large, overlapping, with serrated bristles that lash in unison when the colony is disturbed.
Settlement season: Not recorded.
Distribution: Found throughout New Zealand from the Three Kings Islands to Fiordland, from low tide to 253 m depth. The type locality is Auckland (Hastings 1943).
Remarks: This endemic species has been recorded from wharf piles in Auckland Harbour (Gordon 1967), on experimental submerged panels at Lyttelton (Skerman 1968), and on the Maui-A oil platform from about 26–110 m depth (Foster 1982).

Tricellaria occidentalis (Trask, 1857)
Plate 2, F; Plate 6, F)

Colony form: Erect, bushy.
Size: To 6.0 cm high.
Description: Colonies buff-coloured, the jointed branches variable in length, comprising biserial segments of 3, 5, 7, or 9 zooids. Zooids 0.43–0.71 mm long and about 0.19 mm wide, the membranous frontal wall about two-thirds the zooidal length, the remaining third calcareous, smooth. Generally 3 spines at the outer distolateral corner (the most proximal one often forked), a near-median spine, and 2 spines at the inner corner, on most nonovicelled zooids, plus a scutal spine from the inner zooidal margin that is variably awl-like, bifid, trifid, or, on ovicelled zooids, a large lobate structure with as many as 8 points. Frontal avicularia not evident; lateral avicularia relatively large, projecting, some larger than others, collectively giving a serrated outline to the branch segments, or they are lacking altogether. Ovicell subglobular, smooth with scattered pores.
Settlement season: August to March in Auckland (Harger 1964).
Distribution: Whangarei (Parua Bay), Auckland, Tauranga, Gisborne, Napier, Porirua Harbour and Aotea Lagoon, Tarakohe, Pelorus Sound, Nelson, Lyttelton. Also British Columbia to Southern California, Baja California, China, Japan, Venice, South Australia, Victoria, New South Wales (*see* Remarks). Probably first observed at Santa Barbara, Trask (1857) also noted its occurrence northwards to Cape Flattery, Washington, and on marine debris in San Francisco Bay.
Remarks: This exotic species was first definitely documented in New Zealand by Harger (1964) in his thesis on Auckland marine-fouling organisms, and later by Gordon (1967) and (as *Scrupocellaria*) by Morton and Miller (1968), although it is very likely that the records of *Scrupocellaria* sp. in Auckland Harbour (Skerman 1959) and *Menipea ?patagonica* Busk in Lyttelton Harbour (Skerman 1958) were also of this species — the only known *Scrupocellaria* species around mainland New Zealand is *S. ornithorhyncus* Thomson, reported only from non-fouling situations along the west coast from the Three Kings Islands to Milford Sound (Gordon 1986). *Menipea patagonica* is known only from southern South America, South Georgia, Kerguelen, and Bouvet Island (Hastings 1943), and,

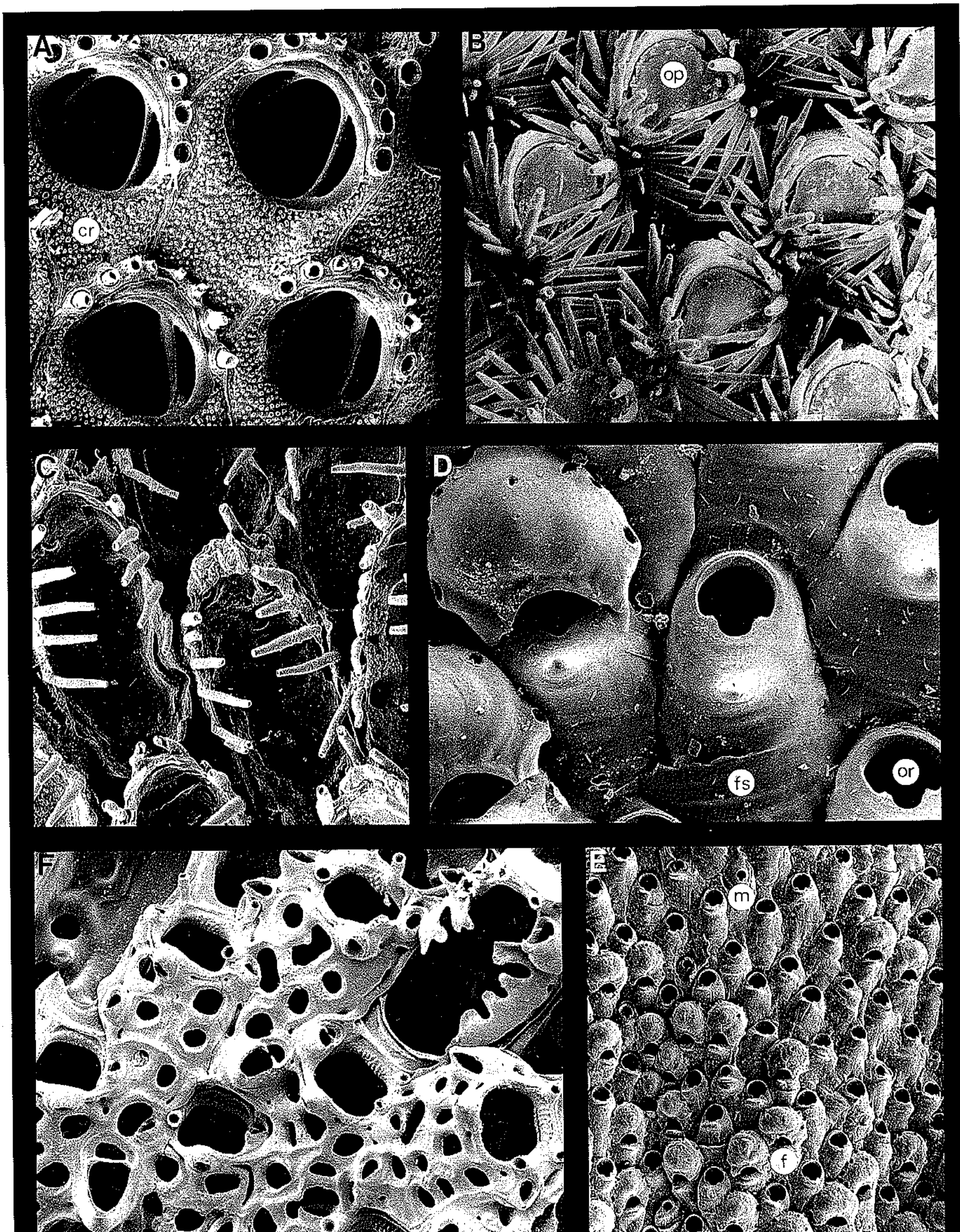

Plate 7. Encrusting Bryozoa: A, *Chaperia granulosa*, x 55. B, *Beania plurispinosa*, x 77. C, *Beania* sp., x 89. D, E, *Celleporella bathamae*: D showing ordinary feeding zooids at right and two ovicelled female zooids at left, x 148; E showing part of a colony with male (m), female (f), and ordinary feeding zooids, x 29. F, *Arachnopusia unicornis*, x 77. (cr = cryptocyst; fs = frontal shield; op = operculum; or = orifice)

significantly, superficially resembles *Tricellaria occidentalis*, which we collected at Lyttelton in 1988. Thus it appears reasonably certain that *T. occidentalis* in New Zealand may be dated from Skerman's (1958) record of colonies of *'Menipea ?patagonica'* on submerged panels at Lyttelton in November 1954.

Tricellaria occidentalis is a distinctive species, often co-occurring with *Bugula* species or alone in dense swards. It dominates the fouling-bryozoan fauna at the port of Gisborne where it may be seen at low tide dangling beneath horizontal concrete beams between pilings, and at Paremata, Porirua Harbour, it can form dense swards on the hulls of pleasure craft, attaining 4–5 cm length in a year.

Although easily recognised, it has intrinsically variable features that have caused taxonomic difficulties. These include the presence or absence of lateral avicularia, the number of zooids per branch segment, and the size and shape of scutal spines. All of these features may vary considerably within a single colony. This condition was superbly illustrated by Mawatari (1951b), which is why it is puzzling that d'Hondt and Occhipinti Ambrogi (1985) saw fit to erect a new species, *T. inopinata*, for colonies occurring in the lagoon of Venice. Their material clearly falls within the range of variation of *T. occidentalis*. This variation was also noted by Robertson (1905), Yanagi and Okada (1918), Okada (1929), and Osburn (1950), among others. Nielsen (1985) has illustrated by scanning electron microscopy developing fertile segments of *T. occidentalis* from San Juan Island, Washington, and these accord with the New Zealand material. According to P.L. Cook (pers. comm.), *Menipea porteri* MacGillivray, 1889 is a junior synonym of *T. occidentalis* — Bock (1982) reported this species as a fouler at Sydney, Port Phillip Bay, and South Australia and Bock (1985) specifically recorded it from the port of Adelaide, South Australia.

Inasmuch as Trask (1857) recorded *T. occidentalis* at Cape Flattery and San Francisco Bay, this would have made the species a candidate for being transported to Asia and Australasia by vessels plying the Pacific. Its late arrival in Europe is surprising, however. Occhipinti Ambrogi (1991) has discussed the invasive capabilities of this species based on its rapid spread in the Lagoon of Venice during the 1980s, where it was unknown as recently as 1978.

Celleporella bathamae (Ryland & Gordon, 1977) (Plate 7, D, E)

Colony form: Encrusting.
Size: Generally less than 1 cm diameter.
Description: Small, circular, white calcareous crusts of elongate zooids — comprising apparently non-reproductive feeding zooids, possibly feeding female zooids with ovicells, and non-feeding dwarf-male zooids. Feeding zooids 0.36–0.56 mm long and 0.16–0.26 mm wide, the frontal surface strongly convex, sometimes transversely striated, often with a suboral bulge. Orifice subcircular with a well-rounded sinus. Lophophore tentacles 12–13. Male zooids scattered, sometimes the same shape as ordinary feeding zooids but with a much smaller orifice. Female zooids generally shorter than ordinary zooids, the orifice broad with a concave proximal rim in which is a small nick or sinus. Ovicell globose, with holes around the margin and some centrally. Embryos and larvae whitish with a pale-apricot flush.
Settlement season: Larvae are known to be liberated in December at least (Ryland & Gordon 1977).
Distribution: South Island, from Marlborough Sounds to Fiordland and Otago Harbour; intertidal to 220 m depth (Gordon 1989). The type locality is Aquarium Point, beside the Portobello Marine Laboratory, Otago Harbour.
Remarks: This endemic species is associated with the kelp *Macrocystis pyrifera* at the type locality but it can also occur on mussel shells and, as in Dunedin and Bluff Harbours, sparingly on the hulls of pleasure craft and fishing boats.

A related northern hemisphere species, *Celleporella hyalina* (Linnaeus), has once been definitely reported for New Zealand (Ryland & Gordon 1977), based on a specimen in the Natural History Museum, London, but its exact provenance and collection details are unknown. This species is therefore not listed here as occurring among the New Zealand marine-fouling bryozoan fauna.

Arachnopusia unicornis (Hutton, 1873) (Plate 7, F)

Colony form: Encrusting.
Size: To several centimetres diameter.
Description: Reddish-orange calcareous crusts. Zooids 0.70–0.75 mm long and 0.25–0.38 mm wide, the boundaries between them not that distinct; the frontal shield perforated by 4 or more small or large irregularly placed holes. Up to 4 small avicularia on the frontal shield and one of these often replaced by a larger avicularium up to half the zooidal length; also 1–2 small avicularia on the proximal rim of the orifice. A long stout spine emerges from one side of the orifice. Tentacles 15–16. Ovicells recumbent, partly concealed by secondary calcification in older zooids. Embryos bright red.

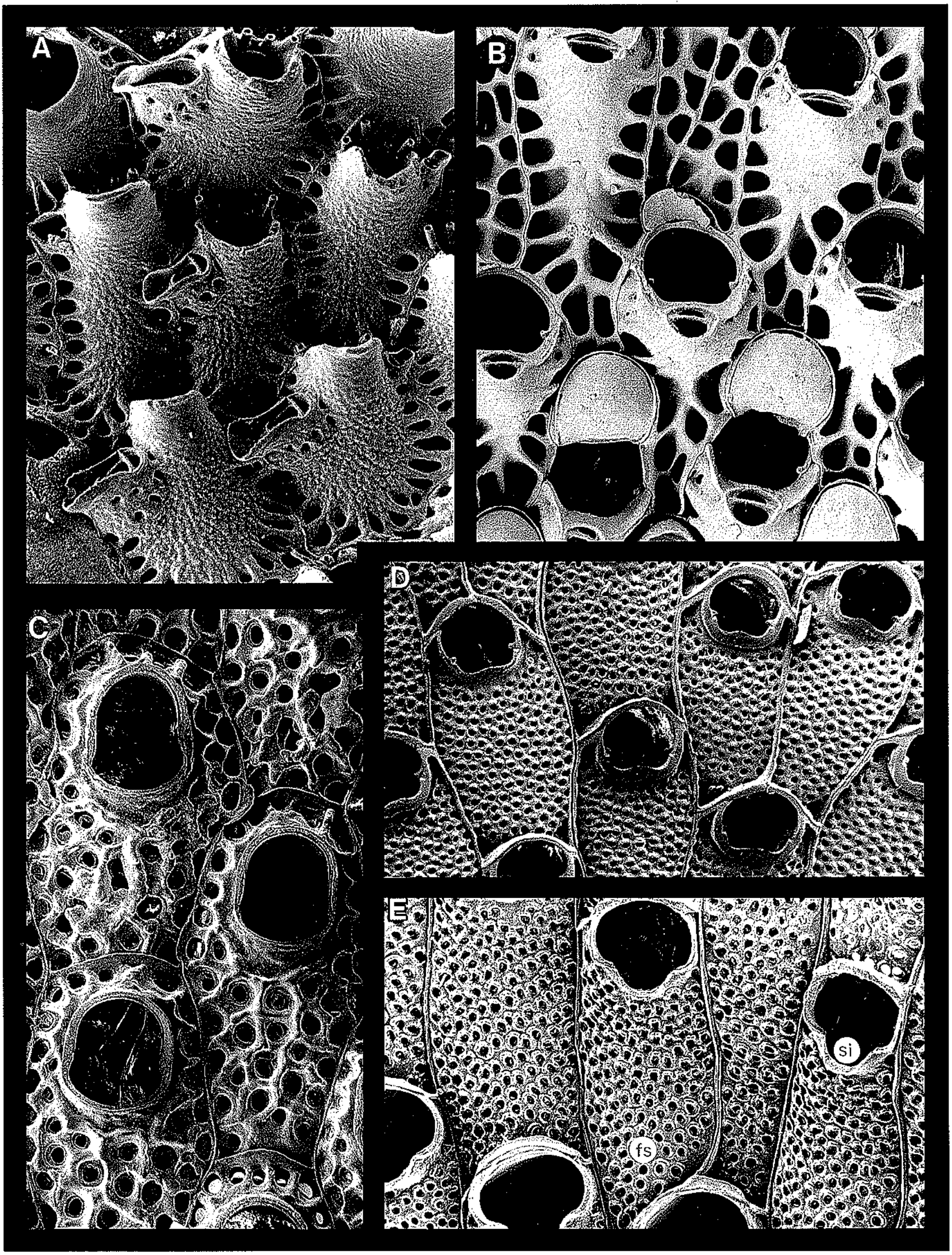

Plate 8. Encrusting Bryozoa: A, *Escharoides angela*, x 55. B, *Hippadenella* cf. *margaritifera*, x 104. C, *Cryptosula pallasiana*, x 69. D, *Watersipora arcuata*, x 51. E, *Watersipora subtorquata*, x 69. (fs = frontal shield; si = orificial sinus)

Settlement season: Not reported.
Distribution: Throughout New Zealand from the Kermadec and Three Kings Islands to Foveaux Strait, from the intertidal zone to 549 m depth. Also known from southern Australia (see Gordon 1984, 1989). The precise type locality in New Zealand is not known (Brown 1952).
Remarks: This common native species has been found in fouling situations, as on the Maui-A oil platform from about 7–49 m depth (Foster 1982), on an experimental panel in Pelorus Sound, and sparsely on the hulls of pleasure craft and fishing boats at Lyttelton and Bluff (this survey).

Escharoides angela (Hutton, 1873)
(Plate 8, A)

Colony form: Encrusting.
Size: To several centimetres diameter.
Description: Orange calcareous crusts. Zooids 0.55–1.13 mm long and 0.50–0.78 mm wide, with a smooth or faintly granular frontal shield rising distally into a large scoop-like peristome in front of the orifice; 11–12 pairs of conspicuous lateral pores. Avicularia single or paired, small or prominent, somewhat spatula-shaped. Oral spines 4, jointed at the base, most obvious in young zooids. Ovicell somewhat immersed in distal zooid, with radiating grooves and marginal pores. Larvae reddish-orange.
Settlement season: More or less year-round, with a decline in numbers of larvae produced during the winter months (Gordon 1970).
Distribution: Widely distributed in the New Zealand region from Curtis Island (Kermadec Ridge) to Foveaux Strait; intertidal to 88 m depth. The precise type locality in New Zealand is unknown (Brown 1952).
Remarks: This endemic species was noted as occurring on mussel shells (*Perna canaliculus*) on pilings at Gisborne (this survey), and on a submerged experimental panel at Lyttelton (Skerman 1958). It has not yet been discovered on boat hulls. Larvae can settle on rock, shell, crab carapaces, algae, and stainless steel (Gordon 1968).

Cryptosula pallasiana (Moll, 1803)
(Plates 1, A–C; Plate 3, C; Plate 8, C)

Colony form: Encrusting.
Size: Up to 3 cm diameter.
Description: Whitish to pinkish-orange or orange crusts. Zooids 0.53–0.92 mm long and 0.29–0.56 mm wide, the frontal shield coarsely perforated by up to 30 relatively large pores in young zooids, with as few as 13 larger pores in older zooids with a thicker shield; low ridges and tubercles usually occur between the pores. Orifice somewhat bell-shaped in outline, widest proximally. Avicularia lacking. No oral spines. No ovicells — yellowish embryos are brooded internally.
Settlement season: Reported only for Lyttelton, where settlement is heaviest during spring and autumn months (Skerman 1958). We encountered colonies with embryos at several locations during August 1988.
Distribution: One of the more ubiquitous fouling bryozoans in New Zealand, occurring at every port between Marsden Point and Bluff (not Westport or Greymouth), and also in Whangateau Harbour near Leigh (DPG), Aotea Lagoon (Porirua), and Akaroa (Dr C.H. Hay). Also widespread around the world, particularly in ports, harbours, and estuarine situations. The type locality in the Mediterranean Sea is unknown.
Remarks: The colour of colonies may be related to salinity in New Zealand, the palest colonies occurring in the upper reaches of harbours, the most orange in waters of near-oceanic salinity. According to Simkina and Turpaeva (1961), salinity as low as 10 psu is sublethal for the species. This naturalised species has been known in New Zealand waters from at least the 1890s when Hamilton (1898) recorded it (as *Lepralia pallasiana*) from the ports of Wanganui, Napier, and Dunedin. It occurs on a variety of substrata — rock, shell, ascidians, glass, pilings, and painted and ferro-cement hulls of pleasure craft and fishing boats.

Watersipora arcuata Banta, 1969
(Plate 8, D)

Colony form: Encrusting, to erect and foliaceous.
Size: Small crusts to extensive overlapping crusts.
Description: Deep black calcareous crusts with brittle, vermilion-tinged growing edges, often curled. Zooids more or less elongate-rectangular, 0.68–1.11 mm long and 0.29–0.60 mm wide, the frontal shield perforated by numerous pseudopores, with a slightly larger pore on each side near the proximal corners of the orifice. Orifice slightly wider than long, the operculum dark, the proximal edge broad, gently convex in the middle or almost straight, the surrounding rim thin, raised. No oral spines or avicularia. No ovicells, the embryos brooded internally, crimson in colour.
Settlement season: Almost year round, with a spring-to-autumn increase in larval settling.
Distribution: *Watersipora arcuata* has been recorded at Opua, Whangarei Harbour, Marsden Point, Leigh Cove, Mahurangi Estuary, Auckland, Tauranga, New

Plymouth, Napier, and Nelson. Also known from the Galápagos Islands, Gulf of California, Southern and Baja California, Queensland, New South Wales, South Australia (*see* Gordon 1989). The type locality is San Diego Bay, Southern California.

Remarks: This is an interesting species with an interesting history. It apparently first arrived in New Zealand, in Auckland Harbour, between the summers of 1955–56 and 1958–59, evidently from Australia, where a *Watersipora* with an arcuate orifice had been studied by Wisely (1958) that was evidently the same species encountered in eastern Australia in the 1940s by Allen and Wood (1950) (Skerman 1960a). This arcuate form was at that time taken to be part of the range of variation of one or more species with a sinusoid orifice, commonly referred to as *Watersipora cucullata* (Busk). It was subsequently appreciated that the arcuate form warranted recognition as a separate species, and was named as such by Banta (1969a). In the New Zealand region *W. arcuata* has sometimes erroneously been referred to as *Dakaria subovoidea*, based on the work of Harmer (1957). In the event, *Dakaria* must be considered a junior synonym of *Watersipora*, and the species name *subovoidea* should be dropped since this species was inadequately characterised and is essentially unrecognisable — *see* discussions in Soule and Soule (1976, 1985) and Gordon (1989).]

The earliest records of an arcuate form like *Watersipora arcuata* are of specimens collected from near the southern tip of Baja California, Mexico, and from the Galápagos Islands. The species was not discovered in Southern California until January 1967, and it was absent (or merely overlooked in surveys) from there before 1960. Banta (1969b) therefore concluded that *W. arcuata* was indigenous to the tropics and subtropics of the eastern Pacific, was transported via shipping to Australasia, and, one to seven years later, was introduced into Southern California from there. This scenario raises the obvious question of why the species did not spread to Southern California sooner and more directly. Banta (1969b) suggested that the Australian populations might be of a mutant form better able to tolerate cooler temperatures.

In this regard, Soule and Soule (1985) have made some interesting observations on the fluctuating occurrence of *W. arcuata* in Southern California, noting that it seems to increase in abundance in El Niño years, which would be a better explanation for its apparent 'sudden arrival' in Southern California in the late 1960s than having been secondarily introduced by shipping from Australasia. The Soules (1985) also noted the apparent coincidental arrival of *W. arcuata* in New Zealand during the 1956–58 El Niño period, but El Niño events in New Zealand are accompanied by cooler-than-usual coastal water temperatures (Greig *et al.* 1988). Whatever the reasons for the timing of its entry to Australia and New Zealand, changes in the abundance and size of colonies have occurred in New Zealand too. After its arrival in the 1950s, *W. arcuata* spread within Auckland Harbour to become one of the dominant intertidal organisms at several locations, and, apparently from Auckland, it spread to several other locations — Bay of Islands by late summer 1972 (McKoy 1981), Mahurangi Estuary by autumn 1974 (Dinamani & Lenz 1977), New Plymouth by winter 1974 (Luckens 1975), and Napier and Nelson (though not at ports further south) by spring 1977 (DPG, pers. obs.). Since that time, *W. arcuata* has regressed dramatically. In April 1985 it was not seen at Nelson at all and in September 1986 it was found there only as dead colonies under crusts of newly discovered *Watersipora subtorquata* (DPG, pers. obs.). It was found at Mission Bay, Auckland, in February 1987, and, during our August 1988 survey, *W. arcuata* was also definitely found alive, or as freshly dead colonies, only at Opua (Bay of Islands), Marsden Point, and Tauranga Harbour. It has not been found since at any port south of Tauranga, whereas *W. subtorquata* (see below) now occurs as far south as Dunedin. Skerman (1960a, b) noted that live *W. arcuata* (as *W. cucullata*) was collected from the hulls of vessels from Australia docked at Auckland and unnamed ports south of Wellington in summer, but that only dead colonies occurred on such vessels at ports south of Wellington in winter. Temperature would therefore seem to be an important factor in the distribution and survival of *W. arcuata* populations near the edge of its range. A re-expansion of the range and abundance of *W. arcuata* in New Zealand shipping harbours during a prolonged period of higher average water temperatures, perhaps between El Niño events, cannot be ruled out, provided that it is not now outcompeted by *W. subtorquata*.

In Auckland Harbour, *W. arcuata* has been noted as settling on a variety of substrata, including rock, shell, wood, ascidians, sponges, other bryozoans, algae, steel, and glass (Gordon 1967).

Watersipora subtorquata (d'Orbigny, 1852)
(Plate 1, D; Plate 3, D, E; Plate 8, E)

Colony form: Encrusting, to erect and foliaceous.

Size: Small crusts to foliaceous growths half the size of a cabbage.

Description: More or less as for *W. arcuata* but less intensely black in colour; often dark greyish-black at the colony centre to dull orange beyond, with broad,

deep-orange margins. Zooids 0.74–1.50 mm long and 0.29–0.68 mm wide, the orifice with a distinct sinus, the proximal rim thin, raised, variable, often with curling edges. Operculum dark overall, with a darker mushroom-shaped area centrally. No spines, avicularia, or ovicells. Lophophore tentacles 24, orange in colour. Larva crimson. Ancestrula resembling later zooids.
Settlement season: More or less year round, with a spring-to-autumn peak.
Distribution: Occurs at almost every port in New Zealand sampled by us (and at Akaroa — Dr C.H. Hay) except for Onehunga, Oamaru, Bluff, and the west coast river ports. We did not encounter it at marinas in the Whangarei Town Basin although it does occur at Marsden Point. Overseas, its exact distribution is uncertain because of taxonomic difficulties, but it certainly occurs in Brazil, the West Indies, Bermuda, Cape Verde Islands, Japan, Torres Strait, and Great Barrier Reef (see Ryland 1974; Soule & Soule 1976; Gordon 1989). Gordon (1989) gives reasons for referring to the species as *Watersipora subtorquata* rather than *W. subovoidea*. The type locality is Rio de Janeiro.
Remarks: *Watersipora subtorquata* was first discovered in New Zealand in December 1982 when Ben J. Wilson, a student at the University of Otago, found colonies growing on experimental panels fixed at 30 cm below low spring tide under Victoria Wharf, Dunedin, and later on wharf piles at Carey's Bay, Port Chalmers.

The year of arrival of *W. subtorquata* is not known, but a collection of bryozoans from under Victoria Wharf in October 1977 by DPG did not yield this species. It was common at the Port of Wellington in June 1983, and not found at Bluff at that time (B.J. Wilson pers. comm.). It was first found at Auckland, by Mr John McCallum, in October 1984 at Westhaven Marina, and DPG collected it at Nelson in April 1985 and Napier in September 1986. As of this writing, *W. subtorquata* is more widespread than *W. arcuata* was at the peak of its distribution and presently outcompetes it where they co-occur. It settles on a variety of substrata including rocks, shells, glass, seaweeds, pilings, and painted and ferro-cement boat hulls.

Chiastosella watersi Stach, 1937
(Plate 9, A)

Colony form: Encrusting.
Size: To 3–4 cm diameter.
Description: Colony purplish-pink. Zooids 0.53–0.85 mm long and 0.23–0.56 mm wide, the frontal shield centrally imperforate, with conspicuous pores around the margin. Orifice with a rounded V-shaped sinus and grooved condyles, the tips of which project into the entrance to the sinus. Basally jointed oral spines 4–5, reduced to 2 in ovicelled zooids. Avicularia sporadic, borne singly, with a cross-bar. Ovicell recumbent, imperforate, but with a distal crescent of pores.
Settlement season: Not reported.
Distribution: Three Kings Islands, Cook Strait, Chatham Rise, Otago Heads, Bluff, Puysegur Bank; intertidal to 235 m depth. The type locality in New Zealand is not known.
Remarks: This endemic species (Gordon 1989) was observed by us on wharf pilings at Oamaru, the only known fouling situation for the species.

Schizoporella errata (Waters, 1878)
(Plate 9, B)

Colony form: Encrusting.
Size: To 2–3 cm in diameter.
Description: Colonies whitish-pink to reddish-brown, the zooids 0.40–0.60 mm long and 0.30–0.50 mm wide, the frontal shield evenly perforated by numerous pores, with a small prominence just proximal to the orifice. Orifice with a broad, rounded-V-shaped sinus. No oral spines. Avicularia paired or single, adjacent to the orifice, directed away from it. Ovicell prominent, with small pores laterally and radiating ridges.
Settlement season: No information in New Zealand.
Distribution: Opua, Bay of Islands, Waitemata Harbour. Also Mediterranean, west Africa, eastern Canada, North Carolina through the Caribbean to Brazil, Pacific coast of North America, Red Sea, Persian Gulf, South Australia (Powell 1970; Hayward & Ryland 1979; Brock 1982). The type locality is Naples, Italy.
Remarks: This species was first noted in New Zealand by R.E. Harger, who encountered it in Auckland Harbour and recorded it on cards in the marine reference collection of the University of Auckland in ?1960. It was subsequently reported on by Gordon (1967) (as *S. unicornis*). It is apparently of sporadic occurrence. During the present survey it was encountered only once, on the hull of a yacht at Opua, Bay of Islands.

Hippadenella cf. *margaritifera* (Lamouroux *in* Quoy & Gaimard, 1825)
(Plate 8, B)

Colony form: Encrusting.
Size: To 2–3 cm diameter.
Description: Orange calcareous crusts. Zooids 0.50–0.54 mm long and 0.30–0.36 mm wide, the frontal

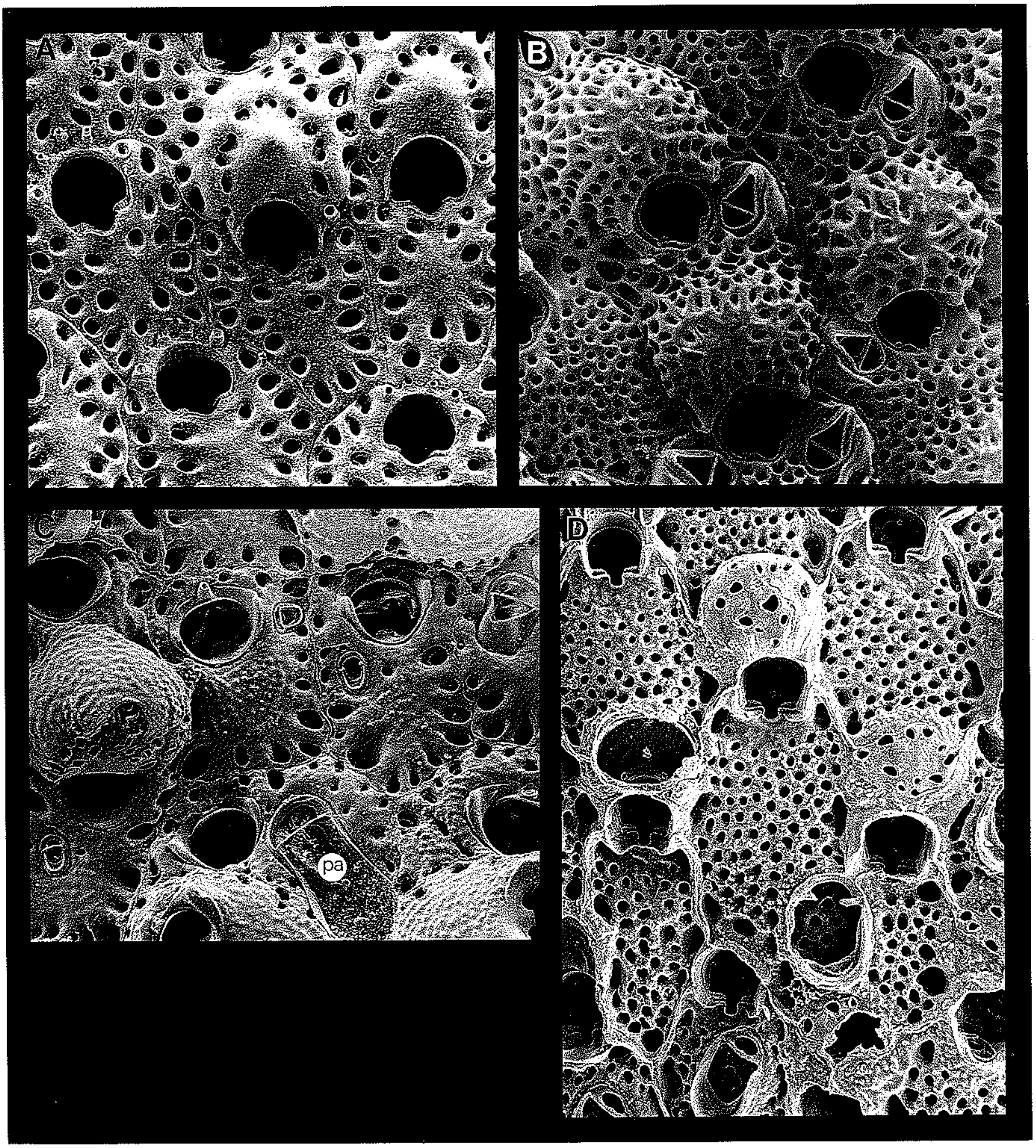

Plate 9. Encrusting Bryozoa: A, *Chiastosella watersi*, x 68. B, *Schizoporella errata*, x 82. C, *Parasmittina delicatula* x 59. D, *Schizosmittina cinctipora*, x 60. (pa = palatal surface of avicularium)

shield smooth, convex, rising to a broad, rounded eminence in front of the orifice, in which is set a small round avicularium with a cross-bar; pores around the margin of each zooid usually conspicuous, with small ridges between. Orifice roundly quadrangular; no oral spines. Giant avicularia occasional. Ovicell conspicuous, subglobular, smooth.
Settlement season: Not reported.
Distribution: In New Zealand, this species has been found only around Otago Peninsula, at Bluff (on the hull of one fishing boat), and near Oban, Stewart Island. The type locality of *H. margaritifera* is the Falkland Islands where it occurs on mussel shells.
Remarks: The New Zealand species differs from *H. margaritifera* in some details and is probably new. Only one small colony was encountered on a fishing boat during the present survey.

Parasmittina delicatula (Busk, 1884)
(Plate 9, C)

Colony form: Encrusting, to multilamellar and suberect.
Size: To 4–5 cm across.
Description: Pinkish-orange crusts, generally with an irregular surface in mature colonies. Zooids elongate-rectangular to subquadrate in outline, 0.48–0.78 mm long and 0.32–0.53 mm wide. Frontal shield in newly formed zooids almost smooth, distinctly granular in older zooids, with 7–9 pores along each lateral margin. Orifice with a straight-edged median tooth (lyrula) flanked by a pair of tiny thorn-like condyles; the lateral edges of the orifice raised somewhat and a single, basally jointed spine on the mid-distal rim in most zooids. Avicularia varied — generally small elongate-oval ones or occasional large avicularia approaching the length of a zooid, with a large palatal surface and a thin cross-bar; intermediate-sized ones also occur. Ovicell moderately large, the distal surface covered with a layer of secondary calcification, the proximal surface with about 20 small perforations.
Settlement season: Not reported.
Distribution: Throughout New Zealand from the Kermadec Ridge and Three Kings Islands to western Foveaux Strait, from the intertidal to 205 m depth. Also Victoria, New South Wales, Great Barrier Reef, Hawaii, Japan (*see* Soule & Soule 1973; Gordon 1984, 1989; Ryland & Hayward (in press).
Remarks: In the present survey, this species was found fouling wharf pilings at Marsden Point, where it is quite prominent at and below low tide.

Schizosmittina cinctipora (Hincks, 1883)
(Plate 9, D)

Colony form: Encrusting.
Size: To 2–3 cm diameter.
Description: Thin reddish-orange crusts, the zooids 0.42–0.63 mm long and 0.30–0.38 mm wide, the frontal shield somewhat flattened in newly formed zooids and evenly perforated by numerous small pores, with 2–4 larger pores along each lateral margin. Orifice sloping inwards distally, with a distinct sinus in the proximal rim; oral spines rare, only in some zooids at the colony margin. Older zooids often with secondary calcification which alters their appearance — the orifice lies deeper and there are fewer, larger pores in the frontal shield, along with small tubercles. Avicularia commoner on secondarily thickened zooids, elongate-oval in shape, from small to moderately large. Ovicell somewhat flattened, with a perforated frontal surface.
Settlement season: Not reported.
Distribution: Kermadec Ridge, North Island from Spirits Bay to Cook Strait, and South Island from Tasman Bay to Foveaux Strait, Stewart Island, and Auckland and Campbell Islands, intertidal to 253 m depth. The type locality in New Zealand is not known.
Remarks: This endemic species was encountered only once in the present survey, on the hull of a yacht at Dunedin.

Calloporina angustipora (Hincks, 1885)
Plate 10, A)

Colony form: Encrusting.
Size: To 3–4 cm diameter.
Description: Thin, bright-pink crusts, the zooids more or less diamond shaped, widest in the middle, 0.40–0.50 mm long and 0.30–0.38 mm wide. Frontal shield not very convex, more or less smooth with 8–9 conspicuous pores along each lateral margin and a slit-like median pore (ascopore) proximal to the orifice. Orifice D-shaped, the proximal border straight; 7–8 basally jointed spines around the curve of the orifice, of which 2–4 remain in ovicelled zooids. Avicularia single or paired, near the widest part of the zooid, directed laterally. Ovicell somewhat flattened, with a pitted crescentic furrow distally. Larva reddish-orange.
Settlement season: Late August to early March in the Leigh marine reserve (Gordon 1970).
Distribution: New Zealand region from the Kermadec Ridge and Three Kings Islands to Chatham Island and Foveaux Strait; intertidal to 235 m depth. The type locality is Napier (Brown 1952).

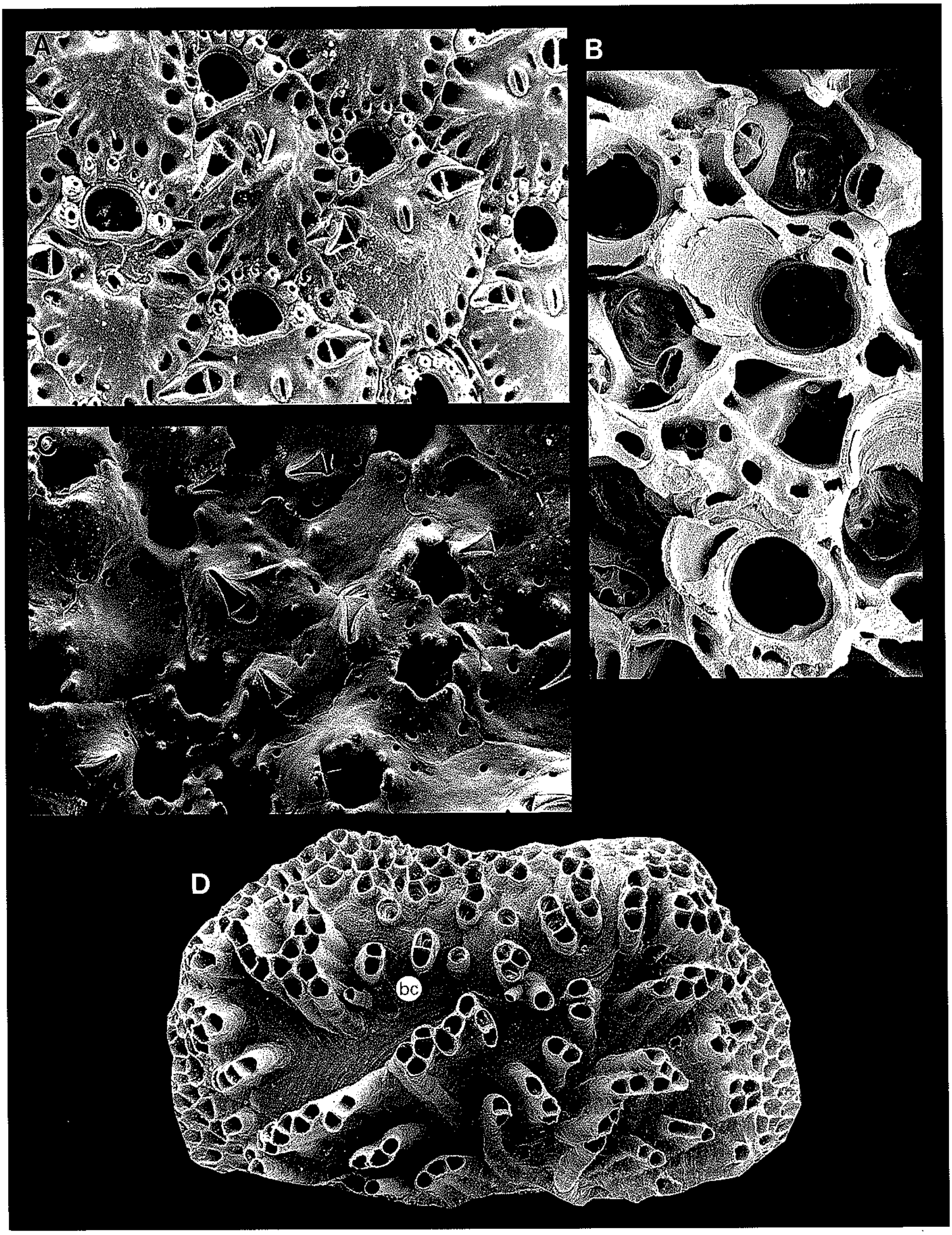

Plate 10. Encrusting Bryozoa: A, *Calloporina angustipora*, x 100. B, *Celleporina proximalis*, x 133. C, *Rhynchozoon larreyi*, x 50. D, *Tubulipora* sp., x 27. (as = ascopore; bc = brood chamber)

Remarks: This endemic species was encountered only once in a fouling situation, on a dinghy at Port Chalmers. Larvae can settle on rock, shell, and glass (Gordon 1968).

Celleporina proximalis (Uttley & Bullivant)
(Plate 10, B)

Colony form: Encrusting, nodular.
Size: Small, generally less than 10 mm diameter.
Description: Colony whitish, the zooids irregularly orientated, with the orifice tending to be somewhat sunken and concealed by a rim that is part of a tall, tapering, proximal projection, partly surrounding the orifice at its base and with a small avicularium near its tip; collectively, these projections give the colony surface a somewhat spiky appearance. Spatulate avicularia not yet known in this species. Ovicells hood-like, with a round or semicircular frontal area with short radial ribbing.
Settlement season: Not known.
Distribution: Cook Strait, Marlborough Sounds. Chatham Islands, Dunedin, Puysegur Point; low tide to 220 m depth.
Remarks: This species is common subtidally on hydroids where it forms small spherical colonies 2–3 mm diameter; if encrusting, the colony is more mound-like. It was found on the hulls of pleasure craft at Picton and Dunedin.

Rhynchozoon larreyi (Audouin)
(Plate 3, B; Plate 10, C)

Colony form: Encrusting.
Size: To about 3 cm diameter.
Description: Pale pinkish-white to reddish crusts of shiny, porcellanous zooids; these 0.42–0.88 mm long and 0.34–0.58 mm wide, more or less recumbent at the colony margin but tending to suberect and irregularly disposed in the colony centre. Orifice somewhat concealed by one or more tubercles or protuberances in front of it, and a transversely set aviculiferous structure above it. Frontal shield more or less smooth, with a row of 2–5 pores along each zooidal margin. Additional avicularia may occur on the frontal side of each zooid, generally only one per zooid, with a pointed mandible, directed proximally or obliquely so. Ovicell becoming somewhat immersed in zooidal calcification, with only a descending frontal area visible. Lophophore tentacles 12. Larva orange.
Settlement season: Year round in the Leigh marine reserve.
Distribution: Widespread throughout New Zealand from Spirits Bay to Fiordland and Foveaux Strait from the intertidal to 235 m depth. Also Turkey, Red Sea (*see* Ristedt & Schuhmacher 1985), Sri Lanka, Indonesia, Lord Howe Island, Victoria (*see* references in Gordon 1989).
Remarks: This common intertidal species was encountered on pilings and rocks and glass under wharves at Leigh Cove and Auckland Harbour.

Tubulipora sp.
(Plate 10, D)

Colony form: Encrusting.
Size: About 0.5 cm diameter.
Description: Colony whitish to pale bluish-white, made up of zooids which have an encrusting adherent portion and an erect tubular portion, the zooidal wall evenly perforated by tiny pores. Openings of tubes circular, without an operculum. Brood chamber inflated between the tubes, densely perforated with small pores, with a short tube for larval release that has a somewhat oval opening.
Settlement season: Possibly in winter, as indicated by Skerman (1958).
Distribution: The exact distribution of this species in New Zealand is uncertain owing to taxonomic difficulties in identifying *Tubulipora* species generally. Also Skerman (1958) did not illustrate the colony he encountered on an experimental panel at Lyttelton. The colony illustrated in plate 10, D was from Auckland.

DISCUSSION

New Zealand Bryozoan Fouling Diversity

Of the 40 species of bryozoans included in this report, 11 are described in the OECD catalogue of main marine-fouling bryozoans encountered on ships coming into European waters (*see* Ryland 1965). A further two species in the OECD catalogue (*Aetea truncata, Scruparia chelata*) occur in the New Zealand region (Hastings 1941; Gordon 1986) but have never been encountered here in a fouling situation. One other species mentioned in the catalogue (*Watersipora subovoidea*) may be synonymous with *Watersipora subtorquata,* in which case 14 of the 31 fouling species then listed for European waters (45%) occur in New Zealand at the present time. More of them may yet come to be recorded for New Zealand, based on past trends, including the fact that nine other exotic species, not in the OECD catalogue, have apparently been introduced to New Zealand. These comprise *Aeverrillia armata, Amathia distans, Electra tenella,* and *Watersipora arcuata,* and, also known from European (especially Mediterranean) waters, *Anguinella palmata, Buskia nitens, Buskia socialis, Conopeum seurati,* and *Tricellaria occidentalis.* Of the 105 fouling-bryozoan species listed by Mawatari and Mawatari (1986) for Japan, 11 occur in New Zealand, viz. *Amathia distans, Bowerbankia imbricata, B. gracilis, Zoobotryon verticillatum, Buskia nitens, Electra tenella, Bugula flabellata, B. neritina, Tricellaria occidentalis, Cryptosula pallasiana, and Watersipora subtorquata.*

The most ubiquitous fouling bryozoans in New Zealand, occurring at a significant number of the ports and berthages (nine or more of the 20 listed in Table 1) and which are also the greatest nuisance species, are, not surprisingly, well-known subcosmopolitan species. In order of their chronological introductions into New Zealand these are — *Cryptosula pallasiana, Bugula neritina, Bugula flabellata, Tricellaria occidentalis, Bugula stolonifera, Conopeum seurati,* and *Watersipora subtorquata.* As Ryland (1965) stated concerning bryozoan fouling at northern hemisphere ports, "Published works indicate a small and constant selection of species as the worst offenders", although, for some parts of the world, bryozoans show the greatest species diversity among fouling organisms and the actual species composition does shift somewhat from the tropics into temperate waters since not all fouling species are eurythermal.

The species diversity of New Zealand marine-fouling bryozoans (40) is greater than that recorded by Ryland (1965) for European waters (31), but considerably less than that recorded by Mawatari and Mawatari (1986) for Japan (105). This may be explained by the fact that the survey of Japanese marine-fouling bryozoans included examination of important anthropogenic substrata such as fixed shore nets for fishing or pisciculture and structures for culture of pearl oysters. The present report includes bryozoans from ropes involved in the cultivation of mussels in Pelorus Sound, but not, for example, cages for salmon culture, as in Big Glory Bay, Stewart Island. If one includes, however, species which may foul (sometimes quite markedly) the steel and nylon-netting traps for rock lobster (*Jasus edwardsii*), then the diversity increases substantially. Appendix 3 lists 61 species (of which only seven are described above from ports and harbours) collected from rock-lobster traps (craypots) from boats operating out of Moeraki, Port Chalmers, and Bluff.

The provenance of the exotic introductions and the exact year of their entry (or entries) into New Zealand can only be guessed at. From Table 2 it can be seen that exotic bryozoans have been coming into New Zealand since at least 1898, and it is also apparent that all introductions have been reported only because of studies of marine-fouling organisms generally or of bryozoans specifically, especially since the late 1940s. Some northern hemisphere species (e.g., *Anguinella palmata, Watersipora arcuata*) may have reached New Zealand via Australia, where they were earlier recorded (e.g., Allen 1953; Allen & Wood 1950, respectively). Japan may have been the provenance for *Watersipora subtorquata,* where it has been known for many years (as *W. cucullata/ subovoidea* [e.g., Mawatari 1952a,b; Kubota & Mawatari 1985; Mawatari & Mawatari 1986]). Inevitably, many, if not most, of the exotic species will have been in New Zealand for many years prior to their having been recorded, especially for the earliest arrivals. The lesson in this, given the dramatic effects on harbour ecology that have been documented for invasive species (Dromgoole & Foster 1983), is that routine monitoring of the biota of ports and harbours is highly desirable.

Table 2.

Earliest-known occurrences of exotic marine-fouling bryozoans in New Zealand ports and harbours (in chronological order of entry).

Species	Year
Cryptosula pallasiana	1898
Bugula neritina	1949
Bugula flabellata	?1949
Tricellaria occidentalis	?1954
Watersipora arcuata	?1957
Anguinella palmata	?1960
Amathia distans	?1960
Zoobotryon verticillatum	?1960
Schizoporella unicornis	?1960
Bugula stolonifera	1962
Conopeum seurati	pre-1963
Bowerbankia imbricata	1967
Bowerbankia gracilis	1967
Buskia nitens	pre-1968
Aeverrillia armata	pre-1968
Electra tenella	1977
Buskia socialis	1977
Watersipora subtorquata	1982
Bugula simplex	1988

Bryozoan invasions show the same kinds of epidemic and endemic aspects as those of other organisms (Mollison 1986). Epidemic aspects are positively exemplified by the seven major nuisance species (*see* above), including the ability to invade, the competitive ability for initial success, and, when successful, the rate and manner of spread. Contrasting endemic aspects of invasion (competitiveness to spread and, if successful, the level and pattern of persistance) are illustrated on the one hand by *Cryptosula pallasiana*, well-established for at least a century, and on the other by *Watersipora arcuata*, which has shown a spectacular decline after an initially successful invasion. As with other organisms, bryozoan invasions are subject to stochastic processes, i.e., pure serendipity, especially in the arrival stages (Gray 1986). Although in hindsight one might acceptably explain many arrivals and subsequent establishment, the predictive power of these explanations is low. Invasive marine-fouling bryozoans are reminiscent of the specialist colonisers among dicotyledonous flowering plants, many of which are relatively short-lived and depend upon chaotic distribution by wind (cf. water) or by human activities (Grime 1986).

Crawley (1986) has shown how, for many kinds of invading species, successful establishment is more likely where levels of competition (for food or space) and predation are lowest. Occhipinti Ambrogi (1991) has argued that these criteria are applicable to the successful invasion of *Tricellaria inopinata* (i.e., *occidentalis*) in the Venice Lagoon, but in the much more speciose and higher-salinity habitats of New Zealand harbours additional criteria must be considered, such as strategies of growth and reproduction (*see* Ross 1979; Dyrynda & Ryland 1982). In terms of r- and K-patterns of life history, the former end of the spectrum would be exemplified by a species that puts a greater relative proportion of energy and nutrients into the rapid production of gametes than into each individual zooid. Such species tend to be faster growing and uncalcified or lightly calcified, with proportionally less colonial integration. They also tend to be opportunistic and can utilise transient substrata. This would go some way toward explaining why buguloideans and ctenostomes are over-represented in many fouling faunas. It may also be significant in this regard that the two most ubiquitous fouling ascophorans (*Cryptosula* and *Watersipora*) lack polymorphic elaborations such as avicularia and ovicells. It appears that bryozoans as suspension feeders lead an energetically marginal existence (Lidgard 1981; Harvell 1986; Gordon *et al.* 1987b), and any contribution that alters the mean metabolic efficiency of individual zooids is highly significant. Thorpe (1979) has calculated that almost negligible variations in this efficiency could lead to massive net variations in, for example, larval production, which in turn would be reflected in ecological competitiveness and survivorship.

Ameliorating the Problem

Insofar as bryozoans are one of the most significant groups of fouling animals in New Zealand ports and harbours, what steps can be taken to reduce the likelihood or impact of fouling, especially of boat hulls? As mentioned in the introduction, the most critical stage in bryozoan fouling is that of larval settlement and metamorphosis, therefore first steps in mitigating the problem should focus on this stage. We list below ways in which this can be done. Obviously, there are problems associated with all of these — the purpose here is merely to highlight what is possible.

1. *Mooring practices.* Most fouling bryozoans have short-lived coronate larvae with limited powers of dispersal. Heaviest settlement occurs in proximity to large numbers of breeding colonies such as can occur on pier pilings or marina pontoons. Boats moored in more open water are less prone to bryozoan fouling. But this is not only because the dispersal powers of coronate larvae are weak but also because delaying settlement in such larvae can lead to reduced competence in metamorphosis and subsequent growth (Crisp 1974; Woollacott *et al.* 1989; Orellana & Cancino 1991). The problem of fouling mainly arises of course when boats are neither moving through water nor are out of water but when they are at rest. An imaginative solution based on this simple fact and that of the limited availability of marina space has been developed in Japan, utilising a mechanical parking device that routinely lifts boats in and out of water and cradles them between use. Thus whenever boats *are* in water they are mostly in motion. This method is not popular, however, and is presently in use only at one crowded marina in Tokyo.

2. *Osmotic controls.* Although many marine bryozoans are euryhaline to a greater or lesser extent, none can tolerate fresh or near-fresh water and salinities as low as 10–12 psu are probably lethal for most species. We encountered no fouling bryozoans at the small berthages in the Whakatane, Waitara, and Hokitika river estuaries, for example, or at the larger river ports of Westport and Greymouth. At these places, green-algal films were the main fouling organisms in evidence. The only bryozoan encountered at

Wanganui, *Cryptosula pallasiana*, was rare, although here turbidity is at least as important as hyposalinity. Generally speaking, even boats fouled with mature (reproducing) bryozoan colonies would benefit from temporary mooring in fresh or near-fresh water. At the other extreme, bryozoan larvae are sensitive to hypersalinity (Soule & Soule 1977; Reed 1988). The Soules have described how cultured oysters fouled by *Bowerbankia gracilis* can be defouled by immersing the shellfish in a vigorously aerated saturated NaCl dip for 1 minute then air-drying them for 1 hour. Hypertonicity causes deciliation (Reed 1988). Since receptor molecules in the cilia may be the means by which cues leading to settlement are detected, this may have application to fouling control.

3. *Physical/chemical deterrents*. In general, larvae of fouling bryozoans avoid wettable surfaces (Eiben 1976; Loeb 1977; Mihm *et al.* 1981; Woollacott 1984; Rittschof & Costlow 1987a, b, 1988; Roberts *et al.* 1991), so paint or varnish formulations that are hydrophobic are to be preferred over hydrophilic ones, although the presence of a film of attractive bacteria can counter avoidance by bryozoan larvae. Self-ablative (sacrificial) coatings may be useful in this situation.

Bryozoan larvae are far less tolerant of biocides (e.g., heavy metals) than established colonies. Many different types of coatings that have been produced over the past several decades have been formulated with invertebrate-larval sensitivities in mind. In recent years some revolutionary new coatings have been developed that have proven very effective in antifouling, such as copolymer paints that self-polish (hydrolyse) on passage through water, releasing biocide (Lorenz 1978; de la Court 1984; Miller 1984). Because of the toxic effect of biocides in the environment, suggestions have been made for investigation into the use of natural biochemicals to deter settlement and metametamorphosis (Houghton 1970; Minichev & Seravin 1988). As Bakus (1988) remarked, sessile marine organisms with exceptionally clean surfaces are worth investigating for antifouling compounds. Such chemicals have already been reported from limited studies on bryozoan chemical defences. Al-ogily and Knight-Jones (1977) and Dyrynda (1983, 1985) have described antifouling activity (antibiotic and larvotoxic) in three species of gymnolaemate bryozoans, based on the presence of novel alkaloids and terpenoids (*see also* references in Colon-Urban *et al.* 1991). Rittschof and Costlow (1987), noting how some bacterial films can be repellent to bryozoan larvae, have suggested that promoting the growth of key micro-organisms on specific surfaces might be used in fouling management. Already, genetic studies of fouling micro-organisms have been undertaken to ascertain what factors are involved in microbial adhesion with the aim of deterring attachment of bacteria and bacteriophilic higher organisms (Simon *et al.* 1988).

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Appendix 1
Classification of New Zealand marine-fouling bryozoans

Phylum BRYOZOA
Class GYMNOLAEMATA
Order CTENOSTOMIDA
Superfamily ALCYONIDIOIDEA
Family ALCYONIDIIDAE
Alyconidium sp.

Superfamily ARACHNIDIOIDEA
Family NOLELLIDAE
Anguinella palmata van Beneden

Superfamily WALKERIOIDEA
Family AEVERRILLIIDAE
Aeverrillia armata (Verrill)

Superfamily VESICULARIOIDEA
Family VESICULARIIDAE
Amathia distans Busk
Bowerbankia gracilis Leidy
Bowerbankia imbricata (Adams)
Zoobotryon verticillatum (delle Chiaje)

Family BUSKIIDAE
Buskia nitens Alder
Buskia socialis Hincks

Order CHEILOSTOMIDA
Suborder SCRUPARIINA
Superfamily SCRUPARIOIDEA
Family SCRUPARIIDAE
Scruparia ambigua (d'Orbigny)

Suborder MALACOSTEGINA
Superfamily MEMBRANIPOROIDEA
Family MEMBRANIPORIDAE
Conopeum seurati (Canu)

Family ELECTRIDAE
Electra pilosa (Linnaeus)
Electra tenella (Hincks)

Suborder NEOCHEILOSTOMINA
Superfamily CALLOPOROIDEA
Family CALLOPORIDAE
Crassimarginatella fossa Uttley

Family CHAPERIIDAE
Chaperia granulosa Gordon
Chaperiopsis cervicornis (Busk)

Superfamily BUGULOIDEA
Family BUGULIDAE
Bugula flabellata (Thompson *in* Gray)
Bugula neritina (Linnaeus)
Bugula simplex Hincks
Bugula stolonifera Ryland

Family BEANIIDAE
Beania plurispinosa Uttley & Bullivant
Beania sp.

Family CABEREIDAE
Caberea rostrata Busk
Caberea zelandica (Gray)
Tricellaria occidentalis (Trask)

Suborder ASCOPHORINA
Superfamily HIPPOTHOOIDEA
Family HIPPOTHOIDAE
Celleporella bathamae (Ryland & Gordon)

Superfamily ARACHNOPUSIOIDEA
Family ARACHNOPUSIIDAE
Arachnopusia unicornis (Hutton)

Superfamily UMBONULOIDEA
Family EXOCHELLIDAE
Escharoides angela (Hutton)

Superfamily SCHIZOPORELLOIDEA
Family CRYPTOSULIDAE
Cryptosula pallasiana (Moll)

Family WATERSIPORIDAE
Watersipora arcuata Banta
Watersipora subtorquata (d'Orbigny)

Family SCHIZOPORELLIDAE
Chiastosella watersi Stach
Schizoporella errata (Waters)

Family SMITTINIDAE
Hippadenella cf.*margaritifera* (Lamouroux *in* Quoy and Gaimard)
Parasmittina delicatula (Busk)
Schizosmittina cinctipora (Waters)

Family MICROPORELLIDAE
Calloporina angustipora (Hincks)

Superfamily CELLEPOROIDEA
Family CELLEPORIDAE
Celleporina proximalis (Uttley & Bullivant)

Family PHIDOLOPORIDAE
Rhynchozoon larreyi (Audouin)

Class STENOLAEMATA
Order TUBULIPORIDA
Superfamily TUBULIPOROIDEA
Family TUBULIPORIDAE
Tubulipora sp.

Appendix 2.
Glossary of technical terms used in the descriptions of marine-fouling bryozoans.

ancestrula The first zooid of a colony, formed by the metamorphosis of the larva; generally differing in size and morphological characteristics from the other zooids in the colony.

avicularium A zooidal polymorph, generally smaller than ordinary feeding zooids, in which the zooidal operculum is modified as a mandible; of various shapes, sometimes bird's-head-like (e.g., Plate 5, E; Plate 6, B).

brood chamber In gymnolaemates, an enclosed space bounded by extensions of zooidal body walls, within which embryos are housed during maturation to larvae; topologically exterior to the maternal zooidal body cavity, able to be occupied by seawater. In stenolaemates (e.g., *Tubulipora*), a coelomic chamber in which embryos develop into larvae (e.g., Plate 10, D).

condyles A pair of tooth-like protuberances at the sides of the zooidal orifice on which the operculum in hinged.

cryptocyst A calcareous wall (shield) or shelf underlying the frontal membranous wall in cheilostomes (e.g., Plate 7, A).

frontal shield Protective and supportive calcareous wall in cheilostomes; either an exterior calcification in place of the membranous frontal wall, or overlying or underlying it (e.g., Plate 7, D; Plate 8, E).

kenozooid In cheilostomes, an enclosed chamber lacking organs and, generally, muscles.

lophophore The tentaculated feeding apparatus of bryozoans (e.g., Plate 1, A).

operculum A lid-like flap of the body wall that is hinged, allowing passage of the lophophore and anterior part of the body to be everted (e.g., Plate 7, B).

orifice That part of the body wall, including the operculum or some other kind of closing apparatus, through which the lophophore is protruded and retracted (e.g., Plate 7, D).

ovicell In cheilostomes, a structure, comprising extensions of zooidal body walls, that encloses the brood chamber in which embryos are matured (e.g., Plate 5, F, G; Plate 6, D).

palate The membranous surface of an avicularium that is exposed when the mandible is folded back in the open position (e.g., Plate 9, C).

pleated collar In ctenostomes, a pleated membranous fold of the anterior body wall that widens upon emergence of the lophophore to feed but constrict together to form part of the closing apparatus of the orifice upon lophophore retraction.

pseudopore A pore that penetrates all or part of the frontal shield or cryptocyst in cheilostomes.

scutum Flattened protective spine over the membranous frontal wall in some cheilostomes (e.g., Plate 6, D).

sinus A concavity i nthe proximal rim of the orifice in many cheilostomes; sealed, when closed, by a proximal tab of the operculum (e.g., Plate 8, E).

vibraculum A highly modified, elongate, type of avicularium (e.g., Plate 6, E) in which the mandible is a long bristle.

zooid One of the physiologically connected, replicated units of the bryozoan colony; either a feeding and/or reproductive unit or one of a variety of polymorphs (e.g., kenozooid, avicularium, vibraculum, rootlet, etc.).

Appendix 3.

Bryozoan species (listed alphabetically by family) fouling rock-lobster traps from boats operating out of Moeraki (M), Port Chalmers (off Cape Saunders [CS]), and Bluff (off Lookout Point [LP]). Descriptions of most of these species can be found in two memoirs by Gordon (1986, 1989).

* Species occurred on algae attached to the traps.

§ Represents a new record for New Zealand

GYMNOLAEMATA

Aeteidae
Aetea ?australis Jullien M, CS*

Arachnopusiidae
Arachnopusia unicornis (Hutton) CS

Beaniidae
Beania intermedia (Hincks) CS

Bugulidae
Bicellariella turbinata (MacGillivray) CS§
Dimetopia barbata (Lamouroux) M, CS, LP
Dimetopia cornuta Busk M, CS

Cabereidae
Amastigia funiculata (MacGillivray) LP
Caberea darwinii Busk M, CS
Caberea darwinii guntheri Hastings CS
Caberea zelandica (Gray) CS, LP
Canda arachnoides Lamouroux M, CS
Emma rotunda Hastings M, CS, LP
Emma triangula Hastings CS, LP
Emma tricellata (Busk) CS
Scrupocellaria ornithorhyncus Thomson CS, LP
Tricellaria aculeata (d'Orbigny) M
Tricellaria monotrypa (Busk) M, CS, LP

Calloporidae
Corbulella corbula (Hincks) LP
Foveolaria cyclops (Busk) CS, LP

Calwellidae
Calwellia bicornis Thomson CS
Calwellia gracilis Maplestone CS, LP

Catenicellidae
Catenicella elegans Busk CS, LP
Claviporella aurita (Busk) CS
Costaticella hastata (Busk) M, CS
Costaticella solida Levinsen M, CS
Cribricellina cribraria (Busk) M, CS
Orthoscuticella innominata Gordon CS
Orthoscuticella margaritacea (Busk) M, CS, LP
Orthoscuticella ventricosa (Busk) CS
Pterocella scutella (Hutton) M, CS
Scalicella crystallina (Thomson) M, CS, LP

Cellariidae
Cellaria pilosa (Kirchenpauer) M, CS
Cellaria tenuirostris (Busk) LP

Celleporidae
Celleporina cribrillifera (Hincks) LP
Galeopsis polyporus (Brown) LP
Osthimosia amplexa Gordon CS
Osthimosia avicularis Gordon CS

Chaperiidae
Chaperia ciliata (MacGillivray) CS§

Cribrilinidae
'Figularia' spinea Brown LP

Exochellidae
Escharoides angela (Hutton) LP
Exochella armata (Hincks) M, LP*

Hippoporinidae
Hippoporina rostrata (MacGillivray) LP
Metroperiella mucronifera (Powell) LP

Hippothoidae
Celleporella bathamae (Ryland & Gordon) LP*

Margarettidae
Margaretta barbata (Lamarck) LP

Microporidae
Manzonella lepida (Hincks) LP

Phidoloporidae
Phidolopora avicularis (MacGillivray) CS, LP
Reteporella sp. CS

Schizoporellidae
Chiastosella watersi Stach LP

Scrupariidae
Scruparia ambigua (d'Orbigny) M, CS*

Smittinidae
Schizosmittina cinctipora (Hincks) LP
Schizosmittina vitrea (MacGillivray) LP§
Smittina purpurea (Hincks) CS
Smittoidea maunganuiensis (Waters) LP

STENOLAEMATA

Crisiidae
Bicrisia edwardsiana (d'Orbigny) M, CS

Lichenoporidae
Disporella gordoni Taylor, Schembri, & Cook LP
Lichenopora novaezelandiae (Busk) CS

Mecynoeciidae
Mecynoecia sp. CS

Theonoidae
Telopora buski d'Hondt CS

Tubuliporidae
Idmidronea sp. LP
Tubulipora sp. LP*