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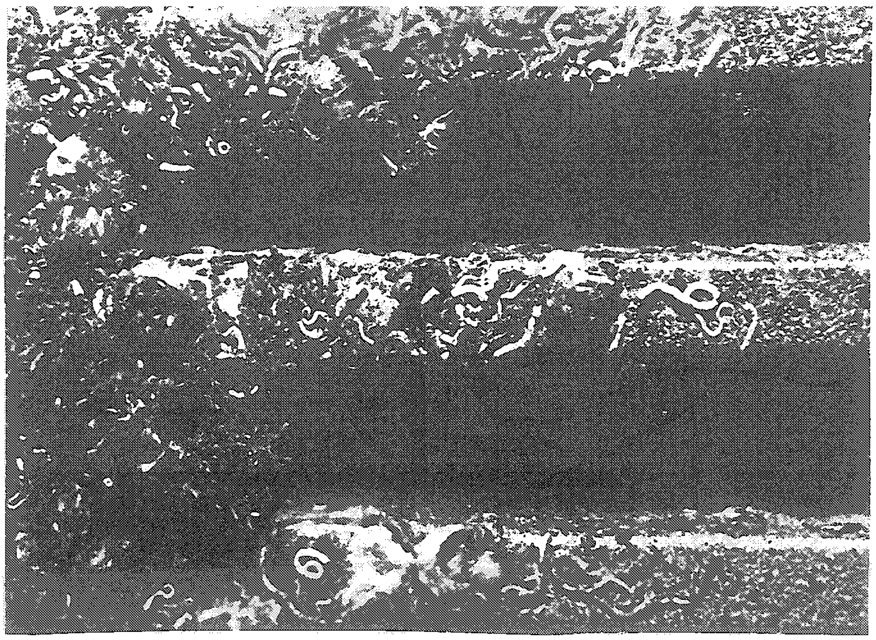

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Cover: Mussels, tubeworms, and barnacles growing on an intake grill on a "clean" ship. Even the best maintained ships are vectors for adventives. Photograph by Steve Mercer

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Abstract

Cranfield, H. J., Gordon, D. P., Willan, R. C., Marshall, B. A., Battershill, C.N., Francis, M. P., Nelson, W. A., Glasby, C. J., & Read, G. B. 1998: Adventive marine species in New Zealand. *NIWA Technical Report 34.* 48 p.

We surveyed the published literature, unpublished reports, and personal communications from systematists on the marine organisms in New Zealand and tested the biogeographical data against nine criteria developed by Chapman and Carlton to identify adventive species. We found 148 species that have been introduced into New Zealand accidentally and that met at least three of these criteria. The types of organisms represented include seaweeds and estuarine grasses among plants, and representatives of several animal phyla ("Protozoa", Porifera, Cnidaria, Annelida, Mollusca, Arthropoda, Entoprocta, Bryozoa, Chordata): 69% of these adventives probably arrived in New Zealand as fouling organisms on vessel hulls, while only 3% probably arrived in ballast water. A further 21% may have arrived by either mechanism, 3% probably arrived in sand ballast, and the remaining 4% arrived in a variety of ways. Although increased vessel speed, faster port turnaround times, and more effective antifouling paints have made it more difficult for exotic species to reach New Zealand in hull fouling, similar numbers of adventives that arrived in hull fouling have become established in New Zealand over the last 40 years as in the previous 50 years.

Three species of *Spartina* and quinnat salmon, *Oncorhynchus tshawytscha*, became established after being deliberately introduced. Seven other deliberately introduced species did not become established. We discuss the reasons for the failure of these introductions and for the failure of many of the species that have reached New Zealand in hull fouling to become established here, as well as why the successful introductions became established. The data suggest that the repeated introduction of an exotic species, the enclosed nature of the receiving water, and the nature of the species themselves have all been important for successful establishment of adventives in New Zealand.

This is a preliminary list of adventive species as other groups of the marine biota await investigation. Furthermore, numbers of cosmopolitan species in New Zealand, currently regarded as part of the native biota, may prove to be adventives that arrived here in the sailing ship era and spread widely at that time.

Introduction

Over the last 30 years many exotic marine species have entered New Zealand waters, spread rapidly from the point of introduction, and become pests. The success of these recent introductions shows how readily exotic species can become established in the New Zealand marine environment. The arrivals in recent years have been well documented because of their conspicuousness and rapid spread. However, many more exotic species were introduced accidentally by shipping during the late 18th century and in the early 19th century before the New Zealand fauna was well known, so their spread has not been observed or recorded. The most successful species may have spread rapidly around the entire New Zealand coast and are now likely to be in equilibrium with the native biota and so widespread that they cannot be readily identified as introductions. The less successful species introduced in the 18th and 19th centuries have characteristically very limited distributions that today render them readily identifiable as adventives.

Investigations of adventive species in other parts of the world have shown that most introductions of marine organisms took place in the era of sailing vessels. It is believed that entire marine communities were introduced in hull fouling of sailing vessels during this period (Chapman & Carlton 1991). As the New Zealand marine algal flora has become better known, the very limited distribution of some species in early ports and roadsteads suggests that a number of them were introduced on sailing vessels late last century (Adams 1983, 1994, Nelson 1994a). Gordon & Mawatari (1992) reviewed the fouling Bryozoa found in New Zealand and suggested that some of them may have also arrived in New Zealand in the sailing ship era. These data point to the likelihood that numerous species in other marine groups were also introduced in the late 18th and early 19th centuries in the same way, though other vectors have been reported.

Many algal and bryozoan species now identified as introductions were not recognised as such earlier because the marine fauna at the time of their arrival was either undescribed or only poorly known (*cf.* Carlton 1989, Chapman & Carlton 1991). Species introduced in the last two decades have been much more obvious interlopers because the marine fauna was by then better known and because of the size, spectacular spread, and local abundance of some of the introduced species (e.g., *Crassostrea gigas, Ficopomatus enigmaticus, Undaria pinnatifida,* and *Musculista senhousia*) made them impossible to overlook (*see* Dinamani 1971, Dromgoole & Foster 1983, Willan 1985, 1987, Hay & Luckens 1987, Read & Gordon 1991, Probert 1993, Nelson 1994a). The most recent arrivals came either as ship fouling or from larvae or propagules discharged from ballast water carried to New Zealand in unladen vessels (*cf.* Hutchings *et al.* 1987, Kelly 1993, Nelson 1995).

Toxic algal blooms in New Zealand (Mackenzie 1997) and pests introduced into fisheries and areas of aquaculture elsewhere (Carlton 1979, 1992 Rosenthal 1980, Stewart 1991, Sindermann 1993) show how vulnerable New Zealand fisheries and aquaculture could be to noxious new species introduced accidentally by humans. New Zealand needs to continue to develop strategies to protect the country from the further introduction of exotic marine species. To help develop these strategies we need to learn more about the exotic species known to have been introduced into New Zealand. This report identifies and documents 159 species within the New Zealand marine biota that are adventive in New Zealand. It tabulates and assesses the evidence for adventism, assesses some of the life history strategies and the nature of the New Zealand habitat of adventive species, and assesses how they arrived here and what other species arrived here but have failed to establish. These data will help our understanding of how some species became established and widespread in New Zealand waters, why some species remained localised around sites of introduction, and why some species that arrived have failed to establish. The characteristics important for the establishment of exotic species reaching New Zealand are identified.

Methods

Chapman & Carlton (1991) investigated the taxonomy and worldwide distribution of the isopod *Synidotea laevidorsalis*, originally described in 1897 as an endemic inhabitant of San Francisco Bay. They established that this species was conspecific with populations in China and the Atlantic coast of South America, and that it had originally spread from China to San Francisco, and from there to South America, as a fouling organism on the hulls of sailing vessels transporting Chinese labourers to California between 1849 and 1888 during the gold rush. Chapman and Carlton developed 10 objective criteria to successfully test the adventism of *S. laevidorsalis*. They later developed and tested a further hypothesis that adventive populations of *S. laevidorsalis* would be found in Brisbane or Sydney, Australia (Chapman & Carlton 1994). They identified such populations in Twofold Bay, Queensland, and Sydney Harbour, as well identifying a further adventive population in the Gironde estuary, France (Chapman & Carlton 1994). They merged 2 of the 10 criteria developed earlier, and these 9 criteria (6 related to national distribution, 3 to international distribution) have been adopted in the present report to test for adventism of the New Zealand marine biota. The present investigation reviewed the published literature and unpublished reports and used personal communications and the experience and knowledge of the authors to collate the biogeographic data required to test these criteria.

The New Zealand distribution of each of the species was tested by the six criteria:

1. **Has the species suddenly appeared locally where it has not been found before?**
2. **Has the species spread subsequently?**
3. **Is the species' distribution associated with human mechanisms of dispersal?**
4. **Is the species associated with, or dependent on, other introduced species?**
5. **Is the species prevalent in, or restricted to, new or artificial environments?**
6. **Is the species' distribution restricted compared to natives?**

The worldwide distribution of the species was tested by a further three criteria:

7. **Does the species have a disjunctive worldwide distribution?**
8. **Are dispersal mechanisms of the species inadequate to reach New Zealand, and is passive dispersal in ocean currents unlikely to bridge ocean gaps to reach New Zealand?**
9. **Is the species isolated from the genetically and morphologically most similar species elsewhere in the world?**

We record the results for all species that met at least three of these criteria. The 20 species that did not become established after entering New Zealand waters as part of fouling assemblages have been included in the Results and Discussion so that factors implicated in their failure to establish may be identified and used to develop strategies to protect New Zealand from future invaders. Only one of the eight deliberately introduced marine organisms became naturalised, but these species are included in the Results and Discussion so factors implicated in the general failure can be contrasted with factors important in the one success.

Results

The probable native range of each species, the date it probably arrived in New Zealand, the distribution of the species in New Zealand at the time of publication of this report, the references from which the information has been culled, and the criteria for adventism that each species meets are given in Table 1.

Table 1: Species identified as adventive in New Zealand from studies of the published literature, unpublished reports, personal communications to the authors, and the taxonomic experience and distributional knowledge of the authors, showing the probable native range of the species, the probable date of introduction, the probable means of introduction (H, in hull fouling communities; B, in ballast water; H or B, by one mechanism or the other), the range of the species within New Zealand (in June 1998), published references for material drawn on and the criteria for adventism of Chapman & Carlton (1994) that the species meet (1–9). Any criterion that is especially marked in any species is highlighted with an asterisk(*). Species that failed to become established (whether they were accidentally or deliberately introduced) are marked with a dagger (†)

Species	Family	Probable native range	Date of introduction	Probable means of introduction	Present range within New Zealand	References	Meets criteria
Algae							
Antithamnionella ternifolia	Ceramiaceae	English Channel	Pre-1904 (may be adventive even there)	H	Timaru & Wellington harbours	Laing (1904) Adams (1983) Nelson & Maggs (1996)	1, 2, 5, 6, 8
Asperococcus bullosus	Punctariaceae	Atlantic Mediterranean	Pre-1957	H	1957 Half Moon Bay Wharf; *Mikhail Lermontov* wreck, Port Gore; Pelorus Sound	Lindauer (1957) Adams (1983) Nelson & Knight (1995)	5, 6, 7, 8
Champia affinis	Champiaceae	Southern Australia	Pre-1855	H	Otago Harbour, Preservation Inlet, Stewart Island	Adams (1983)	6, 7, 8
Chnoospora minima	Chnoosporaceae	Widespread tropical & subtropical distribution Atlantic, Indian, & Pacific Oceans	Early 1800s	H	Port Underwood	Nelson & Duffy (1991)	5, 6, 7, 8
Chondria harveyana	Rhodomelaceae	Tasmania	Early 1800s	H	Porirua Harbour	Adams (1982) Adams (1983)	6, 7, 8

Colpomenia durvilleae	Scytosiphonaceae	Northern Pacific N. Japan – central California	Pre-1980	H	N.E. North Island Hawkes Bay, Napier & Wellington harbours	Parsons (1982) Nelson & Adams (1991)	1, 2, 3, 6
Cutleria multifida	Cutleriaceae	Cosmopolitan in temperate seas	Pre-1870	H	Auckland, Wellington, Picton, Lyttelton, & Otago harbours, Stewart Island	Adams (1983)	1, 2, 5, 6, 7, 8
Griffithsia crassiuscula	Ceramiaceae	Southern Australia	Pre-1954	H	Otago Harbour, Otago Peninsula, Stewart Island	Naylor (1954) Adams (1983)	1, 2, 6, 8
Hydroclathrus clathratus	Scytosiphonceae	Cosmopolitan temperate & tropical seas	Pre-1974	H or B or Range extension	Whangaroa, Whangarei, & Auckland harbours, Kermadec Islands	Johnson & Dromgoole (1977) Nelson & Adams (1984)	1, 2, 6, 7
Polysiphonia brodiei	Rhodomelaceae	Northern Europe	Pre-1940	H	Wellington, Lyttelton, Timaru harbours, Stewart Island, George Sound	Adams (1983)	1, 2, 3, 5, 6, 7, 8
Polysiphonia constricta	Rhodomelaceae	Southern Australia	Pre-1970	H	Otago Harbour	Adams (1983) Adams (1991)	1, 5, 6, 7, 8
Polysiphonia senticulosa	Rhodomelaceae	North America	Pre-1993	H or B	Wellington & Picton harbours	Nelson (1994a) Nelson & Maggs (1996)	1, 5, 6, 7, 8
Polysiphonia sertularioides	Rhodomelaceae	Mediterranean	Pre-1938	H	Bay of Islands, Otago Harbour, Golden Bay, Stewart Island	Adams (1991) Womersley (1979)	1, 2, 6, 7, 8

Species	Family	Probable native range	Date of introduction	Probable means of introduction	Present range within New Zealand	References	Meets criteria
Polysiphonia subtilissima	Rhodomelaceae	West Indies	Pre-1974	H	Wellington, Lyttelton, Whangaroa, & Tauranga harbours, Pelorus Sound	Adams (1991) Womersley (1979)	1, 2, 5, 6, 7, 8
Punctaria latifolia	Punctariaceae	Europe	Pre-1947	H	Otago & Wellington harbours, Stewart Island	Lindauer (1947) Adams (1983)	1, 2, 5, 6, 7, 8
Sargassum verruculosum	Sargassaceae	South Australia	Pre-1845	H	Kaikoura, Akaroa & Otago harbours, Stewart Island, Preservation Inlet, Dusky Sound	Hooker & Harvey (1845) Adams (1983)	1, 2, 6, 7, 8
Striaria attenuata	Striariaceae	Northern Europe	Pre-1957	H	Wellington & Otago harbours, Stewart Island	Lindauer (1957) Adams (1983) Nelson (1994a) Nelson & Maggs (1996)	1, 2, 6, 7, 8
Undaria pinnatifida	Alariaceae	Japan, Korea, parts of China	Pre-1987	B	Napier, Wellington, Picton, Lyttelton & Timaru harbours, Port Chalmers & Marlborough Sounds	Hay & Luckens (1987) Hay (1990)	1, 2, 3, 5, 6 7, 8
unidentified species	Solieriacae	Probably Southeast Asia	Pre-1992	H	Orakei Basin (Auckland Harbour)	Nelson (1994a) Hayward (1997) Dromgoole *et al.* (1993)	1, 3, 5, 6, 7, 8

Angiospermae							
Spartina alterniflora	Poaceae	Eastern USA	1953	Deliberate	NE North Island	Partridge (1987)	
Spartina anglica	Poaceae	Britain	1924	Deliberate	North & South Islands	Partridge (1987)	
Spartina x townsendi	Poaceae	Britain	1913	Deliberate	Auckland, Bay of Plenty, Southland	Partridge (1987)	
Protozoa							
Elphidium vellai	Elphidiidae	?	Pre-1990	B (sand)	First named as a species from Queen Charlotte Sound, but distribution in N.Z. (also found in Waitemata Harbour and ironsand terminal, North Taranaki) strongly suggests an adventive species	Hayward (pers. comm.)	1, 2, 3, 6, 8
Shepheardella taeniformis	Allogromiidae	Southern UK	Pre-1960	B (sand)	Taylors Mistake (Christchurch)	Hedley *et al.*	1, 6, 7, 9
Siphogenerina raphanus	Siphogenerinoididae	Cosmopolitan	Pre-1960	B (sand)	Waitemata Harbour	Hayward (1997)	1, 2, 3, 6, 8
Virgulinella fragilis	Virgulinellidae	Caribbean, also Peru, Australia	Pre-1976	B (sand)	Wellington Harbour	Hayward (pers. comm.)	1, 3, 6, 7, 8

Species	Family	Probable native range	Date of introduction	Probable means of introduction	Present range within New Zealand	References	Meets criteria
Porifera							
Clathrina coriacea	Clathrinidae	North Atlantic, Mediterranean, Japan Indian Ocean, Arctic, Antarctic	Unknown	H	Throughout N.Z. & offshore islands, common fouling organisms in ships & harbours	Battershill *et al.* (1984) Bergquist (1978) Battershill & Bergquist (in press) Dawson (1993)	3, 6, 7, 8
Cliona celata	Clionidae	Arctic, Atlantic coasts of Europe & North America, West Indies, Indian Ocean, Red Sea, Malaysia, Australia, New Guinea	Unknown	H or B (shelly sand)	Around all N.Z. coasts & offshore islands	Battershill *et al.* (1984) Battershill & Bergquist (in press) Doak (1971), Dawson (1993)	3, 7, 8
Dendya poterium	Clathrinidae	Europe, circumglobal	Pre-1896	H	Widespread in N.Z.	Kirk (1896) Dawson (1993)	1, 2, 3, 7, 8
Halichondria panicea	Halichondriidae	Europe, cosmopolitan	Pre-1924	H	Bay of Islands, Hauraki Gulf, Manukau Harbour, Mayor Island, New Plymouth	Brondstedt (1924) Bergquist (1961b, 1970), Dawson (1993)	1, 2, 3, 7, 8
Halisarca dujardini	Halisarcidae	Europe, cosmopolitan	Pre-1973	H or B	Westmere Reef, Auckland	Bergquist & Sinclair (1973)	1, 3, 5, 6, 7, 8
Hymeniacidon perleve	Hymeniacidonidae	Europe, cosmopolitan	Pre-1961	H or B	Common intertidally northern N.Z.	Bergquist (1961b, 1970), Dawson (1993)	1, 2, 3, 6, 7, 8
Leucosolenia botryoides	Leucosoleniidae	Europe, circumglobal	Pre-1894	H	Widespread	Kirk (1894) Dawson (1993)	1, 2, 3, 7, 8

Sycon ciliata	Sycettidae	Europe, circumglobal	Pre-1898	H	Widespread	Kirk (1898) Dawson (1993)	3, 7, 8
Tethya aurantium	Tethyidae	California	Unknown	H	North Island & northern offshore islands common in harbours, & found on ships' hulls	Battershill *et al.* (1984) Bergquist (1961a, 1968) Bergquist & Kelly-Borges (1991) Battershill & Bergquist (in press)	3, 4, 6, 7, 8
Cnidaria							
Amphisbetia operculata	Sertulariidae	Cosmopolitan, especially subtropical Atlantic	Pre-1896	H	First recorded at Auckland Is.; common around N.Z.	Farquhar (1896) Vervoort (pers. comm.)	1, 2, 3
Cladonema radiatum	Cladonematidae	Europe, Mediterranean, Japan	Pre-1953	B	Wellington Harbour	Ralph (1953) Schuchert (1996)	1, 3, 5, 6, 7, 8
Cordylophora caspia	Clavidae	Caspian Sea	Pre-1883	H	Brackish lagoons; Napier, Lake Ellesmere, Dunedin	Hamilton (1883) Schuchert (1996)	1, 2, 3, 5, 6, 7, 8
Coryne pusilla	Corynidae	All European coasts, Mediterranean; now also South Africa, East Asia	Pre-1968	H or B	Devonport wharf (Auckland)	Morton & Miller (1968) Schuchert (1996)	1, 3, 5, 6, 7
Diadumene lineata (Sagartia luciae)	Diadumenidae	Cosmopolitan	Pre-1983	H	Waitemata Harbour	Dromgoole & Foster (1983) Hayward (1997), Ocaña (1997)	1, 3, 5, 6, 7, 8
Ectopleura crocea	Tubulariidae	NE USA, Europe Japan, NE Pacific	Pre-1994	H	Devonport wharf (Auckland)	Schuchert (1996)	1, 3, 5, 6, 7, 8
Ectopleura larynx	Tubulariidae	Atlantic coast of Europe, NE, NW USA, NE Asia	Pre-1953	H	Wellington & Otago Harbours	Ralph (1953)	1, 2, 3, 5, 6, 7, 8

Species	Family	Probable native range	Date of introduction	Probable means of introduction	Present range within New Zealand	References	Meets criteria
Eudendrium ritchiei	Eudendriidae	South Africa	Pre-1953	H	Auckland and Gisborne	Ralph (1953)(as *E insigne*) Vervoort (pers. comm.)	3, 6, 7
Gonothyraea loveni	Campanulariidae	Europe	Pre-1898	H	Dunedin Harbour; sole record	Hilgendorf (1898) Vervoort (pers. comm.)	1, 3, 5, 6, 7, 8
Halecium delicatulum	Haleciidae	Circumtropical	Pre-1876	H	First described from Dunedin probably introduced on ships' hulls	Coughtrey (1876) Vervoort (pers. comm.)	1, 2, 3
Hartlaubella gelatinosa	Campanulariidae	Europe, Atlantic coast of North America	Pre-1957	H	Lake Ellesmere, near mouth of Selwyn River (sole record)	Ralph (1957) Vervoort (pers. comm.)	1, 3, 5, 6, 7, 8
Hoplangia durotrix	Caryophyllidiidae	NE Atlantic	?1940s	H	NE North Island	Cairns (1995)	1, 2, 6, 7, 8, 9
Obelia longissima	Campanulariidae	Europe; widely distributed	Pre-1928	H	First recorded in Dunedin Harbour; now more widespread	Trebilcock (1928) Vervoort (pers. comm.)	1, 2, 3
Pennaria disticha	Pennariidae	Europe; now circum-global in warm water	Pre-1928	H	Waitemata Harbour	Trebilcock (1928) Ralph (1953) (both as *P. australis*), Schuchert (1996)	1, 3, 5, 6
Plumularia setacea	Plumulariidae	Europe; now nearly cosmopolitan	Pre-1896	H	First recorded at Timaru; widespread in New Zealand	Farquhar (1896) Vervoort (pers. comm.)	1, 2, 3
Sarsia japonica	Corynidae	Japan, British Columbia, ?California	Pre-1994	H or B	Wellington Harbour	Schuchert (1996)	1, 3, 5, 6, 7, 8, 9

Tethocyathus cylindraceus	Caryophylliidae	W. Atlantic	?1940s	H or B	Northern North Island	Cairns (1995)	1, 2, 6, 7, 8, 9
Polychaeta							
Dipolydora giardi	Spionidae	West European coastal waters adventive California	Unknown	H	Otago & Wellington harbours	Read (1975)	2, 3, 6, 7, 8, 9
Euchone limnicola	Sabellidae	California	Unknown	H	Timaru Harbour	Read (personal observations)	1, 3, 5, 6, 7, 8
Ficopomatus enigmaticus	Serpulidae	Obscure, European coastal waters	1967	H or B	Whangarei & Waitemata harbours, Hawke Bay	Read & Gordon (1991) Probert (1993)	1, 2, 3, 5, 6, 7, 8, 9
Hydroides elegans	Serpulidae	Unknown, now cosmopolitan	Pre-1952	H or B	Waitemata & Lyttelton harbours	Allen (1953) identified as (*H. norvegicus*) Skerman (1958) Hutchings *et. al* (1987)	1, 2, 3, 4, 5, 6, 8, 9
Polydora armata	Spionidae	Cosmopolitan distribution	About 1900	H	Otago & Wellington harbours, Marlborough Sounds	Rainer (1973) Read (1975)	3, 5, 6, 7, 8
Polydora cornuta	Spionidae	Atlantic Coast North America European coastal waters	Pre-1972	H or B	Whangarei & Waitemata harbours	Read & Gordon (1991)	1, 2, 3, 5, 6, 8
Polydora hoplura	Spionidae	Atlantic coast of Europe Mediterranean coastal waters (adventive? South Africa)	Unknown	H	Wellington Harbour, Marlborough Sounds	Read (1975)	3, 5, 6, 7, 8, 9
Polydora websteri	Spionidae	West coast North America	Early 1990s	H or B	Mahurangi harbour, Admiralty Bay (Marlborough Sounds)	Handley (1995) Handley & Berquist (1997)	1, 2, 3, 4, 5, 6, 7, 8

Species	Family	Probable native range	Date of introduction	Probable means of introduction	Present range within New Zealand	References	Meets criteria
Pseudopolydora paucibranchiata	Spionidae	Now almost cosmopolitan	Pre-1975	H or B	Wellington Harbour	Read (1975)	1, 3, 5, 6, 7, 8
Mollusca							
Aeolidiella indica	Aeolidiidae	Japan (thought to be adventive: California, South Africa, Mediterranean and Australia)	Unknown	H or B	NE coast of North Island	Willan & Morton (1984) Willan & Coleman (1984)	1, 2, 4, 6, 7, 8
Crassostrea gigas	Ostreidae	Japan, Korea and vicinity (adventive: Pacific & Atlantic coast of North America, Hawaii, Okinawa, New South Wales)	1961	H	Northern N.Z. harbours, Waikanae River, Tasman Bay, Pelorus Sound	Dinamani (1971) Dinamani (1991) Dromgoole & Foster (1983)	1, 2, 3, 6, 7, 8, 9
Cuthona alpha	Tergipediidae	Japan (adventive: Pacific coast North America)	1962	H or B	Highly localised within parts of Waitemata Harbour	Miller (1977)	1, 3, 4, 5, 6, 7, 8, 9
Cuthona beta	Tergipediidae	Japan	1958	H or B	Whangarei & Waitemata harbours, Auckland west coast	Miller (1977)	1, 2, 3, 4, 5, 6, 7, 8, 9
Cuthona perca	Tergipediidae	Brazil, Jamaica, Florida, Barbados (adventive, San Francisco, Hawaii)	Unknown (pre-1960)	H or B	Piha, Anawhata, Manukau & Akaroa harbours, Little Papanui (Otago Peninsula)	Miller (1977) (as *Cuthona reflexa* now *C. perca* see Behrens 1984)	1, 2, 3, 4, 5, 8, 9

Cypraea caputserpentis	Cypraeidae	Tropical Indo-Pacific	1975	Fouling on oil rig, found after 4 months in Taranaki waters	Not established (Taranaki)	Hook (1975)	†
Cypraea erosa	Cypraeidae	Tropical Indo-Pacific	1975	Fouling on oil rig	Not established (Whangarei Harbour)	Hook (1975)	†
Eubranchus agrius	Eubranchidae	Chile	1959	H or B	NE & NW coasts North Island, Waitemata & Akaroa harbours, Otago Peninsula	Miller (1971)	1, 2, 3, 4, 6, 8, 9
Goniodoris castanaea	Goniodorididae	Europe & Mediterranean coasts	1913	H	Not established Hull fouling on vessel in Otago Harbour in 1913	Suter (1913) Powell (1979)	†
Janolus hyalinus	Zephyrinidae	European and Mediterranean coastal waters (adventive:Australia)	Pre-1981	H or B	Northeast coast North Island	Miller & Willan (1986)	1, 4, 6, 7, 8, 9
Limaria orientalis	Limidae	Japan, Philippines & widely distributed in Indo Pacific	Pre-1972	H or B	Waitemata Harbour, Hauraki Gulf, Bay of Islands, Coromandel Peninsula	Grange (1974) Dromgoole & Foster (1983)	1, 2, 3, 6, 7, 8, 9
Lyrodus mediolobatus	Teredinidae	Tropical cosmopolitan	Unknown	H	Whangaroa to Tauranga Harbour (North Island east coast)	McKoy (1980)	3, 5, 8
Lyrodus pedicellatus	Teredinidae	Tropical to temperate seas, cosmopolitan	Unknown	H	Waitemata, Tauranga, Wellington, Nelson, Wanganui, New Plymouth, Napier, & Gisborne, harbours, Bay of Islands	McKoy (1980)	3, 5, 8

Species	Family	Probable native range	Date of introduction	Probable means of introduction	Present range within New Zealand	References	Meets criteria
Microtralia. sp.= *M. insularis*	Ellobiidae	Unknown	Pre-1933	Discarded dunnage	Rangitoto Island (Waitemata Harbour), Manukau Harbour	Powell (1933)(*Rangitotoa insularis*), Climo (1982) (*Microtralia occidentalis*) Martins (1996)	1*, 3, 5, 6, 7, 8
Musculista senhousia	Mytilidae	Eastern Asia from Singapore to Siberia	1978	B or H	Whangarei &Waitemata harbours, Parengarenga, Whangaparaoa Peninsula, Great Barrier Island, Firth of Thames, East Cape	Willan (1985, 1987) Morley (1988)	1, 2, 3, 6, 7, 8, 9
Nototeredo edax	Teredinidae	Tropical Pacific	Unknown	H	Tauranga, Gisborne, Wellington Wanganui, & New Plymouth harbours	McKoy (1980)	3, 5, 6, 8
Okenia pellucida	Goniodorididae	Australia	probably about 1960 (with bryozoan *Zoobotryon verticillatium*)	H	Waitemata Harbour (in channels on *Zoobotryon verticillatum*)	Willan & Coleman (1984) Gordon & Mawatari (1992)	1, 3, 4*, 6, 8, 9
Okenia plana	Goniodorididae	Cosmopolitan	unknown	H	Northern New Zealand	Willan & Coleman (1984)`	4, 6, 7, 8, 9
Ostrea edulis	Ostreidae	European coastal waters	1869	Deliberate attempt to naturalise	Not established, two survivors of a transfer transplanted among native oysters at Portobello (Otago Harbour)	Thomson (1922)	†
Phytia myosotis	Ellobiidae	Spain, England, Europe (adventive in South Africa, Tasmania, South Australia and North America)	Pre-1980	Discarded Dunnage	Aramoana (Otago Harbour entrance)	Climo (1982)	1, 3, 5, 6, 7, 8, 9

Polycera hedgpethi	Polyceridae	Unknown, now almost cosmopolitan	1970s	H	Waitemata Harbour, Northeast coast North Island, feeding on adventive bryozoa *Bugula neritina* & *B. flabellata*	Willan & Coleman (1984)	1, 2, 3, 4*, 6
Theora lubrica	Semelidae	Japan, the tropical Pacific, Indonesia, Thailand, China Philippines and Australia	1971	B	Northeast coast North Island, Bay of Islands, Herekino, Whangaroa, Waitemata, & Wellington harbours, Pelorus Sound	Climo (1976) Morley (1995)	1, 2, 5, 6, 7, 8, 9
Thecacera pennigera	Polyceridae	Unknown; temperate cosmopolitan (perhaps originally temperate latitude of eastern South America)	1973	H or B	Waitemata Harbour	Willan (1976) Willan & Coleman (1984)	1, 2, 3, 4, 5, 6, 7, 8
Teredo princessae	Teredinidae	Tropical Indo-Pacific	1979	Driftwood	Not established	McKoy (1980)	†
Xiphosura							
Carcinoscopius rotundicauda	Xiphosuridae	India, Bengal, Gulf of Thailand, Penang, Moluccas, Philippines	1910	H	Not established: one specimen found in 1908 on stone facing of Calliope dock (Waitemata Harbour)	Chilton (1910)	†
Limulus polyphemus	Xiphosuridae	Coasts of Maine to Yucatan, N. America	1940	H	Not established: one specimen found on low tide rocks at Great Barrier Island	Powell (1949)	†

Species	Family	Probable native range	Date of introduction	Probable means of introduction	Present range within New Zealand	References	Meets criteria
Cirripedia							
Balanus albicostatus	Balanidae	Japan	1975	Fouling on oil platform	—	Foster & Willan (1979)	†
Balanus amphritrite	Balanidae	Cosmopolitan warm temperate & tropical seas	1960	H	Orakei Basin (Waitemata Harbour)	Foster (1978) Dromgoole & Foster (1983)	1, 5*, 6*, 7, 8
Balanus cf. *flos*	Balanidae	California	1970	Fouling on turtle	Piha Beach	Foster (1978)	†
Balanus improvisus	Balanidae	Atlantic coast of America	1975	Fouling on oil platform	—	Foster & Willan (1979)	†
Balanus reticulatus	Balanidae	Circumtropical	1975	Fouling on oil platform	—	Foster & Willan (1979)	†
Balanus trigonus	Balanidae	Cosmopolitan warm temperate & tropical seas	1960	H	Whangarei & Waitemata harbours, northeast coast North Island from Whangarei through Hauraki Gulf south to Mercury Bay	Foster (1978) Dromgoole & Foster (1983)	1, 2, 6, 7, 8
Balanus variegatus	Balanidae	Indo-Malaysia to Australia	1960	H	Mangonui, Kaipara, Mahurangi, Waitemata & Manukau harbours	Foster (1978) Dromgoole & Foster (1983)	1, 2, 5, 6, 7, 8
Lepas anserifera	Lepadidae	Cosmopolitan	1975	Fouling on oil platform	—	Foster & Willan (1979)	†

Lepas hilli	Lepadidae	Australia	1910	H	—	Chilton (1910) Jennings (1915)	†
Megabalanus rosa	Balanidae	Japan, Taiwan	1975	Fouling on oil platform	—	Foster & Willan (1979)	†
Megabalanus volcano	Balanidae	South Japan Taiwan	1975	Fouling on oil platform	—	Foster & Willan (1979)	†
Megabalanus zebra	Balanidae		1975	Fouling on oil platform	—	Foster & Willan (1979)	†
Platylepas hexastylos	Platylepadidae		1970	Fouling on turtle	Piha Beach	Foster (1978)	†
Tetraclita squamosa japonica	Tetraclitidae	Japan, Korea	1975	Fouling on oil platform	—	Foster & Willan (1979)	†
Ostracoda							
Loxoconcha parvifoveata	Loxoconchidae	New South Wales, South Australia	1960s	B	McCormacks Bay (Christchurch), Moa Point (Wellington)	Eagar (pers. comm.)	1, 2, 3, 5, 6, 8
Isopoda							
Cymodoce tuberculata	Sphaeromidae	Australia	1910	H	Found in hull scrapings Lyttelton Harbour	Chilton (1919)	†
Limnoria rugosissima	Limnoriidae	NSW, SA, Victoria Tasmania, Bass Strait	Unknown	H, probably in attached algae	Snares Islands	Cookson (1991)	3, 4, 6, 7, 8

Species	Family	Probable native range	Date of introduction	Probable means of introduction	Present range within New Zealand	References	Meets criteria
Limnoria tripunctata	Limnoriidae	Cosmopolitan warm to tropical waters	Unknown	H	Auckland Harbour	McQuire (1964) Cookson (1991)	3, 5, 6
Amphipoda							
Chelura terebrans	Cheluridae	Cosmopolitan	Pre-1914	H	Auckland Harbour	Chilton (1919) Haywood (1997)	1, 3, 4, 5, 6, 8
Corophium acherusicum	Corophiidae	Mediterranean, U.K., now circumglobal	Pre-1921	H	Lyttelton Harbour	Hurley (1954)	3, 5, 6, 8
Corophium acutum	Corophiidae	Coasts of Europe; now circumglobal	Pre-1921	H	Auckland & Otago harbours, Kenepuru Sound, Chatham Islands	Hurley (1954)	3, 6, 8
Corophium sextonae	Corophiidae	Britain, Portugal	Pre-1921	H	Lyttelton, on wharves, Portobello, Otago Harbour	Hurley (1954)	3, 5, 6, 7, 8
Decapoda							
Cancer pagurus	Cancridae	European seas	1907–13	deliberate attempt to naturalise	Not established	Thomson & Anderton (1921)	†
Dromia wilsoni	Dromiidae	Australia (adventive South Africa, Japan)	1914	H	NE coast N.I. south to Hawkes Bay, west coast N.I.from Wanganui south to Tasman Bay	Bennett (1964) Dell (1968)	1, 2, 6, 7, 8
Homarus gammarus	Nephropidae	European & Mediterranean Coasts	1906–13	Deliberate attempt to naturalise	Not established	Thomson & Anderton (1921)	†

Merocryptus lambriformis	Leucosidae	Southern Australia (adventive Japan)	1924	H	Hauraki Gulf, Taranaki Coast	Bennett (1964) Dell (1968)	1, 6, 7, 8
Penaeus canaliculatus	Penaeidae	Australia	1892, 1894	Deliberate attempt to naturalise	Not established	Thomson (1922)	†
Pilumnopeus serratifrons	Xanthidae	South Australia	1876	H	Whangateau, Auckland, & Whangarei harbours	Dell (1968)	1, 5, 6, 8
Plagusia chabrus	Grapside	West Indo-Pacific	1840	H	Northern distribution generally in harbours, from Bay of Islands in north to Nelson Harbour in the south	Dawson (1987) Dell (1968) Chilton (1910)	2, 3, 6, 8
Plagusia depressa tuberculata	Grapsidae	Indo-Pacific	1979	H	Not established	Foster & Willan (1979)	†
Pyromaia tuberculata	Majidae	West coast North America (adventive Japan)	1975	H (probably as megalopa or juvenile)	Firth of Thames, Tamaki Estuary	Foster & Willan (1979) Webber & Wear (1981) Wear & Fielder (1985)	1, 2, 3, 6, 7, 8
Entoprocta							
Barentsia matsushimana	Barentsiidae	Japan, also Europe	Pre-1995	H or B	Otago Harbour	Wasson (pers. comm.)	1, 3, 5, 6, 7, 8
Amathia distans	Vesiculariidae	Atlantic coast of America, North Carolina to Brazil	Pre-1960	H or B	Auckland Harbour	Gordon & Mawatari (1992) Morton & Miller (1968)	1, 4, 5, 6* 7, 8
Anguinella palmata	Nolellidae	Southern Europe	1960	H or B	Devonport (Waitemata Harbour), Nelson Harbour	Gordon & Mawatari (1992) Morton & Miller (1968)	1, 2, 5, 6*, 7, 8
Bowerbankia gracilis	Vesiculariidae	Eastern North America	Pre-1965	H or B	Waitemata, Napier, & Onehunga harbours, Oaonui, Tataraimaka, Totaranui, Oban	Gordon & Mawatari (1992)	1, 2, 5, 6, 7, 8

Species	Family	Probable native range	Date of introduction	Probable means of introduction	Present range within New Zealand	References	Meets criteria
Bowerbankia imbricata	Vesiculariidae	Southern Europe	Pre-1967	H or B	Goat Island, Whangateau Auckland & Nelson harbours	Gordon & Mawatari (1992)	1, 5, 6, 7, 8
Bugula flabellata	Bugulidae	Probably European waters	Pre-1949	H	In 1992 present in all N.Z. ports from Opua to Bluff, except Whangarei, Onehunga, Gisborne, Tarakohe, & Timaru harbours	Gordon & Mawatari (1992) Morton & Miller (1968) Ralph & Hurley (1952) Skerman (1958, 1959, 1960)	1, 2, 3, 5, 6, 7, 8
Bugula neritina	Bugulidae	Mediterranean and southern Europe	Probably 1949	H	All N.Z. ports from Opua in north to Dunedin in south apart from Onehunga, Gisborne, & Oamaru harbours	Gordon & Mawatari (1992) Skerman (1958, 1959, 1960) Ralph & Hurley (1952)	1, 5, 6*, 7, 8
Bugula simplex	Bugulidae	Mediterranean and Europe	1988	H or B	Lyttelton Harbour	Gordon & Mawatari (1992)	1, 5, 6*, 7, 8
Bugula stolonifera	Bugulidae	Europe	1962	H	Waitemata, New Plymouth, Napier Tarakohe, Nelson, Lyttelton, Timaru, & Bluff Harbours, Opua, Kawau Island, Pelorus Sound	Gordon & Mawatari (1992)	1, 2, 3, 5, 6, 7, 8
Buskia nitens	Buskiidae	European seas	1967	H or B	Auckland & Oamaru harbours	Gordon & Mawatari (1992)	1, 2, 5, *6, 7, 8
Buskia socialis	Buskiidae	Mediterranean and Adriatic seas	Pre-1977	H	Kawau Island	Gordon & Mawatari (1992)	1, 5, *6, 7, 8

Conopeum seurati	Electridae	Caspian Sea, Sea of Azov, Mediterranean, North Africa	Pre-1963	H	Whangarei, Whangateau, Waitemata, Onehunga, Gisborne, Napier, Nelson & Lyttelton harbours, Opua, Patea, Whanganui Inlet	Gordon & Mawatari (1992) Read & Gordon (1991)	1, 3, 4, 5, 6, 7, 8
Cryptosula pallasiana	Cryptosulidae	Cosmopolitan	1890s	H	Present in every port from Marsden Point to Bluff including Whangateau Harbour, Aotea Lagoon, Akaroa	Gordon & Mawatari (1992) Skerman (1958, 1960)	1, 2, 3, 5, 6, 7, 8
Electra tenella	Electridae	Atlantic coast of Florida, Puerto Rico, Brazil	1977	Drift Plastic	Northeast coast of Northland & Hauraki Gulf	Gordon & Mawatari (1992)	1, 3, 5, *6, 7, 8
Schizoporella errata	Schizoporellidae	Mediterranean	Pre-1960	H	Auckland Harbour, Bay of Islands	Gordon & Mawatari (1992)	1, 2, 3, 6, 7, 8
Tricellaria porteri	Candidae	Southern Australia or Japan, now cosmopolitan	1954	H	Whangarei, Auckland, Gisborne, Napier, Porirua, Tarakohe, Nelson, & Lyttelton harbours & Pelorus Sound	Gordon & Mawatari (1992) (as *T. occidentalis*)	1, 2, 5, 6, 7, 8
Watersipora arcuata	Watersiporidae	California to Galapagos Islands	Pre-1957	H	Auckland, Whangarei, & Tauranga harbours, Bay of Islands	Gordon & Mawatari (1992) Skerman (1960)	1, 2, 3, 5, 6, 7, 8
Watersipora subtorquata	Watersiporidae	Brazil, Bermuda, Cape Verde Islands	Pre-1982	H or B	Whangarei, Auckland, Tauranga, Napier, Wellington, Nelson, Lyttelton, & Otago harbours	Gordon & Mawatari (1992)	1, 2, 3, 5, 6, 7, 8
Zoobotryon verticillatum	Vesiculariidae	Mediterranean	1960	H or B	Waitemata & Manukau harbours	Gordon & Mawatari (1992) Morton & Miller (1968)	1, 2, 5, *6, 7, 8

Species	Family	Probable native range	Date of introduction	Probable means of introduction	Present range within New Zealand	References	Meets criteria
Ascidiacea							
Aplidium phortax	Polyclinidae	Northeastern Australia, Solomon Islands	Pre-1900	H	Tauranga, D'Urville Island, Otago, Stewart Island, Chatham Islands	Millar (1982) Brewin (1946) Stocker & Battershill (in press)	2, 3, 7, 8
Ascidiella aspersa	Ascidiidae	Europe	1900s	H	Lyttelton Harbour, Portobello, Half Moon Bay (Stewart Island)	Brewin (1946,1950b, 1958a) Millar (1982) Stocker & Battershill (in press)	1, 2, 3, 4, 5, 6, 7, 8
Asterocarpa cerea	Styelidae	South Australia & Sub-Antarctica	Pre-1900	H	Hauraki Gulf, Queen Charlotte Sound, D'Urville Island, Southern New Zealand, Sub-Antarctic Islands	Millar (1982) Brewin (1946, 1948)	2, 5, 6, 7, 8
Botrylloides leachii	Styelidae	English Channel	Pre-1900	H	Whangarei, Tauranga, & Wellington harbours, Hauraki Gulf, Cook Strait, Portobello, Stewart Island, Chatham Islands, Auckland Islands	Sluiter (1900) Millar (1982) Brewin (1946, 1948, 1950b, 1951, 1956, 1958a, 1960)	1, 2, 3, 5, 6, 7, 8
Botrylloides magnicoecum	Styelidae	Southern African coasts (now adventive on coasts of Australia, New Zealand, and the Mediterranean)	Pre-1922	H	Tauranga Harbour, Hauraki Gulf, Stewart Island	Millar (1968, 1982) Brewin (1951, 1957, 1958a)	1, 2, 3, 5, 6, 7, 8
Botryllus schlosseri	Styelidae	Atlantic	Pre-1922	H	Auckland, Wellington, & Lyttelton harbours, Hauraki Gulf, Heathcote Estuary, Half Moon Bay (Stewart Island)	Morton & Miller (1968) Millar (1982) Brewin (1946, 1948, 1950b, 1958a, 1960)	1, 2, 3, 5, 6, 7, 8

Ciona intestinalis	Cionidae	Europe?	Pre-1950	H	Wharf piles in Lyttelton Harbour	Brewin (1950b) Morton & Miller (1968)	1, 3, 5, 6, 8, 9
Corella eumyota	Rhodosmatidae	Southern & western Australia	Early 1900s	H	Widespread through all New Zealand ports, Chatham Islands, Sub-Antarctic Islands	Skerman (1958, 1959, 1960), Ralph & Hurley (1952), Millar (1982) Stocker & Battershill (in press), Brewin (1946, 1948, 1950b, c, d, 1951, 1952b, 1956, 1957, 1958a, b, 1960) Millar (1982)	1, 2, 3, 5, 7, 8
Cystodytes dellechiajei	Polycitoridae	Warm water cosmopolitan	Late 19th Century	H	North Cape, Auckland, Hauraki Gulf, Cook Strait Otago, Stewart Island Chatham Islands	Millar (1982) Brewin (1948, 1951, 1952a, 1956, 1958a, 1960), Stocker & Battershill (in press)	6, 7, 8
Didemnum "candidum"	Didemnidae	Now cosmopolitan	Pre-1924	H	Hauraki Gulf to Stewart Island Chatham Islands	Millar (1982) Stocker & Battershill (in press) Brewin (1946, 1948, 1950a, b, 1951, 1952b, 1956, 1957, 1958a, b, 1960)	3, 4, 7, 8
Diplosoma listerianum	Didemnidae	South Africa, now cosmopolitan	Pre-1996	H	Hauraki Gulf, Napier, Lyttelton Harbour, Banks Peninsula, Otago Harbour Stewart Island	Brewin (1946, 1948, 1950b 1951, 1952b, 1958a, 1960) Millar (1982)	1, 2, 5, 6, 7, 8
Styela plicata	Styelidae	Cosmopolitan	Pre-1948	H	Auckland Harbour & Hauraki Gulf	Brewin (1948, 1958b) Millar (1982) Stocker & Battershill (in press)	1, 2, 5, 6, 7, 8
Tridemnum cerebriforme	Didemnidae	South Africa, Australia	Pre-1924	H	Stewart Island	Millar (1982)	6, 7, 8

Species	Family	Probable native range	Date of introduction	Probable means of introduction	Present range within New Zealand	References	Meets criteria
Teleostei							
Abudefduf vaigiensis	Pomacentridae	Indo-west central Pacific	1975	Oil platform fouling	A pair identified as (*A. saxatilus*) recorded among fouling of oil rig, there is no evidence this circum-tropical fish has become established	Foster & Willan (1979)	†
Engraulis japonica	Engraulidae		1981, 1982	Deliberate discharge of live bait fish	No trace of this species since	Paulin & Stewart (1985)	†
Sardinops melanostica	Clupeidae		1981, 1982	Deliberate discharge of live bait fish	No trace of this species since	Paulin & Stewart (1985)	†
Oncorhynchus tshawytscha	Salmonidae		1870s 1901–1907	Deliberate attempt to establish a commercial fishery	Now present along much of the east coast of the South Island and spawning in many South Island rivers	McDowall (1990)	Successful deliberate introduction
Scophthalmus maximus	Scophthalmidae	Coastal North Atlantic Ocean, Ireland, Norway to UK & southern France	1913	Deliberate attempt to naturalise	Not established	Thomson & Anderton (1921)	†

Discussion

How individual species meet the nine criteria of Chapman & Carlton (1994) is discussed below, followed by some preliminary analyses of deliberate introductions, where the adventives originated, how most of them arrived in New Zealand, which species have been most successful and what their general impact has been on the New Zealand marine environment. Quantitative statements refer to the information in Table 1.

Criterion 1: Previously unknown in New Zealand

We have analysed the biogeography of species within that part of the New Zealand marine biota that has been well described so that the sudden appearance of new species (at least in recent years) could be readily detected. This criterion has been useful to identify only recent arrivals and has not been helpful in identifying species that arrived here in the sailing vessel era. As Carlton (1989) stated, "One reason we do not yet know exactly how many species were moved (but with considerable systematic and biogeographic work we will come a great deal closer) is that most biological surveys commenced well after most of these taxa had been transported globally." Such systematic and biogeographic work is progressing in New Zealand as part of the NIWA FRST-funded Marine Biodiversity and Systematics programme, new NIWA programmes examining New Zealand's coastal resources, and marine research programmes within museums.

Between 1938 and 1987, 14 species of algae became established in New Zealand and 5 of them have not spread from where they were first found. Between 1949 and 1988, 18 species of newly recorded Bryozoa appeared in New Zealand, 5 of which have not spread from where they were first found. Since 1960, 3 species of barnacles have become established in New Zealand and 10 others have arrived here in fouling communities but have not become established. Between 1933 and 1993, 20 species of mollusc were newly recorded in New Zealand. Similar taxonomic novelty has been recorded for a number of other invertebrates.

Criterion 2: Post-introduction range extension

Of the 159 species listed in Table 1, 98 (66%) are established at more than one locality, 32 (21%) occur at only a single locality, and 29 (19%) failed to become established. Eight of the 14 algal species introduced since 1938 have spread widely to other ports and one has spread only within southern New Zealand. The spread of *Undaria* can be tracked to particular ship and pleasure craft movement (Hay 1990). Spread of this alga throughout the country, together with other species, particularly ascidians, is increasing rapidly as movement of aquaculture structures becomes commonplace around New Zealand (Miller *et al.* 1997). Two species of Bryozoa introduced since 1949 have spread within the vicinity of their arrival site and 11 have spread widely to other New Zealand ports. *Watersipora arcuata* was found first in Auckland Harbour in 1957 where it spread widely and became one of the dominant intertidal organisms. It subsequently spread around ports and bays in northern New Zealand and south to the port of Napier on the east coast, and to New Plymouth and Nelson on the west coast by 1977. Since then it has regressed dramatically to Auckland, Opua, Bay of Islands, Marsden Point, and Tauranga Harbour. Colonies on ships' hulls died in the winter of 1960 at all ports south of Wellington; the range contraction in the 1980s may have been due to widespread temperature changes or competition with the newly arrived *W. subtorquata* (Gordon & Mawatari 1992).

Four species of molluscs introduced since 1933 have not spread from the vicinity of their arrival site, 10 species have spread along the northeast coast of the North Island from their original harbour entry point, and 6 species have spread more widely around New Zealand.

Only two of the three adventive barnacles have spread from Auckland (the site at which they were first found) to northern harbours and the northeast coast. Records are not sufficiently detailed to permit analyses of the spread of species within other taxa. It is likely, however, that those species introduced as fouling organisms will be readily spread around New Zealand, either by shipping or movement of aquaculture structures.

Criterion 3: Human mechanisms of dispersal

All the adventive algae so far recognised (other than *Undaria*, which has spread from harbours on to outer exposed coasts (Miller *et al.* 1997, Battershill *et al.* 1998)), many of the fouling Bryozoa, and all the adventive barnacles are confined to ports or anchorages, particularly some of those used in the early days of whaling and sealing (e.g., southern fiords). This is in agreement with the hypothesis of Chapman & Carlton (1991) that sailing vessels of this era normally were heavily fouled with masses of hydrozoans, bryozoans, barnacles, tunicates, and algae and much of this biota was spread around the world with vessel movement, but also shows that even among the recent arrivals the pattern of confinement to ports or anchorages continues to reveal the human mechanism of introduction on hull fouling. Fifteen of the recently introduced molluscs occur solely in harbours.

Chilton (1910) recorded the first information on hull-fouling organisms introduced to New Zealand. He examined fouling organisms scraped from the British Antarctic ship *Terra Nova* in the Lyttelton dry dock in 1910 and identified the barnacles *Lepas hilli, L. australis, Conchoderma auritum, C. virgatum,* and *Balanus tintinnabulum* as well as the isopod *Cymodoce tuberculata*. He concluded that much of this fouling fauna had been acquired during port calls at Trinidad, South Africa, Hobart, and Melbourne on the passage from England. However, *L. australis* occurs in southern New Zealand, and *C. auritum* and *C. virgatum* are common on whales and sharks and other floating or nektonic objects in New Zealand waters. A re-examination of Chilton's material has shown that *B. tintinnabulum* was the same subspecies, *B. tintinnabulum linzei*, found in northern New Zealand anyway and specimens from the *Terra Nova* were small and many were coated with *Balanus decorus*, pointing to the fouling having occurred in New Zealand waters (Foster 1978). *Lepas hilli* and *C. tuberculata* have not been recorded in New Zealand since.

Skerman (1960) recorded hull-fouling organisms found on a variety of vessels visiting New Zealand in the late 1950s. Modern vessels employ more effective antifouling paints, travel at higher speeds, and spend less time in port, so the opportunity for organisms to foul hulls is much lower today. The life-history strategies and characteristics of the main fouling species and their low profile are, however, adapted to withstand the increased shear forces encountered at these higher speeds and result in fouling species being most successful in spreading widely around the globe (*see* Watts *et al.* 1998). Recent examples of such oceanic transfers in hull fouling are an actinarian and polyclad species (*Haliplanella* (= *Diadumene*) *luciae* and *Cryptostylochus hullensis*) that reached Europe from North America as hull-fouling species (Faubel & Gollasch 1996, Gollasch & Reimann-Zurneck 1996). On the other hand, New Zealand ports are visited by growing numbers of seagoing yachts and fishing vessels that have spent considerable periods in overseas ports where they frequently have acquired a rich fouling biota. This biota could readily be introduced here when these same vessels spend considerable periods in New Zealand ports.

Foster & Willan (1979) and Hook (1975) recorded organisms introduced to New Zealand on oil platforms towed here in 1974 and 1975 respectively. Oil platforms carried much higher levels of fouling and a greater diversity of forms than cargo vessels. The much lower speed of oil platforms (they were towed at a mean speed of 6 km/h), their lack of anti-fouling paint, their much less streamlined construction (especially when towed on the side with two legs and many cross beams submerged), as well as the prolonged times the platforms spent in port resulted in them acquiring a major tropical fouling community that was not lost in transit. In these respects, oil platforms provided an opportunity for marine organisms to reach New Zealand similar to the sailing vessels of old. But, unlike sailing vessels, the platforms did not spend time in New Zealand ports where the imported organisms themselves, or their larvae, could have migrated to other habitats and become established in our fauna. All the barnacle species introduced were overwhelmed by local fouling organisms within a very short time (Foster 1982).

The data presented in this report are consistent with the suggestion of Chapman & Carlton (1991, 1994) that whole communities were introduced in the last two centuries on the slow, poorly streamlined, wooden sailing vessels with no anti-fouling. The ability of a replica of a 16th century sailing vessel to transport hull and test plate fouling from one port to another along 800 km of the western U.S. seaboard was confirmed by Carlton & Hodder (1995). The vessel sailed slowly (averaging 3.5 to 4 km/h) for the 1 to 3 day journeys between ports. There were no significant changes in abundance nor in numbers of taxa in hull or test panel fouling after each of these short passages. This vessel settled on the harbour floor periodically in one port and benthic organisms entrained were carried 390 km to the next port, so even non-fouling organisms could have been transported this way. The arrival of two species of king crab in New Zealand (Chilton 1910, Powell 1949) shows this to be a feasible mechanism of introducing non-fouling species from thousands of kilometres away.

Many of the adventive algae found in southern New Zealand originated in southern Australia and are localised in harbours or anchorages that were heavily used by sealers and whalers in the late 18th and early 19th centuries (Adams 1983, 1994, Nelson 1994a). In the early 19th century sealers regularly worked in both southeastern Australia and southern New Zealand (Ross 1987) and these algal species clearly arrived on their hulls. Two other species of adventive algae are localised at important whaling stations in central New Zealand and they are also presumed to have arrived in the same manner (Adams 1982, 1983, Nelson & Duffy 1991). Closer investigations of all these early anchorages will probably reveal other adventive organisms. All algae, bryozoans, and barnacles so far recognised as adventives have been found in or around major ports, indicating arrival on vessels. As many of the Bryozoa, some of the algae, and all of the barnacles have been found fouling vessel hulls they have probably also arrived in this way. Many of New Zealand's introductions are probably the result of progressive adventism, with adventive populations becoming established progressively around the world and then finally reaching New Zealand from Australia.

Ballast water contains many planktonic larvae and on its discharge in port has the potential to introduce these species into a country (Carlton & Geller 1993). High-salinity ballast water of tropical origin discharged from ironsand carriers loading at Taharoa had little living plankton after the 3-week transit from Japan (Mackenzie 1997). On the other hand, a two-year programme sampling the ballast water of vessels entering New Zealand ports (Hay *et al.* 1997) found a wide range of living invertebrate larvae in the wider variety of vessels examined. The risk of any of these species entering or becoming established in New Zealand has yet to be assessed. Studies in Australia (Williams *et al.* 1988) point to ballast water containing more organisms that could potentially be introduced than are found externally fouling the hulls. Nevertheless, only 14 species appear to have been introduced to Australia by this means (Jones 1991). In New Zealand the introduction of only one species can be ascribed with any certainty to this mechanism. As *Undaria pinnatifida* arrived here without a small crustacean that infests almost 100% of Asian plants and eats holes in the blades of the plant, it probably arrived in New Zealand as a gametophyte in ballast water (Nelson 1994a). Furthermore, at least two distinct forms of this species are now found in New Zealand suggesting that it may have been introduced more than once (Nelson 1995). Nelson (1995) considered that three other species, *Pyromaia tuberculata, Musculista senhousia,* and *Theora lubrica,* also may have entered New Zealand in this manner.

Criterion 4: Association with known introductions

None of the algae identified as adventive is associated with other adventives. The bryozoan *Conopeum seurati* is generally an estuarine species able to live in calm muddy water and in other parts of the world is closely associated with the adventive polychaete *Ficopomatus enigmaticus*. Their association is not recorded in New Zealand and *C. seurati* has spread more widely here than *F. enigmaticus*. The bryozoan *Amathia distans* may settle on another adventive bryozoan *Zoobotryon verticillatum* (that is preyed on by a further adventive, the nudibranch *Okenia pellucida*). Among the introduced molluscs, many of the nudibranchs are intimately associated with other introduced species on which they prey. *Thecacera pennigera* feeds on the adventive bryozoan species *Bugula neritina* and *B. flabellata*, as does the more widespread *Polycera hedgpethi* (Willan & Coleman 1984). *Cuthona perca* elsewhere preys on the adventive Asian anemone *Diadumemene (= Haliplanella) luciae* (Behrens 1984) but is not yet recorded as doing so in New Zealand where it has been recorded feeding on the adventive hydroid *Ectopleura larynx*, as has the extremely localised Japanese species *C. alpha* and probably also the more widespread Japanese species *C. beta* (Miller 1977). *Okenia pellucida* lives on the adventive bryozoan *Zoobotryon verticillatum,* which is confined to channels in the Waitemata and Manukau harbours, whereas *O. plana*, which feeds on the widespread, possibly adventive, bryozoan *Membranipora membranacea*, is widespread around northern New Zealand (Willan & Coleman 1984). The adventive *Eubranchus agrius* feeds on the adventive hydroid *Plumularia setosa* (Miller 1971b).

Criterion 5: Association with new or artificial environments

Most currently recognised adventive species are confined to harbours in New Zealand. Although this reflects their arrival on hull fouling of vessels, it also seems to reflect the availability of clean artificial surfaces of harbour structures, ropes, and buoys that some of these species are adapted to colonise. The alga *Punctaria latifolia* grows primarily on rope, buoys, plastic debris, and wooden pilings (Adams 1983, 1994). *Undaria pinnatifida* rapidly colonises new or disturbed surfaces on seawalls and grows like a weed on vessel hulls, buoys, and wharf pilings (Hay & Luckens 1987, Hay 1990). *Undaria pinnatifida* can grow outside harbours and has the ability to modify habitat (Battershill *et al.* 1998). In North America, *Codium fragile tomentosoides* has caused great problems for oyster growers. The buoyant alga fouls cultivated oysters and lifts them off the bottom so the oysters are washed ashore and die. In New Zealand, however, this adventive species has not caused problems in the rock oyster industry, possibly because the adventive has not out-competed local algae (Dromgoole 1975, Nelson 1995). *Electra tenella* is frequent on drifting plastic debris and probably arrived along the northeast coast of New Zealand this way. The adventive Bryozoa are restricted to harbours in New Zealand (Gordon & Mawatari 1992), where they are found predominantly on wharf piles and breakwaters. Although many of the adventive molluscs are confined to harbour environments, none is restricted to new or artificial environments. Most adventive sponges and ascidians appear tightly restricted to specific harbour habitats.

Criterion 6: Discontinuous regional distribution compared to natives

Harbours have been the chief entry point for adventive species. Because they are sheltered and enclosed waters, larvae and propagules produced by adventives are generally retained within their confines, frequently resulting in the settlement of enough invaders to develop local self-sustaining populations. Orakei Basin, an enclosed tidal basin in Waitemata Harbour, Auckland, has provided such conditions within an already enclosed harbour. Several adventive species have become established in Orakei Basin only. An as yet unidentified alga that has not reproduced sexually (as summer temperatures are too low) is growing vegetatively there and has not spread outside the basin. Even as a free-floating adventive this species has become very abundant with an estimated biomass of about 70 t (Dromgoole *et al.* 1993, Nelson 1994a). The sea anemone *Diadumene luciae* was found in Orakei Basin in 1977, and by 1983 had spread from there to Westmere Reef and Bucklands Beach within Waitemata Harbour (Dromgoole & Foster 1983). It still remains confined to Waitemata Harbour (Hayward 1997). *Balanus amphrite* is also confined to Orakei Basin. An Australian euryhaline copepod, *Sulcanus conflictus*, was found in Orakei Basin in 1977 (Bradford-Grieve in press). It may be confined to Orakei Basin as it has not been recorded in other Auckland Harbour waters or elsewhere in New Zealand and may be adventive here. Orakei Basin has been the initial habitat for populations of other adventives that have subsequently spread more widely around northern New Zealand.

Six adventive algal species have extremely localised distributions. *Chnoospora minima,* a widespread tropical brown alga adventive at one very local site in Port Underwood, is unattached, forming a vegetatively expanding mass of drift in 8 m of water. As summer temperatures are too low there for sexual reproduction, the lack of spores has prevented the alga spreading or developing attached plants. The site was the centre of a busy whaling station in the 1800s harbouring vessels fishing the whole Pacific Ocean and *C. minima* probably arrived on their hull fouling (Nelson & Duffy 1991). *Chondria harveyana,* an adventive red alga from Tasmania, is found only in Porirua Harbour, the site of an old whaling station that was regularly supplied from Hobart in the early 19th century, and it probably arrived on hull fouling during that period. The further spread of this alga appears to have been halted by inhospitable topography and currents (Adams 1982, 1983). *Asperococcus bullosus*, an adventive alga from the Atlantic and Mediterranean, was found originally on the wharf at Halfmoon Bay, Stewart Island, but has since been found on the *Mikhail Lermontov* wreck in Port Gore as well as in Pelorus Sound. *Polysiphonia constricta*, an epiphytic Australian species first found in 1970, has been recorded only in Otago Harbour (Adams 1983, 1991). *Polysiphonia senticulosa*, an adventive from North America, was first found originally in Wellington Harbour in 1993 and has since been found in Picton Harbour (Nelson 1994a, Nelson & Maggs 1996). The as yet unidentified red alga in Orakei Basin is confined to this locality, where it is very abundant (Nelson 1994a, Hayward 1997). All the adventive bryozoan species have limited harbour distributions, seven of them limited to just one harbour.

A number of adventive algal species have disjunctive distributions in southern harbours and anchorages heavily used in the whaling and sealing days. Three of them, *Champia affinis, Griffithsia crassiuscula,* and *Sargassum verruculosum,* were introduced from southern Australia and one, *Polysiphonia brodiei*, was introduced from Europe (Adams 1983, 1991). The ascidian *Ascidiella aspersa,* introduced to Portobello from Europe with fish and crustaceans to be reared at the hatchery in the early 1900s, was absent from all other South Island localities examined at the time of its first discovery. It spread to Lyttelton Harbour by 1950 and Halfmoon Bay, Stewart Island, by 1958 (Brewin 1946, 1950b, 1958a).

Criterion 7: Disjunct global distribution

Most of the introduced species have a wide-ranging and frequently global distribution. In the same way that *Synidotea laevidorsalis* remained a covert adventive until its taxonomy was clarified (Chapman & Carlton 1991), populations of some species have been identified as new species in New Zealand and only later been recognised as conspecific with populations elsewhere in the world. *Sargassum verruculosum*, an adventive alga from South Australia, was first described as a new endemic species, *S. raouli*, in New Zealand in 1845 (Hooker & Harvey 1845). It was properly identified in 1983 when its adventive status was recognised (Adams 1983). Correct identification has been very important in identifying adventive molluscs. *Cuthona perca* was described originally as a new endemic species, *C. reflexa*, by Miller (1977), but was later identified as an adventive from the West Indies (Behrens 1984). Other nudibranchs currently identified as New Zealand species may also turn out to be adventives (e.g., *Cuthona scintillans*, Miller 1977). *Phytia myosotis*, an ellobiid snail with direct development, probably reached Otago Harbour from Australia where it had been described as a new species *Auricularia meridionalis*. In New Zealand, it was identified as *P. myosotis*, an adventive from Europe (Climo 1982). *Microtralia* sp. another ellobiid snail with direct development, was originally described as a new New Zealand species, *Rangitotoa insularis*, by Powell (1933). It was subsequently identified as conspecific with *M. occidentalis* from Bermuda and the West Indies (Climo 1982) thus rendering it an adventive. Martins (1996) recognised the great similarity of both species but he concluded that the wide Indo-Pacific range of the genus and anatomical changes in another species precluded the immediate synonymisation of both species without further investigation. Because of the limited power of dispersal of ellobiid snails, and the geological youth of the habitat, this New Zealand species is likely to be adventive. This species also clearly belongs to the genus *Microtralia* (Martins 1996), and its full identification must await further investigation.

Criterion 8: Insufficient life-history adaptations to reach New Zealand actively or passively in currents

The dispersal capacity of bryozoans, hydroids, most ascidians, and all sponges with short-lived larvae is insufficient to bridge ocean gaps to New Zealand. Teleosts, molluscs, and echinoderms with long-lived larvae, particularly those forms that can successfully postpone metamorphosis, can readily bridge ocean gaps from Australia, Norfolk Island, and Lord Howe Island to northern and northeastern New Zealand. The dispersal opportunities for oviparous teredinids, such as *Bankia* species, result in them having more restricted distributions in temperate regions, whereas tropical species generally have a wide circum-tropical distribution. Larviparous teredinids, such as *Lyrodus* species, are considered to have become widespread because of their long larval life while being transported on driftwood or wooden ships (Turner 1966).

In recent years increased diving, especially in northern New Zealand, has resulted in more habitats becoming more accessible and has shown the need to reappraise earlier interpretations of the distribution of northern fauna. For example, Powell (1976) listed 76 species that he considered had invaded northern New Zealand waters in years of high water temperatures. Diving records suggest that these species have been continuously present in northern waters, even if rare, and are naturally occurring parts of the New Zealand biota that are generally recruited from larvae from more northern breeding populations (Marshall & Crosby 1998). Francis & Evans (1993) concluded that even among the well documented groups it is not easy to prove that newly recorded species are not simply rare, permanent members of the flora and fauna that had been previously overlooked. Furthermore, range extensions of subtropical fish and molluscs (species which produce long-lived larvae, but which do not necessarily breed in New Zealand) into northern New Zealand, have coincided with periods of much warmer conditions which may have brought their larvae 750 km southeast from Norfolk Island or 1300 km southeast from Lord Howe Island or from the Australian coast. Fish species include *Cheilodactylus fuscus* found at Mercury Island and Kawau Island in 1970; *Dactyloptena orientalis* found just north of Whangarei in 1970 (Moreland 1975); *Aulacocephalus temmincki* found at the Poor Knights Islands in 1968 (Stephenson 1970); *Stegastes gascoynei* found at the Poor Knights in 1972, *Thalassoma amblycephalum* found at the Poor Knights in 1973, *Synodus similis, Leptoscarus vaigiensis,* and *Thalassoma lunare* found at the Poor Knights in 1975, and *Purupeneus spilurus* (first recorded as *P. signatus)* found at the Poor Knights in 1976 (Russell & Ayling 1976); *Cyprinocirrhites polyactis* found at the Poor Knights in 1975 (Francis & Evans 1993); *Acanthurus dussumieri* found at Cape Brett in 1989 and more widely since (Francis & Evans 1993, Francis 1996). In 1962 small numbers of the large portunid crab *Scylla serrata* were caught at widely dispersed locations along the northern east coast of the North Island from Doubtless Bay to Bay of Islands. Small numbers continued to be caught in 1963 and 1964 with the last recorded one being captured in December 1965. All specimens caught were large and none of the females were in berry. Although this crab is a powerful swimmer, this invasion is likely to have been the result of settlement of a single pulse of larvae, probably from northeastern Australia reaching New Zealand and settling here (Dell 1964, Manikiam 1967, Wear & Fielder 1985). A single specimen of *Diadema savignyi* was collected in the Bay of Islands in April 1991, and others were reported from the Poor Knights Islands in the same summer. These specimens probably resulted from the settlement of larvae that reached the northeast coast of New Zealand well to the south of their normal range in a period of warm sea temperatures (Francis & Evans 1993).

In contrast to an expansion into northern New Zealand, one pelagic fish species has spread to southeastern New Zealand in a pattern apparently unrelated to water temperature changes. The Peruvian jack mackerel, *Trachurus murphyi*, recently extended its eastern range and suddenly appeared along the South Island coast and the Chatham Rise in 1985. By 1991 it made up 80% of the southern jack mackerel landings and since then has become very common in the Bay of Plenty and further north (Annala 1993).

Evidence points to ocean currents transporting many species with long pelagic development (especially fish and molluscs) to New Zealand in recurring episodes as northern waters became warmer in the 1960s (Moreland 1975). In the La Niña years 1989–90, northern coastal waters became warmer as the East Auckland Current became stronger and moved closer inshore (Francis & Evans 1993, Francis 1996). The Kermadec Islands, which are always bathed by the East Auckland Current, support established populations of many of the warm-water forms that only infrequently occur the Poor Knights or off mainland New Zealand. The alga *Hydroclathrus clathratus*, identified in this report as an adventive of tropical origin (Johnson & Dromgoole 1977), has recently been established as part of the indigenous biota of the Kermadec Islands (Nelson & Adams 1984) and may have extended its range to the mainland in a period of high water temperatures. In contrast, Furlani (1996) identified the alga *Caulerpa racemosa* in southern Queensland as an adventive from Japan, whereas *Caulerpa racemosa* in New Zealand is considered an indigenous member of the Kermadec flora (Nelson & Adams 1984, Adams 1994).

Invasions of subantarctic species in the south during colder years do not seem to occur, because few subantarctic species have long-lived pelagic larvae, there are only a few small subantarctic islands to act as stepping stones or sources of larvae, and subantarctic surface currents do not impinge on the New Zealand continental shelf.

Although driftwood floating in currents is cited as an important means of transport and dispersal of shipworms (Turner 1966), examination of 1500 pieces of driftwood from New Zealand shores (McKoy 1980) identified only one species, *Teredo princessae*, that had not been recorded from New Zealand. The distribution around the New Zealand coast of the five teredinid species that occur here appears to be maintained by transport of infestations in driftwood (McKoy 1980). These five species also occur in southeastern Australia, yet a further six teredinid species that also occur there have not reached New Zealand, even though driftwood could float there in the current systems. Long-distance transport of teredinids in driftwood may be more difficult than Turner (1966) suggested. The fossil record suggests that *Bankia australis* (described as *B. turneri*) has been in New Zealand since the lower Miocene, and *B. neztalia* since the upper Cretaceous. Species of *Lyrodus* and *Nototeredo* have so far not been found in the New Zealand fossil record (McKoy 1978). The three species of these genera that are present here now were unlikely to have reached New Zealand in driftwood, so they may have arrived from Australia within the hulls of wooden sailing vessels in the early 19th century. There is some evidence that human mechanisms are still important today in expanding the range of these species within New Zealand. *Lyrodus pedicellatus* was found at Bluff, well to the south of its normal range, in 1964 and probably reached this port in timber of a wooden vessel (McQuire 1964, 1965, McKoy 1980) and *L. mediolobatus* has been transported from Warkworth on the northeast coast of the North Island to Kaipara Harbour on the west coast (a new habitat for this species) in oyster-spat sticks (McKoy 1980). The other species, *Nototeredo edax*, even though moderately common in driftwood, has very limited and primarily harbour distribution in New Zealand and, although a tropical to warm-temperate species, is absent from the northeast coast of the North Island suggesting that it did not arrive here passively in driftwood which the East Auckland Current would deposit on this coast.

Criterion 9: Isolation from genetically and morphologically similar species

There is a high degree of endemism in southern marine faunas, and those of New Zealand in particular, especially the deeper water biota (Vine 1977, Gordon 1986, 1989, Newman & Foster 1987, Newman 1991, Cairns 1991, 1995) suggesting that the New Zealand marine region has been isolated from the rest of the world for a long time. The investigations of Carlton and others (Carlton 1989, 1992, 1995, Chapman & Carlton 1991, 1994, Carlton & Hodder 1995,) suggest that, with further investigation, many of the cosmopolitan species of the New Zealand coastal biota may prove to be adventives. The assumption that the coastal marine biota of New Zealand is endemic or has spread here naturally has not been upheld for the 133 established species examined here. The degree of endemism (and numbers of adventives) may vary between groups and is about 90% in molluscs. Endemism is no higher in New Zealand polychaetes (about 50%) than it is in the polychaete fauna of other southern landmasses that have not been isolated from the rest of the world (Glasby & Alvarez, in press). This conclusion may, however, be influenced by inadequate taxonomy that misidentifies some New Zealand endemic species as cosmopolitan polychaete species (Glasby & Read, in press).

Deliberate introductions that failed to establish fishery species

Although many species of freshwater fish have been successfully naturalised in New Zealand and have established important sport fisheries (McDowall 1990), apart from one Pacific salmon all attempts to naturalise marine organisms in New Zealand to develop fisheries have failed. Many of these introductions have been well documented and allow analysis of why they failed to become naturalised. This information may prove useful in formulating management strategies that will reduce or eliminate the chances of accidental introductions becoming established.

Numbers of the European oyster, *Ostrea edulis*, from the River Roach, Essex, were imported into New Zealand in 1868. Only two oysters survived the voyage and were relaid on a bed of native oysters (*Tiostrea chilensis*) at Portobello in Otago Harbour (Thomson 1922). No sign of this species has been seen since. Numbers of the Australian penaeid prawn *Penaeus canaliculus* were released in Nelson in 1892, and 200 imported in 1894 were released at the Otago Harbour Heads that year (Thomson 1922). The Portobello hatchery and marine station was established in 1904, and between 1905 and 1918 was used in attempts to naturalise a further four European species, the crab *Cancer pagurus*, the lobster *Homarus gammarus,* the turbot *Scophthalmus maximus*, and the herring *Clupea harengus* (Thomson & Anderton 1921). All data in the following paragraphs are drawn from Thomson & Anderton (1921) and Thomson (1922).

The first shipment of *Cancer pagurus* died in the tropics in 1885. Eight were imported in 1907 and a further eight in 1908. These were held in tanks at the Portobello hatchery where they bred. By 1911, when all the adults had died, they were estimated to have produced 20 million larvae which were released in or just outside Otago Harbour. In 1913, 43 more adult crabs were imported. Some died after arrival, 19 were released into Otago Harbour, and the remainder kept in tanks where they bred releasing an estimated 12 million larvae before all the adult crabs died. The crab has a long pelagic larval life and, apart from being exposed to high mortality in this period, could have been dispersed widely once flushed from the harbour. The crab never became established.

In 1885, 1891, and 1892 a few adult *Homarus gammarus* were shipped to New Zealand but all died in transit. In 1893, 12 more were imported and the 9 that survived were released off the Otago Heads that year. A further 25 lobsters were imported in 1906 and 2 reached New Zealand alive; 50 more were imported in 1907 and 14 reached New Zealand alive; 33 more were imported in 1908 and 31 survived; and in 1913, 43 more were imported with 32 surviving the trip. These lobsters were held in tanks at the hatchery and allowed to breed. Twelve of these adult lobsters were released into Otago Harbour in 1914 and over the years the captive adults are estimated to have reared 1 million eggs and the larvae hatching from them were released into Otago Harbour through the pond overflows. Thomson (1922) believed that once the young larvae were flushed from the harbour, they would have been swept well to the north in the weeks of their free-swimming developmental stages. The lobster never became established.

About 300 small turbot, *Scophthalmus maximus*, 50–75 mm long, were imported in 1913. Of these, 195 survived the voyage and were on-grown in hatchery tanks at Portobello. In 1916, when the turbot reached 250–450 mm in length, 128 were released in a trawl-free area of Tautuku Bay, Southland. The remaining 57 were grown on for a further year to maturity (330–480 mm) in the expectation that they would breed in the tanks. When these fish did not spawn in the hatchery, a further 42 fish, up to 560 mm long, were released at the same site in Tautuku Bay in 1917. The remaining 14 turbot were kept in the hatchery to breed, but apparently none ever reached spawning condition.

The first attempt to introduce herring to New Zealand, in 1886, involved shipment of 2–3 million fertilised herring eggs in a circulating refrigerated water system. Ice blocked the circulating water and all the eggs died 16 days into the voyage. Experiments between 1908 and 1910 showed that cooling could slow hatching time of the eggs to 40 days, though only 1% of these eggs hatched. In 1912, 60 000 fertilised ova were shipped in a refrigerated water system, but the filter system became fouled and all the eggs were lost after 37 days. Because of the cost, and because many shipments would clearly be required to establish this species, no further attempts have been made to introduce herring.

In these importations, considerable difficulty was experienced in keeping the fish or shellfish alive in running seawater, particularly on the passage through the tropics (even when using a refrigerated water supply). These species encountered the same thermal challenge crossing the tropics in running seawater on deck as did those organisms fouling vessel hulls. Although the individuals of each species were released in suitable habitats in New Zealand, the numbers of potentially reproductive adults was small and movement of the water mass into which their larvae would be released could readily result in larvae never encountering suitable habitat for settlement. Alternatively, larvae could become so widely dispersed at settlement that the distribution of individuals when grown could be too dispersed to allow successful breeding.

Ova of the diadromous Pacific salmon, *Oncorhynchus tshawytscha*, were first imported from California between 1875 and 1880 and the hatched fish released in Hawkes Bay rivers. These introductions failed to establish the species here. In 1901, the Government embarked on a project to establish a commercial fishery. A hatchery was built on a tributary of the Waitaki River and between 1901 and 1907 1.5 million young salmon were raised from ova imported from California and released in the Waitaki River system. A run of salmon returning from the sea was established by 1906 and from 1908 to 1942 the hatchery continued to rear ova from New Zealand salmon and release small fish in the Waitaki River system. By 1916 runs had become established in rivers to the north and south of the Waitaki River and salmon were widespread along the east coast of the South Island (McDowall 1990). The success of this introduction points to the need not only to select a species suited to the New Zealand habitat, but also to confine the introductions to one site and continue them in large numbers over many years.

In spite of the failure to establish the other fishery species, a fouling organism, the European ascidian *Ascidiella aspersa*, that accidentally accompanied these shipments to Portobello was released in sufficient numbers locally to establish itself in Otago Harbour.

Much greater numbers of adventive species have been established in other countries from shipments of live shellfish for trade or aquaculture. Two New Zealand species of crab, five species of mollusc, one brachiopod, and two asteroid species were introduced into Tasmania with live Foveaux Strait oysters imported there between 1900 and 1935 (Greenhill 1965, Dartnell 1969, Allmon *et al.* 1994). These shipments of oysters were emptied into holding beds in harbour areas and continued over many years to introduce organisms associated with the oysters into these sheltered waters. Carlton (1979) recorded that of the 96 marine species then known to have been introduced into San Francisco Bay, 37% appeared to have been transported with the great tonnage of oysters imported from the east coast and Japan to develop aquaculture in the bay, and a further 46% may have been transported with oysters and/or in hull fouling. In both countries great numbers of each species that became established were introduced annually for many years into the enclosed embayments.

Numbers of the pelagic fishes *Engraulis japonica* and *Sardinops melanostica* were released in New Zealand waters by Japanese vessels in 1981 and 1982 as live bait during pole and line fishing for tuna. The five geographically distinct species of *Sardinops* are morphologically indistinguishable and electrophoretic studies indicate that they are not genetically distinct either, but are geographically isolated populations of a single species (Whitehead 1985). Interbreeding of *S. melanostica* with the New Zealand sardine (*"S. neopilchardus"*, the western South Pacific species recorded in New Zealand) may therefore have merely increased gene flow between populations. Exactly the same situation exists with the five named species of *Engraulis* (Whitehead *et al.* 1988). *Engraulis japonica* may have interbred with the New Zealand anchovy (*"E. australis"*, the Australasian species that occurs in New Zealand) and also have increased gene flow between these populations.

What has been the most important method of transfer to New Zealand?

Most (69%) of the adventive species recognised in this report arrived in New Zealand as part of hull-fouling communities. Numerous species already established in New Zealand have been recorded in studies of fouling on vessels in New Zealand ports (Ralph & Hurley 1952, Skerman 1958, 1959, 1960), confirming the importance of this mode of introduction. Modern vessels travel faster and use more effective antifouling paints than vessels of the past. However, this does not seem to have slowed the rate of arrival of adventives in hull fouling. If we assume that the date a hull-fouling adventive is first recorded in New Zealand is related to the date it arrived here, 31 arrived here between 1900 and 1950 and 34 arrived between 1950 and the present. In 1975, eight species of barnacles, one species of fish, and two species of mollusc arrived in New Zealand from fouling populations on the slow-moving Maui oil platform that had not been antifouled (Hook 1975, Foster & Willan 1979). This shows that higher vessel speeds and effective antifouling paints are probably very important in protecting New Zealand from the invasion of hull-fouling adventives. Nevertheless, some species of fouling organisms can overcome even these obstacles to transportation across oceans (Faubell & Gollasch 1996, Gollasch & Reimann-Zurneck 1996), and the continued arrival of hull-fouling adventives in New Zealand over the last 40 years shows that this is still an efficient means of entry. This is probably the result of the increased traffic of poorly maintained pleasure craft or fishing vessels. The discharge of ballast water provides an important mechanism introducing alien species as free-swimming larvae or propagules (*see* Williams *et al.* 1988, Jones 1991, Carlton & Geller 1993). However, only five adventive species (3% of the total) in New Zealand are considered to have become established from ballast water discharge with another 3% being introduced in ballast sand: a further 32 adventive species (21% of the total) are thought to have arrived either this way or in fouling on vessel hulls (*see* Table 1).

Plastic debris is an interesting part of the flotsam of the ocean that is frequently colonised by fouling species (Winston 1986, Gregory 1990). Two species of Bryozoa were reported as having been introduced to New Zealand by this pathway (Stevens *et al.* 1996). One is *Electra tenella*, the other, *Jellyella eburnea* (as *Membranipora*), also occurs naturally in our waters on shells of *Spirula spirula* and the violet snail *Janthina*, so is not listed here as an adventive. Two barnacle species, *Platylepas hexastylos* and a balanid, tentatively identified as *Balanus flos*, arrived in New Zealand on the flippers of a hawksbill turtle stranded on Piha beach in 1970 (Foster 1978) and floating driftwood has brought in one teredinid (McKoy 1980) and may have brought in other fouling organisms. The two ellobiid gastropods probably arrived in New Zealand on dunnage.

What are the most important characteristics of the New Zealand environment for successful establishment of adventives?

Harbour breakwaters specifically built to shelter vessels from wave action and the calm conditions found within them seem propitious for the establishment of many adventives: breakwaters enclose harbour waters, reducing circulation and water exchange with that outside the immediate harbour area. Thus harbour environments can retain larvae or propagules and minimise their loss and dispersal so that sufficient numbers can settle in high enough densities for them to breed successfully as adults.

The hull-fouling communities of early sailing vessels were frequently scraped off while vessels were careened intertidally in sheltered inlets. These sites were probably ideal to contain both adults and larvae and enable invaders to quickly establish self-sustaining populations. In more recent times hull fouling has typically been removed in dry dock (Chilton 1910, Hay & Dodgshun 1997) with little chance of exotic species becoming established. However in the last 30 years, scuba divers using air-driven wire brushes have frequently been employed to scrub badly fouled vessel hulls in port. *Crassostrea gigas* was transferred to the South Island this way when barges heavily fouled in Auckland Harbour were scrubbed by divers in Croisilles Harbour, Tasman Bay (Dinamani 1991). The extent of hull fouling recorded by Hay & Dodgshun (1997) suggests that hull scrubbing in port could provide a significant route for invaders to enter New Zealand waters.

What was the rate of entry of adventives?

If we allow for a minimum of 136 species since 1900, then the rate of entry this century is 1.4 species per year. The rate becomes lower if we include earlier European ship visits but exclude Polynesian vessels. Although 159 species are recorded in this report, the actual number of introduced marine species is probably much closer to 200, so the rate of entry averaged over 356 years is 0.6 species per year since Abel Tasman's (1642) visit or 0.9 per year since James Cook in 1769.

Where did the adventive species come from?

The data have large margins of error. For many species now regarded as cosmopolitan/circumglobal or circumtropical, sources may be secondary, deriving from previous introductions. Taking the data at face value, the provenances of adventive species are: U.K./Europe/Mediterranean 48%, Japan/east Asia 11%, tropical Indo-Pacific 11%, southern Australia/Tasmania 10%, Caribbean/south Florida 6%, western USA 4%, northeastern USA 3%, South Africa 1%, Chile/western South America 1%, all other sources 5%. From the early 1800s until the 1920s, southern Australia appears to have been the next most important source after Europe, apparently declining subsequently relative to increasing introductions from Japan/east Asia and the tropical Indo-Pacific. The numbers from Europe are almost certainly inflated by including those now-cosmopolitan species that were first described from British and European specimens. Inasmuch as some of these species were recorded from southeastern Australia in the decades before they arrived in New Zealand, it is likely that Australia (or, in a few instances, Japan) was the more immediate source. In the 1990s, more species may have had Europe as their source than those from east Asia and elsewhere.

What has been the impact of adventives on the New Zealand environment?

So few biological studies have been carried out on New Zealand marine adventive species that the effects of most of them are not formally recognised. For the most part their distributions are limited to ports and harbours and this limits their effects on native assemblages between major harbours or harbour entrances. The most obvious effects are from species that occur so abundantly that either through competitive exclusion and/or habitat modification they negatively affect native species and assemblages (*see* Griffiths *et al.* 1992, Crooks 1998). Alternatively the impact may be economic or potentially economic.

The best-documented habitat-modifiers are bivalves (Pacific oyster, *Crassostrea gigas;* Asian mussel, *Musculista senhousia;* file shell *Limaria orientalis;* fragile bivalve *Theora lubrica* (*see* Hayward 1997)). Large sheet-encrusting bryozoans like *Watersipora subtorquata* and *Cryptosula pallasiana* competitively exclude slower-growing or less robust native species in intertidal or immediately subtidal habitats (Morton & Miller 1968, Gordon & Mawatari 1992). Species of cord grass (*Spartina*) become weeds that alter upper-harbour habitats and cost money to eradicate. Recent ecological studies of wakame (*Undaria pinnatifida*, the best-documented candidate for ballast-water introduction (Nelson 1995) have shown reduction in the diversity of understorey invertebrates (Miller *et al.* 1997, Battershill *et al.* 1998). Two species of polychaete worms have more direct economic impacts — *Ficopomatus enigmaticus* in warm years can significantly foul marinas and hulls of pleasure craft in estuaries and cooling-water intake pipes for power stations (Read & Gordon 1991), and *Polydora websteri* can foul cultured Pacific oyster, causing blistering of shells with entrapped pockets of hydrogen sulphide gas, spoiling them for market use (Handley 1995). The now globally widespread, shell-boring sponge *Cliona celata* is a significant eroder of biogenic carbonate. Locally (as in the Orakei Basin, Auckland), adventive species (*Musculista senhousia, Balanus amphitrite, Diadumene luciae, Conopeum seurati*, and a filamentous red alga) can completely dominate the biota.

Conclusions

By surveying the literature, we have established the adventive status of 148 marine species that have arrived in New Zealand accidentally over the last 200 years and recorded the history of a further 11 species that were introduced deliberately. Many of the species that became established have highly disjunctive local distributions (criteria 3 and 6) and many of the most recent arrivals suddenly appeared locally where they had not occurred before (criterion 1). These criteria are suitable for identifying recent arrivals that are still spreading or have remained localised at their site of entry.

The criteria are not useful in identifying species that arrived on sailing vessels before the marine biota was described. Some of these arrivals can be identified by their present-day, highly localised distribution in harbours and roadsteads heavily used by sailing vessels over 100 years ago (*see* Adams 1983, 1994, Gordon & Mawatari 1992, Nelson 1994a). Other cosmopolitan species that spread rapidly around the country at that time cannot be identified as adventives by these criteria today and are now considered part of the non-adventive biota of New Zealand. The extreme isolation of New Zealand and the high levels of endemism in many marine groups, however, suggest that most of these cosmopolitan species are really adventives that fouled sailing vessels.

Although some criteria help identify adventive species, genetic studies may ultimately be required to determine the true origin of some widespread marine organisms. For example, the blue mussel, *Mytilus galloprovincialis*, common throughout New Zealand, could have readily been introduced here in the sailing ship era. Allozyme studies suggest that *M. galloprovincialis* is a native of the coasts of Europe and the Mediterranean, but that it has been introduced into southern California, Japan, Hong Kong, and South Africa (Grant & Cherry 1985 Koehn 1991). Mitochondrial DNA studies (T. J. Hilbish, University of South Carolina, pers. comm.) suggest that the populations of *M. galloprovincialis* in Chile, New Zealand, and Australia have spread naturally from an invasion from the South Atlantic 0.8 million years ago. These same studies have, however, revealed the presence of a species with *M. edulis*-like mitochondrial DNA adventive in the North Island of New Zealand.

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