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RESEARCH ARTICLE

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Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia

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Abstract Port Phillip Bay (PPB) is a large (1,930 km^2), temperate embayment in southern Victoria, Australia. Extensive bay-wide surveys of PPB have occurred since 1840. In 1995/1996 the Commonwealth Scientific and Industrial Research Organization (CSIRO) Centre for Research on Introduced Marine Pests (CRIMP) undertook an intensive evaluation of the region with the aims of developing a comprehensive species list of native and introduced biota and contrasting previous bay-wide assessments with a current field survey in order to detect new incursions and discern alterations to native communities. Two methods were used to meet these aims: a re-evaluation of regional museum collections and published research in PPB to identify and determine the timing of introductions; and field surveys for benthic (infauna, epifauna and encrusting) organisms between September 1995 to March 1996. One hundred and sixty introduced (99) and cryptogenic (61) species were identified representing over 13% of the recorded species of PPB. As expected, the majority of these are concentrated around the shipping ports of Geelong and Melbourne. Invasions within PPB appear to be increasing, possibly due to an increase in modern shipping traffic and an increase in aquaculture (historically associated with incidental introductions); however the records of extensive biological surveys suggest that this may, in part, be an artefact of sampling effort. In contrast to Northern Hemisphere studies, PPB (and Southern Hemisphere introductions in general) have significantly different suites of successfully invading taxa. PPB is presented as one of the most invaded marine ecosystems in the Southern Hemisphere.

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Introduction

Human-mediated change to the marine environment has recently become a focus of the biodiversity and conservation debate (Lubchenco et al. 1991; Vitousek et al.1997) with human-mediated biological introductions recognised as one of the top five threats to native biodiversity (e.g., Elton 1958; Carlton 1989; Drake et al. 1989; Vitousek et al. 1997). Despite recognition of the seriousness this threat poses, detailed information on the scale of marine invasions, the relative importance of transport mechanisms and the underlying biological processes associated with successful introductions remains sparse. The processes and dynamics of invasions in terrestrial and freshwater habitats are well documented (e.g., Groves and Burdon 1986; Kitching 1986; MacDonald et al. 1986; Mooney and Drake 1986; Joenje et al. 1987; Kornberg and Williamson 1987; Drake et al. 1989; di Castri et al. 1990; Williamson 1996); however, our understanding in the marine environment lags far behind. As first steps in documenting the scale of the marine invasion problem, several broadly targeted evaluations of introduced marine biota have been conducted in regional and local (port) areas around the world (e.g., Cohen and Carlton 1995; Cranfield et al. 1998; Cohen et al. 1999; Coles et al. 1999; Ruiz et al. 1997, 2000; Gollasch and Leppäkoski 1999; Hewitt et al. 1999; Leppäkoski and Olenin 2000; Occhipinti-Ambrogi 2000; CIESM 2002; Hewitt 2002; Leppäkoski et al. 2002). These broad-scale surveys typically indicate highly diverse introduced assemblages from widely different taxonomic associations.

The transport of non-indigenous species is often, but far from exclusively, associated with commercial shipping activities (e.g., hull fouling, hull boring, wet and dry ballast), and typically results in port environments becoming major points of biotic invasion (e.g., Carlton 1985; Cohen and Carlton 1995, 1998; Ruiz et al. 1997, 2000; Hewitt et al. 1999; Hewitt and Campbell 2001; Hewitt 2002). As a consequence, in 1995, the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Centre for Research on Introduced Marine Pests (CRIMP) began a two-part effort to determine the extent of invasions and inferred invasion mechanisms in Australian coastal waters. First, in conjunction with the Australian Association of Ports and Marine Authorities, port surveys were initiated in representative ports around Australia, using a consistent design and sampling protocol (Hewitt and Martin 1996, 2001). To date, approximately half of Australia's 62 first ports of call for foreign vessels have been surveyed as part of the Australian National Introduced Species Port Baseline Surveys Program (Hewitt 2003).

The second component was a detailed analysis of the invasion history and introduced species status of a major Australian embayment. Port Phillip Bay (PPB) was selected for this analysis on the basis of its long history of use by maritime trade (extending back to the early 1800s) previous (and at times extensive) surveys and evaluations for the physical and biological characteristics of the bay, the availability of relevant taxonomic expertise with local knowledge of PPB, and CSIRO's previous work in the region relating to taxonomy, distribution and ecology of the biota.

This paper provides a synopsis of the CSIRO PPB Introduced Species Study (Hewitt et al. 1999), which was a collaborative effort involving scientists from Australia and New Zealand with taxonomic expertise in the range

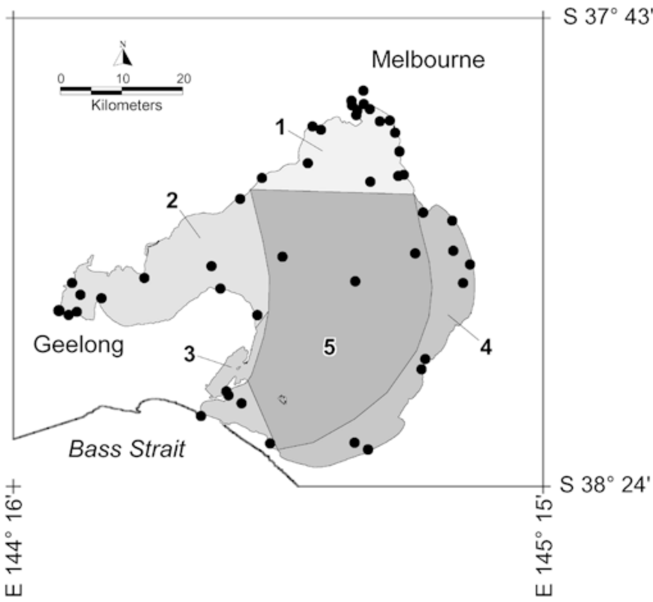


Fig. 1 Port Phillip Bay (PPB), regions (1–5) and CRIMP sampling locations (for detailed information on locations of specific sampling techniques see Hewitt et al. 1999). Note the major shipping ports of Geelong and Melbourne and the concentration of sampling effort in these areas

of taxa represented in these collections. This study is one of the most thorough investigations of the introduced species status of a single embayment in the world, and the only major study of introduced marine species in a Southern Hemisphere port environment.

The study area

PPB is a large (1,930 km^2), sheltered, temperate embayment on the southern coast of Victoria, Australia (Fig. 1). First "discovered" by Europeans in 1802, European settlement began in 1834 and immigration in 1836. Today the shores of PPB host Australia's second largest metropolitan area (Melbourne, Geelong and associated areas) with a total human population of 3.5 million. PPB represents one of the largest throughput ports in Australia with over 150 international and 400 domestic ship visits in the ports of Melbourne and Geelong each year.

Physically, PPB is a drowned river system, formed approximately 8,000 years ago. The physical characteristics of the bay were described in detail by Harris et al. (1996). In brief, the bay is relatively shallow, with a maximum depth of approximately 24 m and the vast majority at less than 8 m. The salinity of most of PPB is >32 PSU except near the mouth of the Yarra River. Temperatures fluctuate seasonally between 11°C and 21°C, and are relatively uniform across the bay. The bottom of the bay is predominantly silt, fine sands and clay, with coarser sediments in shallower areas and a high-organic loose floc in the deeper center of the bay. Water movement is driven by tides, winds and density differences, the latter due to seawater entry from Bass Strait and freshwater sources from, in particular, the Yarra River, which is close to the Port of Melbourne. The general circulation pattern, driven by the dominant west winds, consists of two large gyre systems. Residence time for water in PPB is 10–16 months.

Major habitat types in PPB were detailed by Coleman et al. (1999). Soft, subtidal sediments provide the major benthic habitat type in the bay. Sediments are sandy near the edge of the bay and become progressively muddier towards the deeper waters in the centre of the bay. Other habitat types include subtidal reefs, intertidal sandy and rocky areas and estuarine areas. The bay as a whole is considered "healthy" (see Harris et al. 1996), but is subject to a range of diverse disturbances, including commercial fishing, scallop dredging (discontinued in 1996), channel dredging, substantial nutrient loading from urban run-off and sewage treatment and, historically, metal and other inorganic pollutants from industrial and urban point sources.

Several extensive, bay-wide biotic surveys of PPB were undertaken during the last two centuries. Over 500 species of benthic macrophytes (algae, mangroves and seagrasses) and more than 700 species of benthic invertebrates are known from the region (see Black 1971; Poore et al. 1975). Overviews of the biota are provided by the Marine Research Group of Victoria (1984), Gomon et al. (1994) and Edgar (1997). Over the last 25 years, significant changes have been observed in the soft sediment infauna (Wilson et al. 1998; Currie and Parry 1999). One introduced species (the bivalve *Theora lubrica*) was identified in the ten most abundant species during the 1970s, but since then four additional introduced species (the polychaetes *Sabella spallanzanii* and *Euchone limnicola*, the bivalve *Corbula gibba* and the crab *Pyromaia tuberculata*) have displaced native species from the list, resulting in five of the top ten most abundant species being non-indigenous in 1999 (Currie and Parry 1999).

Vectors, shipping and trade

The history of European influence in Australia is relatively short (Crosby 1986). Despite the long history of aboriginal culture in the region, the history of marine biological invasions most likely began with European contact. PPB was first "discovered" by Europeans in 1802, and European settlement began in 1834 with significant immigration starting in 1836. The first marine biological collections were not made until the early 1840s, but no detailed surveys were conducted until the 1860s. The establishment and development of trading in PPB group into four periods (see Campbell and Hewitt 1999a for further details): exploration/colonisation (pre-1839); immigration (1839–1851) and Gold Rush (1852–1860); the modern period up to and including just post-World War I (1861–1920); and the remaining modern period post-World War I to the present (1921–present).

Exploration/colonisation (pre-1839)

Sealing and whaling operations were established in the Bass Strait islands by 1796, often using Western Port (the embayment to the immediate east of PPB) as a home base (Shaw 1997). These sealers and whalers were typically from North America, and frequently had contact with Asia (Shaw 1997). British entry into the Port Philip Heads by John Murray of the "Lady Nelson" in 1802 led to the establishment of a convict colony in 1803 (Shillinglaw 1972). Trade during this period was largely with other Australian colonies; however, periodic visits from Great Britain occurred. From 1803 to 1835 only three ocean-going vessels entered PPB (Shaw 1997). By 1839, regular intra- and inter-colony (South Australia, New South Wales, and Tasmania, Australia; New Zealand) trade routes were established, as were regular international routes to Great Britain. Due to the East India Company's monopoly of British trade between the Cape of Good Hope and the Straits of Magellan, there was limited direct trade between British colonies until 1834 (Staples 1966; Bach 1976). During this period, international vessels trading with PPB followed the Admiralty and later the Great Circle routes (Fig. 2a). Vessels originating in Europe would typically travel to South America (e.g., Recife, Rio de Janeiro), South Africa (e.g., Cape Town, Durbin), then to Australia (with some exceptions to trade via India).

Immigration (1839–1851) and the Gold Rush (1852–1860)

Free British immigrants arrived in Melbourne in 1839 from Sydney, and the "David Clarke" arrived from Great Britain later in that year (Strahan 1994). Over 11,500 immigrants arrived at the Point Ormond quarantine station in PPB during 1839 (Shaw 1997). Pacific trade began in 1840, catering for the demand for Newcastle coal in California (Bach 1976). The repeal of British navigation laws in 1849 allowed foreign vessels entry into British colonial ports. Simultaneously the signing of the Treaty of Nanking ceded Hong Kong to Great Britain and opened Chinese Ports to British residence and trade (Lubbock 1933). The announcement of gold in Victoria in 1851 had an effect on immigration much like that in California following the California gold strike: the population swelled from $<40{,}000$ to 416,000 in 5 years (Bach 1976; Wild 1950) with immigrants from all continents often abandoning the vessels to rot in PPB. Port facilities expanded to meet the needs of a burgeoning population and new domestic (coastal) and international trade routes were opened (Fig. 2b).

Modern era—up to World War I (1861–1920)

As noted by Carlton (1985, 1996b), shipping changed considerably between the 1860s and the present. The

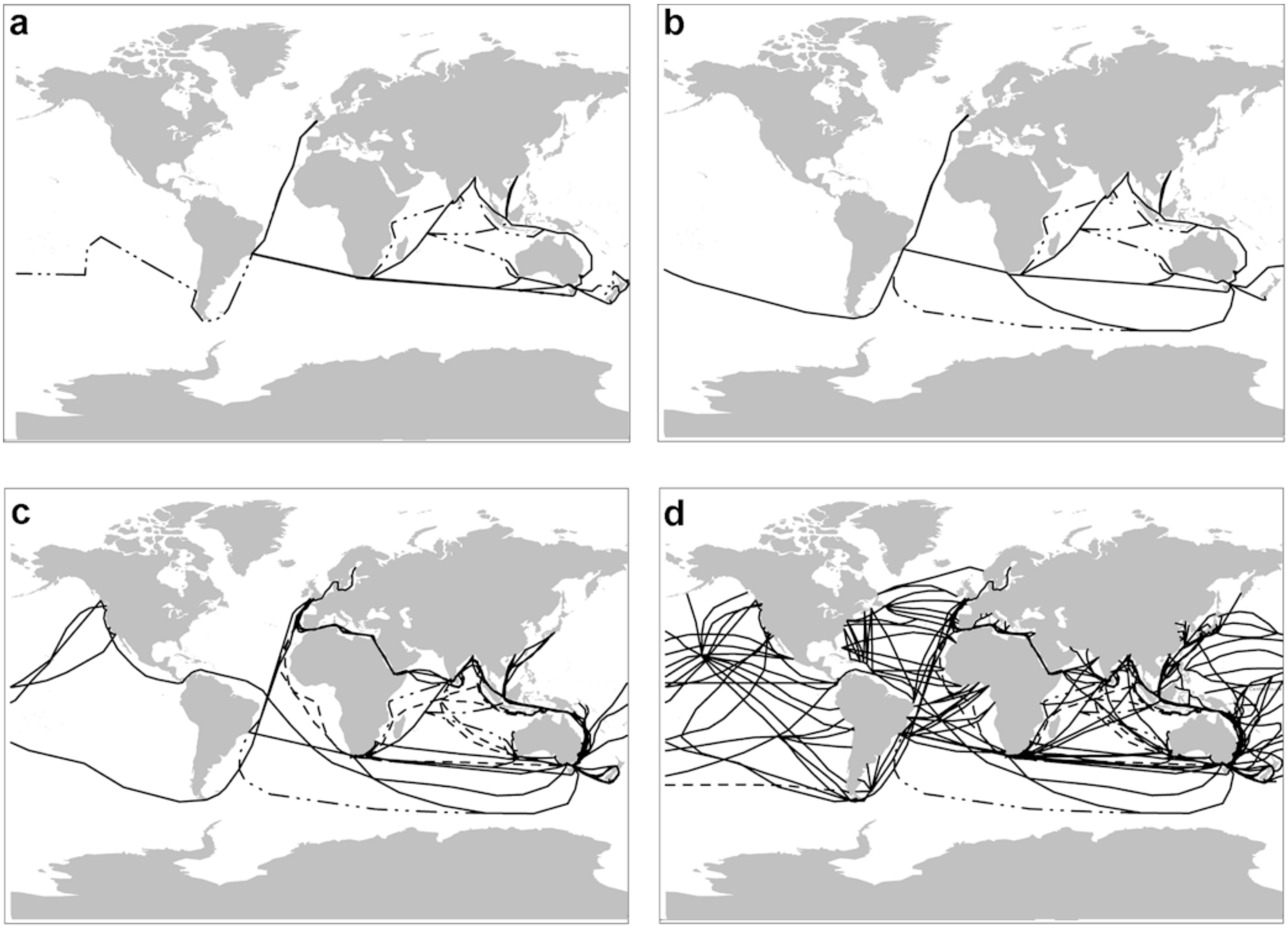


Fig. 2a–d Historical trade route maps of four periods. **a** Exploration/colonisation (pre-1839). **b** Immigration (1839–1851) and the Gold Rush (1852–1860). **c** Modern era to Post-World War I (1861–1920). **d** Modern era pre-World War II to present (1921–present). *Solid lines* represent common routes; *dashed lines* represent rare or itinerant routes

shift from wooden-hulled to steel-hulled vessels reduced the transport of marine borers. Simultaneously the shift from dry ballast (rock, cobble, sand) to water ballast (in steel ships) reduced the transport of near-shore meiofauna and adult benthic encrusting and epifauna, while providing a new vector for holo-, mero- and tychoplanktonic organisms.

Australian shipping tonnage was 93% British until the early 1900s. As trade became increasingly commercial, more ports of call were added to Conference shipping routes (established routes and cargo). By 1870 the trans-Pacific route went from Melbourne to Honolulu, Vancouver, Seattle, Tacoma, Portland, San Francisco and Los Angeles before returning to Melbourne (Bach 1976). The opening of the Suez Canal in 1869 and its subsequent deepening in 1875 led to increasing shipping traffic through the Mediterranean. The increasing global activity included the transport of military personnel and equipment from Australia during World War I (Fig. 2c).

Mariculture transfers of flat oysters (*Ostrea lutaria*) from New Zealand to Tasmania may have increased the likelihood of New Zealand species arriving in PPB via trade with Tasmania. No *O. lutaria* transport directly to PPB was known to occur.

Modern era—post-World War I to the present (1921–present)

Post-World War I wooden-hulled vessels in international and coastwise transport were significantly phased out (and almost non-existent by 1950). This resulted in the concomitant increase in reliance on ballast water and the disappearance of dry (or semi-dry) ballast as a vector. Similarly, the increased speeds of vessels and advent of more effective anti-fouling paints probably reduced the transport of encrusting and fouling organisms in numbers, if not diversity. During this period, the exponential growth in global trade led to a proliferation of trade routes (Fig. 2d).

Mariculture transport of *Crassostrea gigas* adults from Japan to PPB by CSIRO fisheries may have resulted in the inoculation of associated species.

Materials and methods

Reviews of all major groups in PPB for which taxonomic expertise was available were undertaken to provide the broadest and most in-depth coverage possible. Taxa were allocated as follows: J. Lewis (Defence Science and Technology Organisation (DSTO) - macroalgae; M. Lockett (University of Technology Sydney) and M. Gomon (Museum Victoria) - fish; M. Keough (University of Melbourne) and J. Ross (CRIMP/University of Tasmania) - fouling species; J Watson (Marine Science and Ecology) - hydroids; S. Boyd (Museum Victoria) - molluscs; R. Wilson (Museum Victoria) - polychaetes; G. Poore (Museum Victoria) - crustaceans; T. O'Hara (Museum Victoria) - echinoderms; and P. Bergquist (Auckland University) - sponges. Each author drew on previous collections or observations of marine and brackish-water organisms in PPB, scientific papers, monographs and books, and reports by and for Commonwealth and State governments and private organizations. We also reviewed the national and state Herbaria collections of algae, and the Museum Victoria catalogues of invertebrates and fishes for records of all marine or estuarine organisms collected in PPB. Dates of first record were assumed to represent the date of first introduction.

The ten-point criteria of Chapman and Carlton (1991, 1994) were used as a guide to determine native, introduced and cryptogenic (of undetermined origin, sensu Carlton 1996a) status. The probable origins or previously known geographic ranges of the introduced species occurring in PPB were derived from the general literature and from expert opinion (see Hewitt et al. 1999). Synthesis of the results was the responsibility of the first four authors.

Three field-sampling programs complemented the taxonomic reviews. First, in 1995 and 1996, CRIMP undertook targeted surveys to fill apparent gaps in the geographic or habitat coverage of previous surveys. The geographic extent of PPB (1,930 km^2) precluded a systematic survey of all locations and habitats; instead a targeted survey was performed in regions of high historic and modern shipping traffic with an overview of the remaining regions (Fig. 1). With a few exceptions, collection methods were consistent with the protocols developed for the Australian National Introduced Species Port Baseline Surveys Program (Hewitt and Martin 1996, 2001). At each pier or wharf station, fouling organisms growing on hard surfaces were semi-quantitatively collected from the intertidal zone to the bottom (maximum 26 m depth), preserved in formalin or alcohol and sorted into taxa. Sediment-dwelling organisms and their substrata were collected from depths ranging down to 26 m by inserting a 15-cm-diam hand core, 25 cm into the sediment and sieving through 1-mm mesh. Additional sampling for sediment-dwelling organisms was conducted off beaches using hand cores at 0, 1, 2, 5, and 10 m depth (mean low water (MLW)) contours; beam trawls along 100 m transects perpendicular to shore at depths of 1, 2, 5, and 10 m (MLW); and benthic sled trawls along 100 m transects at depths of 5, 10, 15, 20, and 25 m depth (MLW) (for specific station locations see Campbell and Hewitt 1999b). No algal samples were collected during the CRIMP surveys. Preserved sediment-dwelling organisms were wet-sieved in the laboratory through a 500-micron-mesh screen. All fouling and sediment-dwelling specimens were sorted and identified to species or lowest practicable taxon. Vouchers of all taxa were distributed for identification or verification of preliminary identifications.

Second, the Victorian Marine and Freshwater Resources Institute (MAFRI) surveyed the Port of Geelong for exotic marine species between 28 August and 23 October 1997. The principal objective was to determine if any of a suite of "target" pests were present in the Geelong area, with incidental information collected on all other non-indigenous species. Sampling focused on the seven commercial shipping facilities in the Geelong Arm of PPB (Point Henry Pier, Rippleside Pier, Bulk Grain Pier, Corio Quay, Lascelles Wharf, Refinery Pier and Point Wilson Jetty) (Currie et al. 1997, 1999). The MAFRI sampling protocols, outlined in Table 1, broadly followed Hewitt and Martin (1996, 2001) and were detailed by Currie et al. (1997, 1999).

Finally, as it was suspected that past surveys of fishes inadequately covered port areas of the bay, the Museum Victoria carried out sampling for exotic fish. Divers using the ichthyocide rotenone sampled hard substrates. Soft substrate sites were sampled using a 6 m beach seine net with a mesh size of 1 cm. Generally, two shots were conducted at each site. Virtually all specimens collected were preserved, identified and registered in Museum Victoria collections. Two fish surveys were conducted, in spring (November–December) and mid-summer (February). The detailed results are presented by Lockett and Gomon (1999; 2001).

The bioregion scheme developed by the International Union for the Conservation of Nature (IUCN; Kelleher et al. 1995) was used to evaluate species origins and changes in trade route patterns through time.

Transport vectors were compiled into five broad categories: hull fouling/boring, mariculture, dry and semi-dry ballast, water ballast, mariculture and intentional introduction (Carlton 1979, 1985; Coles et al. 1999). To assess the role of each vector in PPB, we scored each species for most probable vector(s) based on the biology of each life history phase (e.g., planktonic larvae for ballast water, attached benthic phase for hull fouling) and the timing of invasions (e.g., before or after the advent of ballast water use). Species assignments to vectors were not exclusive; any vector by which a life history phase could be transported (see expert chapters in Hewitt et al. 1999) *and* that was operating at the time of first collection, was given equal weighting (the total for an individual species summing to 1), and a percentage of all species calculated for each vector.

Table 1 Summary of sampling methods, habitats sampled and target taxa, for the Centre for Research on Introduced Marine Pests (CRIMP) surveys and the Marine and Freshwater Resources Institute (MAFRI) Port of Geelong survey (from Hewitt and Martin 1996, 2001)

Sampling methods	Habitat sampled	Target taxa
Non-targeted:		
Qualitative surveys:		
Diver searches	Piles, breakwaters, soft sediment	Algae, invertebrates, fish
Video/still photography	Piles, breakwaters, soft sediment	Algae, invertebrates, fish
Ockelmann sled	Soft sediment	Epifauna
Beach seine	Soft sediment, seagrass	Mobile epifauna, fish
Plankton net – 100-μm	Water column	Zooplankton
Quantitative surveys:		
Diver scrapings	Piles	Algae, invertebrates
Video/still photography	Piles	Algae, invertebrates
Smith-McIntyre grabs	Soft sediment	Infauna
Large cores	Soft sediment	Infauna
Targeted:		
Diver searches	Piles, breakwaters, soft sediment	*Asterias, Sabella, Carcinus*
Traps	Piles, breakwaters, soft sediment	*Carcinus*
Small cores	Soft sediment	Dinoflagellate cysts
Shore surveys	Intertidal wrack	*Undaria*
Plankton net – 20-μm	Water column	Dinoflagellates

Results

The first biological surveys and collections in PPB began after the 1840s for flora (Harvey 1847, 1855, 1858–1863, 1869; Sonder 1852, 1853, 1880; Wilson 1886, 1889, 1890, 1892, 1894, 1895) and for benthic fauna (surveys by Wilson, Agardh, Carpenter, Hickson, Spencer, Sendy, and Pritchard among others; Anon 1890, 1892, 1894, 1895). After the death of J.B. Wilson in 1895, few other surveys were conducted in the region until the early 1950's. From these surveys, more than 1,191 taxa have been identified from the PPB benthos alone (Harris et al. 1996). Of these, 154 were determined to be either introduced (93; 7.8% of all species) or cryptogenic (61; 5.1% of all species) marine and brackish water taxa (see Table 2) (Boyd 1999; Keough and Ross 1999; Lewis 1999; Lockett and Gomon 1999; O'Hara 1999; Poore and Storey 1999; Watson 1999; Wilson 1999; P Bergquist in Keough and Ross 1999). In addition, one species had been intentionally introduced but had subsequently become locally extinct (the oyster *Crassostrea gigas*), one species (the flatworm *Euplana gracilis*) was recognised in the literature but not found, while another 18 species were identified as "potentially" introduced into the region but no records were found in PPB. These 20 species are not incorporated into the remaining analyses (but are presented in Table 2).

Three hundred and one additional taxa held in Museum Victoria collections or collected in previous bay-wide surveys could be identified only as far as family or genus and appeared not to belong to any known described species. Given the known high percentage of specific endemicity in the southern Australia fauna and flora and the fact that many local species remain to be described, these taxa were classed as endemic rather than cryptogenic by the taxonomic experts.

In the CRIMP survey more than half (456) of the known native *animal* species were collected. Forty-five of these were found to be introduced and four cryptogenic. Six introduced species not previously recorded from PPB were collected in the CRIMP survey, bringing the total numbers to 99 introduced and 61 cryptogenic species.

These additional species are three sponges (*Dysidea fragilis, Haliclona heterofibrosa,* and *Halisarca dujardini*) and three crustaceans (*Cirolana harfordi, Corophium sextonae,* and *Paracerceis sculpta*). *Dysidea fragilis* is widely distributed on the Atlantic coast of northern Europe. Previous records of this sponge from Australian waters exist (Burton 1934), but P. Bergquist considers the sponge to be misidentified. This species is now established in Port Melbourne. *Haliclona heterofibrosa* is native to the northern hemisphere common on cold-water European Atlantic coasts and has been introduced to New Zealand. The species is established in the Geelong Arm of PPB. *Halisarca dujardini* is native to European Atlantic coasts, but has spread to North America, New Zealand, and South Africa. This is the first record of the species in Australia where it has established in Port Melbourne. *Cirolana harfordi* was previously known from western North America, British Columbia to Baja California (Richardson 1905), and has been introduced to Japan, eastern Russia, Malaysia, and other places in Australia (NSW, WA). It is established in Port Melbourne and the Point Henry Pier in the Geelong Arm. *Corophium sextonae* is native to England and has subsequently been reported in France, Portugal, The Netherlands, the Mediterranean, New South Wales (Australia), and New Zealand. It is established in the Geelong Arm and at Queenscliff in PPB. *Paracerceis sculpta* is native to the Pacific Coast of Mexico (Menzies 1962) and central California, North America, and has since been found in Hawaii, Brazil, and Townsville, Queensland (Harrison and Holdich 1982). This species has since been detected in other ports of Australia during the course of introduced species port surveys (Hewitt and Campbell 2001). A single male specimen was found in the port of Melbourne.

The MAFRI survey of the Port of Geelong collected 18 introduced (16) and cryptogenic (2) species from the commercial structures, all of which had been included in the taxonomic reviews. These species were: the algae *Ulva lactuca* and *Undaria pinnatifida*; the annelid polychaetes *Euchone limnicola, Myxicola infundibulum,* and *Sabella spallanzanii*; the bryozoans *Bugula neritina* and *Watersipora subtorquata*; the chordates—ascidians *Ascidiella aspersa, Ciona intestinalis, Styela clava,* and *S. plicata*; the fish *Acentrogobius (Amoya) pflaumi*; the crustaceans *Carcinus maenas, Cirolana harfordi,* and *Jassa marmorata*; and the molluscs *Corbula gibba, Musculista senhousia,* and *Theora lubrica*.

The targeted fish surveys by Lockett and Gomon (1999, 2001) identified four introduced species in PPB. Two species, *Acanthogobius flavimanus* and *Tridentiger trigonocephalus*, both native to the Northwest Pacific bioregion, were previously known from PPB (Middleton 1982; Paxton and Hoese 1985, respectively). A further species from the Northwest Pacific, *Acentrogobius (Amoya) pflaumi*, was detected during sampling (Lockett and Gomon 1999, 2001). A New Zealand tripterygiid, *Forsterygion lapillum*, was also collected in the Corio Bay region (Lockett and Gomon 1999, 2001).

All taxa examined or collected had non-indigenous representatives, however, the introduced and cryptogenic species are not evenly spread among taxonomic groups (Fig. 3). Four groups in particular (cnidarians, crustaceans, chordates and bryozoans) dominate, jointly comprising more than 75% of all non-indigenous species.

Introduced and cryptogenic species are found in all regions of the bay. The richness of the invasive biota, however, varies widely across the bay. Most of the reported introduced (72.7%) and cryptogenic (95%) species are found on hard substrata (i.e., pilings, breakwalls, natural and artificial reefs). These habitats are predominantly found in regions 1 and 2 (Fig. 1), which is also where: shipping activities are focused; disturbances to native communities have historically been concentrated; and most non-native species were

Table 2 Introduced and cryptogenic species reported in the literature, collected or observed in Port Phillip Bay (including those species without voucher specimens). *Taxon: boldfaced and underlined* new report, *solid circle* questionable identification or no available specimen, ‡ locally extinct, [na]not incorporated into analyses. *Status: I* introduced; *C* cryptogenic; *Source:* citation of first record where available, or of the examined specimen including those in collections: *AD* Adelaide Herbarium; *MELU* Melbourne University; *MUCV* Museum of Central Victoria; *MV collections* Museum Victoria. *First PPB* year first collected or published where collection dates are unknown, *NR* not recorded in PPB but from Victoria; *Origin* for introduced species the presumed native region, for cryptogenic species the current known distribution. *Vectors: HF* hull fouling; *M* mariculture; *SDB* semi-dry ballast; *BW* ballast water; *I* intentional; *solid circle* potential primary vector; *solid triangle* transport in sea-chests

Taxon	Status	Source	First PPB	Presumed origin (I) or distribution (C)	HF	M	SDB	BW	I
Plantae									
Chlorophyta									
Bryopsidaceae									
Bryopsis plumosa	C	Womersley 1966	1966	NE Atlantic	●				
Cladophoraceae									
Chaetomorpha aerea	C	King et al.1971	1971	NE Atlantic	●				
Chaetomorpha capillaris	C	Lewis 1983	1983	Mediterranean	●				
Chaetomorpha linum	C	O'Brien 1981	1981	Baltic Sea	●				
Cladophora prolifera	I	Ducker 1964, MELU[a]	1964	Mediterranean	●				
Codiaceae									
Codium fragile ssp *tomentosoides*	I	Parry 1997, MELU[a]	1997	NE and NW Atlantic	●				
Derbesiaceae									
Derbesia marina	C	Lewis 1977	1977	Arctic	●				
Ulvaceae									
Enteromorpha compressa	C	Lewis 1977	1977	Baltic Sea	●				
Enteromorpha intestinalis	C	O'Brien 1981	1981	Cosmopolitan	●				
Ulva fasciata	I	Parish 1978, MUCV[a]	1978	Mediterranean	●	●			
Ulva lactuca	C	Womersley 1984	1984	NE Atlantic	●	●			
Ulva rigida	C	Lewis 1983	1983	Mediterranean	●	●			
Ulva stenophylla	C	Phillips 1988	1988	NE Pacific	●	●			
Dinophyaceae									
Alexandrium catenella	I	Hallegraeff et al. 1988	1988	Cosmopolitan				●	
[na]*Alexandrium minutum*	C	Hallegraeff et al. 1988	NR	Cosmopolitan				●	
Alexandrium tamarense	C	Arnott 1998	1993	Cosmopolitan				●	
· [na]*Gymnodinium mikimotoi*	C	Harris et al. 1996	< 1970	Cosmopolitan				●	
· [na]*Gymnodinium pulchellum*	C	Harris et al. 1996	< 1970	Cosmopolitan				●	
Phaeophyta									
Alariaceae									
Undaria pinnatifida	I	Campbell and Burridge 1998	1996	NE and NW Pacific	●			●	
Cladostephaceae									
Cladostephus spongiosus	C	Womersley 1966	1966	NE Atlantic	●				
Cutleriaceae									
Cutleria multifida	C	Womersley 1966	1966	NE Atlantic	●				
Dictyotaceae									
Dictyota dichotoma	C	Womersley 1966	1966	NE Atlantic	●				
Ectocarpaceae									
Acinetospora crinita	C	King et al.1971	1971	NE Atlantic	●				
Ectocarpus fasciculatus	C	King et al.1971	1971	NE Atlantic	●				
Ectocarpus siliculosus	C	Womersley 1966	1966	NE Atlantic	●				
Feldmannia globifera	C	Womersley 1966	1966	Mediterranean	●				
Feldmannia irregularis	C	King et al.1971	1971	Mediterranean	●				
Feldmannia lebelii	C	King et al.1971	1971	NE Atlantic	●				
Ectocarpaceae									
Hincksia granulosa	C	King et al.1971	1971	NE Atlantic	●				
Hincksia mitchellae	C	King et al.1971	1971	NW Atlantic	●				
Hincksia ovata	C	King et al.1971	1971	NE Atlantic	●				
Hincksia sandriana	C	King et al.1971	1971	Mediterranean	●				
Kuckuckia spinosa	C	King et al.1971	1971	Mediterranean	●				
Pilayella littoralis	C	King et al.1971	1971	Mediterranean	●				
Sorocarpus micromorus	I	Clayton 1970, MELU[a]	1970	NE and NW Atlantic	●				
Stictyosiphon soriferus	I	King 1969, MELU[a]	1969	NE and NW Atlantic	●				
Leathesiaceae									
Leathesia difformis	C	King et al.1971	1971	NE Atlantic	●				
Petrospongium rugosum	C	King et al.1971	1971	NW Pacific	●				

Table 2 (Contd.)

Taxon	Status	Source	First PPB	Presumed origin (I) or distribution (C)	HF	M	SDB	BW	I
Myrionemataceae									
Myrionema strangulans	C	King et al.1971	1971	NE Atlantic	●				
Punctariaceae									
Asperococcus compressus	I	Kraft 1976, MELU[a]	1976	NE and NW Atlantic	●				
Punctaria latifolia	C	King et al.1971	1971	NE Atlantic	●				
Scytosiphonaceae									
Colpomenia peregrina	C	King et al.1971	1971	NE Atlantic	●				
Colpomenia sinuosa	C	Womersley 1966	1966	Mediterranean	●				
Petalonia fascia	C	King et al.1971	1971	Baltic Sea	●				
Scytosiphon lomentaria	C	King et al.1971	1971	Arctic	●				
Sphacelariaceae									
Sphacelaria fusca	C	Lewis 1977	1977	NE Atlantic	●				
Rhodophyta									
Acrochaetiaceae									
Audouinella pacifica	C	O'Brien 1981	1981	NE Pacific	●				
Audouinella simplex	C	Lewis 1977	1977	NE Pacific	●				
Bangiaceae									
Bangia atropurpurea	C	King et al.1971	1971	Baltic Sea	●				
Ceramiaceae									
Antithamnionella spirographidis	I	Lewis 1977, MELU[a]	1976	Mediterranean	●				
Antithamnionella ternifolia	C	Lewis 1977	1977	SE Pacific	●				
Centroceras clavulatum	C	King et al.1971	1971	SE Pacific	●				
Ceramium flaccidum	C	O'Brien 1981	1981	NE Atlantic	●				
Ceramium rubrum	C	O'Brien 1981	1981	NE Atlantic	●				
Deucalion levringii	I	Kraft et al. 1975, MELU[a]	1975	S Pacific	●				
Gymnothamion elegans	C	Millar and Kraft 1993	1993	Mediterranean	●				
Medeiothamnion lyalli	I	Halder 1962, MELU[a]	1962	Australia and New Zealand	●				
Erythrotrichiaceae									
Erythrotrichia carnea	C	Womersley 1994	1994	NE Atlantic	●				
Gelidiaceae									
Gelidium pusillum	C	King et al.1971	1971	NE Atlantic	●				
Pterocladia capillacea	C	Womersley 1966	1966	Mediterranean	●				
Hildenbrandiaceae									
Hildenbrandia occidentalis var *yessoensis*	C	O'Brien 1981	1981	NW Pacific	●				
Hildenbrandia rubra	C	O'Brien 1981	1981	Mediterranean	●				
Liagoraceae									
Nemalion helminthoides	C	King et al.1971	1971	NE Atlantic	●				
Peyssonneliaceae									
Peyssonnelia conchicola	C	O'Brien 1981	1981	Arabian Seas	●				
Phyllophoraceae									
Gymnogongrus crenulatus	I	King 1969, MELU[a]	1969	NE and NW Atlantic	●				
Schottera nicaeensis	I	O'Brien and Kraft 1975, MELU[a]	1975	Mediterranean	●				
Porphyridiaceae									
Stylonema alsidii	C	Lewis 1977	1977	Mediterranean	●				
Rhodomelaceae									
Chondria arcuata	I	Kraft 1975, MELU[a]	1975	NE and NW Pacific	●				
Polysiphonia brodiaei	I	Womersley 1959, AD[a]	1959	NE and NW Atlantic	●			●	
Polysiphonia senticulosa (pungens)	I	King 1969, MELU[a]	1969	NE and NW Pacific	●			●	
Polysiphonia subtilissima	C	Lewis 1983	1983	Mediterranean	●			●	
Solieriaceae									
Solieria filiformis	I	Womersley 1966	1957	NE and NW Atlantic	●				
ANIMALIA									
Annelida									
Nereididae									
Neanthes succinea	I	Wilson 1984	1978	NE Atlantic	●	●		●	

Table 2 (Contd.)

Taxon	Status	Source	First PPB	Presumed origin (I) or distribution (C)	HF	M	SDB	BW	I
Sabellidae									
Euchone limnicola	I	McArthur 1997	1984	NE Pacific	●	●	●	●	
Myxicola infundibulum	C	Poore et al.1975	1975	Mediterranean			●	●	
Sabella spallanzanii	I	Carey and Watson 1992	1984	Mediterranean and NE Atlantic	●	●		●	
Serpulidaea									
Ficopomatus enigmaticus	I	Russ and Wake 1975	1975	NE Atlantic or Central Indian Ocean?	●	●		●	
Hydroides norvegica	I	Russ and Wake 1975	1975	Arctic		●		●	
Spionidae									
Boccardia proboscidea	I	Blake and Kudenov 1978	1978	NE and NW Pacific		●		●	
Pseudopolydora paucibranchiata	I	Blake and Kudenov 1978	1978	NE and NW Pacific		●		●	
Bryozoa									
Aeteidae									
Aetea anguina	I	MacGillivray 1887	1887	Cosmopolitan	●				
Bugulidae									
· [na]*Bugula avicularia*	C	Russ and Wake 1975	1975	Cosmopolitan	●				
Bugula calathus	I	Watson 1978	1978	NE Atlantic, Mediterranean and W Africa	●				
Bugula flabellata	I	Holmes 1982	1982	NE Atlantic	●				
Bugula neritina	I	MacGillivray 1881	1881	NE Atlantic	●				
Bugula simplex	I	Holmes 1982	1982	NE Atlantic, Australia and New Zealand and NE Pacific	●				
Bugula stolonifera	I	MacGillivray 1880's	1880's	NE Atlantic, Australia and New Zealand, Mediterranean and Baltic	●				
Candidae									
Scrupocellaria bertholettii	I	Vigeland 1971	> 1900	Cosmopolitan	●	●			
Scrupocellaria scrupea	I	MacGillivray 1887	1887	Cosmopolitan	●	●			
Scrupocellaria scruposa	I	Vigeland 1971	> 1900	Cosmopolitan	●	●			
Tricellaria occidentalis (robertsonae)	I	MacGillivray 1889	1889	NE Pacific, NW Pacific and Australia and New Zealand	●				
Cryptosulidae									
Cryptosula pallasiana	I	MV collections	Late 1880's	NE and NW Atlantic; Cosmopolitan	●				
Cycliporidae									
· [na]*Cyclicopora longipora*	C	MacGillivray 1883	NR	NE Pacific	●				
Electridae									
Electra pilosa	I	MacGillivray 1869	1860's	Cosmopolitan	●			●	
Hippothoidae									
Celleporaria albirostris	C	Vigeland 1971	1971	Wider Caribbean	●				
Celleporella hyalina	I	MacGillivray 1889	1889	NE, NW, South Atlantic, NE, NW, South and SE Pacific	●				
· [na]*Hippothoa aporosa*	C	Bock 1982	< 1980	Cosmopolitan	●			●	
· [na]*Hippothoa distans*	C	Bock 1982	< 1980	Cosmopolitan	●			●	
Hippothoa divaricata	C	Vigeland 1971	1971	Cosmopolitan	●			●	
Lepraliellidae									
Celleporaria albirostris	I	MacGillivray 1888	1888	NW Atlantic; Wider Caribbean	●				
Membraniporidae									
· [na]*Biflustra (as Membranipora) savarti*	C	Vigeland 1971	< 1967	Cosmopolitan	●			●	
Conopeum reticulum	I	MacGillivray 1879	1879	Cosmopolitan	●			●	
· [na]*Conopeum seurati*	I	Gordon and Mawatari 1992	NR	Mediterranean and NE Atlantic	●			●	
Membranipora membranacea	I	MacGillivray 1879	1879	Cosmopolitan	●			●	
· [na]*Membranipora tuberculata*	C	Vigeland 1971	< 1967	NE and NW Pacific	●			●	
Microporellidae									
Fenestrulina malusii	I	MacGillivray 1879	1879	Cosmopolitan	●			●	
Microporella ciliata	I	MacGillivray 1879	1879	Cosmopolitan	●			●	
· [na]*Microporella lunifera*	C	Parker (unpublished)	NR	NW Pacific	●			●	

Table 2 (Contd.)

Taxon	Status	Source	First PPB	Presumed origin (I) or distribution (C)	HF	M	SDB	BW	I
Schizoporellidae									
· [na]*Schizoporella errata*	C	Parker (unpublished)	NR	Mediterranean	●			●	
Schizoporella unicornis	I	Hincks 1880	1800's	Cosmopolitan (NW Pacific)	●				
· [na]*Stylopoma duboisii*	C	MacGillivray 1879	NR	Indo-Pacific	●				
Scrupariidae									
Scruparia ambigua	I	MV collections	1881	Cosmopolitan	●	●			
Smittinidae									
· [na]*Parasmittina delicatula*	C	MacGillivray 1887	NR	NW Pacific	●				
Parasmittina trispinosa	C	Vigeland 1971	1950	Cosmopolitan	●				
Vesiculariidae									
Amathia distans	I	Campbell and Hewitt 1999b	?	Cosmopolitan	●				
Bowerbankia spp	I	Russ 1977	1977	Cosmopolitan	●				
· [na]*Zoobotryon verticillatum*	I	Russ and Wake 1975	NR	Cosmopolitan	●				
Watersiporidae									
Watersipora arcuata	I	Holmes 1982	1973–1976	NE Pacific	●				
Watersipora subtorquata	I	Holmes 1982	1973–1976	Australia and New Zealand, NW Pacific, Wider Caribbean, S Atlantic	●				
Chordata									
Ascidiidae									
Ascidiella aspersa	I	Kott 1985	?	Baltic Sea	●				
Cionidae									
Ciona intestinalis	I	Miller 1966	1958	NE and NW Atlantic	●	●		●	
Gobiidae									
Acanthogobius flavimanus	I	Parry et al.1995	1990	NW Pacific	▲			●	
Acentrogobius pflaumi	I	Lockett and Gomon 1999	1996	NW Pacific	▲			●	
Tridentiger trigonocephalus	I	Paxton and Hoese 1985	1977	NW Pacific	▲			●	
Molgulidae									
Molgula manhattensis	I	Kott 1976	1967	NE and NW Atlantic	●			●	
Styelidae									
Botrylloides leachi	I	MV collections	1901	Baltic Sea	●	●			
Botryllus schlosseri	I	Russ 1977	1977	NE Atlantic	●	●			
Styela clava	I	Holmes 1976	1976	NW Pacific	●			●	
Styela plicata	I	Miller 1966	1966	East Asian Seas	●			●	
Tripterygiid									
Forsterygion lapillum	I	Lockett and Gomon 1999	1996	Australia and New Zealand				●	
Cnidaria									
Bougainvilliidae									
Bougainvillea muscus (ramosa)	I	Southcott 1971	1971	Cosmopolitan (NE Atlantic)	●	●		●	
Campanulariidae									
Clytia hemisphaerica	I	Watson 1999	1980	Cosmopolitan	●	●		●	
Clytia paulensis	I	Watson 1999	1985	E Africa, NE Atlantic, NW Atlantic	●	●		●	
Obelia dichotoma (australis)	I	Ralph 1966	1966	Cosmopolitan	●	●		●	
Clavidae									
Turritopsis nutricula	I	Southcott 1982	1982	Cosmopolitan	●	●		●	
Corynidae									
Sarsia eximia (radiata)	I	von Lendenfeld 1884	1884	Cosmopolitan	●	●		●	
Haleciidae									
Halecium delicatulum	I	Ralph 1966	1966	Cosmopolitan	●			●	
Lafoeidae									
Filellum serpens	I	Watson 1999	1984	Cosmopolitan	●			●	
Phialellidae									
Phialella quadrata	I	Mulder and Trebilcock 1915	1915	Cosmopolitan	●	●		●	

Table 2 (Contd.)

Taxon	Status	Source	First PPB	Presumed origin (I) or distribution (C)	HF	M	SDB	BW	I
Plumulariidae									
Antennella secundaria	I	Mulder and Trebilcock 1910	1910	Cosmopolitan	●	●		●	
Monotheca obliqua	I	Bale 1884	1884	Cosmopolitan	●	●		●	
Plumularia setacea	I	von Lendenfeld 1885	1885	Cosmopolitan	●	●		●	
Sertulariidae									
Amphisbetia operculata	I	Bale 1884	1884	Cosmopolitan	●	●		●	
Tubulariidae									
Ectopleura crocea	I	Bale 1884	1884	NE Atlantic	●	●			
Crustacea									
Balanidae									
Balanus amphitrite	I	see Keough and Ross 1999	?	Cosmopolitan	●			●	
Cancridae									
Cancer novaezelandiae	I	McNeil and Ward 1930	1930	Australia and New Zealand	●		●	●	
Caprellidae									
· [na]*Caprella acanthogaster*	C	Haswell 1885	NR	NW Atlantic	●	●		●	
Caprella equilibra	C	Haswell 1885	1885	NW Atlantic	●		●	●	
Caprella penantis	C	Poore et al.1975	1975	NW Atlantic	●	●		●	
Caprella scaura	C	Poore et al.1975	1971	S Atlantic	●	●		●	
Cirolanidae									
Cirolana harfordi	I	Campbell and Hewitt 1999b	1996	NE Pacific		●		●	
Corophiidae									
Corophium acherusicum	I	Fearn-Wannan 1968	1968	Cosmopolitan		●		●	
Corophium insidiosum	I	Storey 1996	1996	Cosmopolitan		●		●	
Corophium sextonae	I	Campbell and Hewitt 1999b	1995	NE Atlantic		●		●	
Ischyroceridae									
Jassa marmorata	I	Conlon 1990	1997	Mediterranean, NE and NW Pacific, East Africa and NE, NW and S Atlantic	●	●		●	
Majidae									
Pyromaia tuberculata	I	Parry et al. 1995	1995	NE Pacific	▲			●	
Portunidae									
Carcinus maenas	I	Uncertain; Campbell and Hewitt 1999b	Early 1800s	Baltic Sea	▲		●	●	
Sphaeromatidae									
Paracerceis sculpta	I	Campbell and Hewitt 1999b	1995	NE Pacific				●	
Echinodermata									
Asteriidae									
Asterias amurensis	I	O'Hara 1995	1995	NW Pacific	▲	●		●	
Ophiuroidea									
Amphiura (Ophiopeltis) parviscutata	C	Clark 1966	1966	?		●			
Mollusca									
Corbulidae									
Corbula gibba	I	Coleman 1993	1987	East Asian Seas	▲			●	
Hermaeidae									
Aplysiopsis formosa	I	Harris et al. 1996	1994	NE, NW and S Atlantic				●	
Mactridae									
Raeta pulchella	I	J Watson (personal comment); Campbell and Hewitt 1999b	1991	NW Pacific	▲		●	●	
Mytilidae									
Musculista senhousia	I	Coleman 1993	1980s	NW Atlantic	●	●		●	
Okeniidae									
· [na]*Okenia plana*	C	Hutchings et al. 1987	?	NW Pacific	●	●			
Ostreidae									
‡ [na]*Crassostrea gigas*	I	Coleman and Hickman 1986	1940's	NW Pacific	▲			●	●

Table 2 (Contd.)

Taxon	Status	Source	First PPB	Presumed origin (I) or distribution (C)	HF	M	SDB	BW	I
Polyceridae									
Kaloplocamus ramosus	C	Burn 1989	?	Mediterranean		●	●		
Polycera hedgpethi	C	Burn 1989	?	NE Pacific	●				
Semelidae									
Theora lubrica	I	Macpherson 1966	1958	NW Pacific				●	
Zephyrindae									
Janolus hyalinus	I	Miller and Willan 1986	1986	NE Atlantic and Mediterranean	●			●	
Platyhelminthes									
· [na]*Euplana gracilis*	I	Prudhoe 1982	1982	NW Atlantic	●	●			
Porifera									
Anchinoidea									
Phorbas cf tenacior	C	Weidenmayer 1989	1989	Mediterranean		●			
Callyspongidae									
Callyspongia pergamentacea	C	Keough and Ross 1999	1895	Australia and New Zealand and South Atlantic	●	●			
Darwinellidae									
Aplysilla rosea	I	Weidenmayer 1989	1981	Mediterranean, West Africa and NE Pacific	●	●			
Darwinella australianensis	C	Carter 1886	1885	Mediterranean and NE Pacific	●	●			
Darwinella gardineri	C	Weidenmayer 1989	1981	West Africa, Central Indian Ocean and East Africa	●	●			
Dysideidae									
Dysidea avara	I	von Lendenfeld 1889	1889	Mediterranean and NE and SE Pacific	●	●			
Dysidea fragilis	I	Bergquist (unpublished); Campbell and Hewitt 1999b	1996	Arctic, NE Atlantic and Mediterranean	●	●			
Haliclonidae									
Haliclona heterofibrosa	I	Bergquist (unpublished); Campbell and Hewitt 1999b	1996	Arctic and NE Atlantic	●	●			
Halisarcidae									
Halisarca dujardini	I	Bergquist (unpublished); Campbell and Hewitt 1999b	1996	NE Atlantic	●	●			
Myxilidae									
Lissodendoryx isodictyalis	C	Carter 1882	1882	NE, NW and S Atlantic and NE, NW, S and SE Pacific	●	●			
Pilakinidae									
· [na]*Corticium candelabrum*	C	Weidenmayer 1989	NR	Mediterranean and NE Atlantic	●	●			
Tedabiidae									
Tedania anhelans	C	Carter 1886	1886	Mediterranean, West Africa, East Africa and Central Indian Ocean	●	●			

[a]After Lewis 1999

reported. Species introduced pre-1940 have wider distributions in the bay than post-1940 introductions ($t_{[42]} = 2.70$, $P < .05$), which suggests that older introductions, often associated with hull fouling, are now widely distributed.

An increase in the numbers of recognised introduced and cryptogenic species was observed through time (Fig. 4a); however, an understanding of the invasion history of PPB is severely limited by survey intensity (see solid line in Fig. 4a). For the PPB biota, dates at which introduced and cryptogenic species were first reported were reliably available for 153 species. These dates are conspicuously bi-modal, with one peak of reports in the late 1800s and a second after 1960 (Fig. 4a). A strong correlation between apparent invasion dates (numbers of new introduced species records per decade) and survey intensity (number of surveys per decade) is evident (Fig. 4a; $r^2 = 0.84$; $P < 0.05$), and is mirrored by cryptogenic species. One possible approach to separating the effects of sampling intensity on invasion dates is to

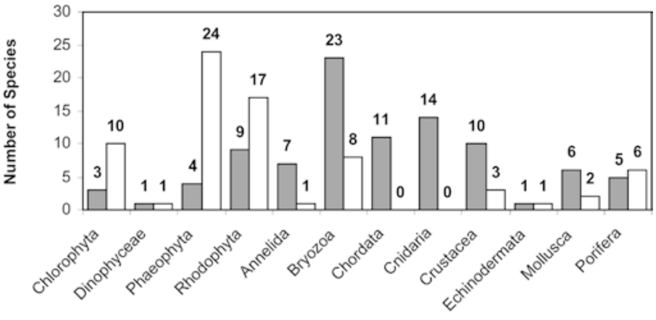


Fig. 3 The number of *(shaded bars)* introduced and *(open bars)* cryptogenic species in PPB by taxonomic group (does not include unidentified species or species excluded from analyses, see text and Table 2 for explanation)

examine the introductions in a subset consisting of well-known and conspicuous groups (e.g., molluscs, fish, and echinoderms) that appear to have had a consistent sampling effort. For these groups, there is a clear increase in introductions post-1950 (Fig. 4b).

Species origins can only be determined in retrospect based upon the date of first collection in PPB, the known trading activities prior to collection date and the known international distribution of the species. Based on these criteria, species introduced to PPB have come from all regions of the world except Antarctica, the Central Indian Ocean, and the South East Pacific (Fig. 5). Both the North Atlantic (Northeast and Northwest) and the North Pacific (Northeast and Northwest) have been significant donor regions for successful invaders. Since 1990, North Pacific species represent 11 introductions; many have subsequently been classified as pests (the primary criteria have been: known invasive history; causing social, economic, or environmental impacts) by Australian authorities (e.g., the Commonwealth Agencies Agriculture, Forestry and Fisheries – Australia and Environment Australia, as well as several State and Territory Governments).

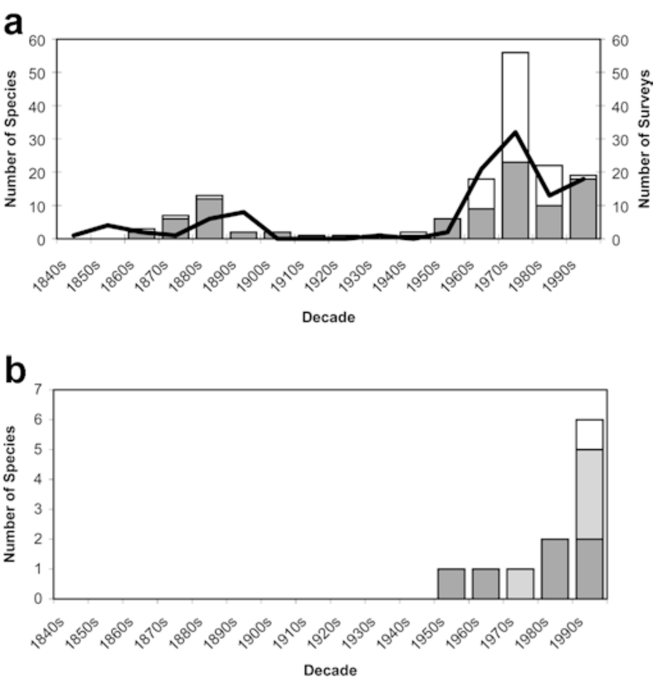


Fig. 4a, b First reports of non-indigenous species by decade. **a** Numbers of *(shaded bars)* introduced and *(open bars)* cryptogenic species identified and the numbers of bay-wide floral and faunal surveys *(solid line)* per decade in PPB. **b** Numbers of introduced species for commonly surveyed groups per decade in PPB; numbers of *(solid bars)* molluscs , *(shaded bars)* fish, and *(open bars)* echinoderms

Based on the criteria for assigning species to invasion vectors, many of the introduced species recorded in this study were likely to have been transported by hull fouling (78.3%), whereas only 19.9% were likely to have been transported by ballast water (Fig. 6).

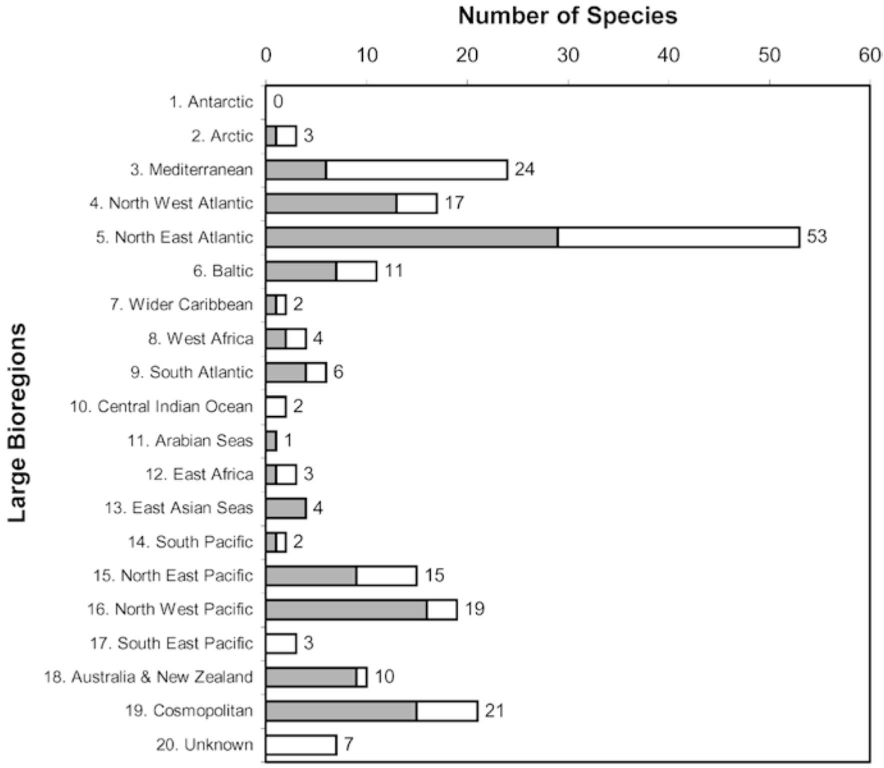
Discussion

Reviews of the literature and museum collections, combined with additional field sampling during 1995–1997, have identified 99 introduced and 61 cryptogenic species in PPB. Therefore, depending upon the criteria used, we identified 99 (definite introductions, with voucher specimens), 160 (introduced and cryptogenic species with voucher specimens) or 180 (all reports) of non-indigenous species in PPB. Harris et al. (1996) reported 713 zoobenthic and 478 benthic algal species in PPB. Of these, introduced species (99) constitute at least 8.3% of the recognised biota.

These are minimum estimates. The actual number of introduced species in PPB is likely to be higher as additional habitat types are evaluated and further taxonomic evaluations occur. A number of the expert evaluations covered only some habitats, for example, the crustaceans, molluscs, and polychaetes only undertook detailed evaluations of soft-substrate habitats. The boring fauna was not evaluated or sampled, even though representatives of specific groups, such as the shipworms (Teredinidae), have well-documented invasive histories and are known to occur in PPB (e.g., *Teredo navalis*). Similarly, no planktonic assemblages were evaluated. Given the propensity of ballast water to transport holo- and mero-plankton, planktonic assemblages would be expected to host significant numbers of introduced and cryptogenic species (e.g., Wyatt and Carlton 2002). Although we sought to minimise these effects through expert evaluations, such biases are common to all "check-lists" of invasive marine species and reflect a global lack of taxonomic expertise in many marine phyla and a lack of historic record for many groups and habitats. Taking these biases into account, we anticipate a significant number of unidentified invaders currently exist in PPB.

All taxa examined in this study had at least one introduced species; however, taxonomic representation was uneven. Four groups (bryozoans, cnidarians, chordates, and crustaceans) dominate, jointly comprising more than 75% of all non-indigenous species. This

Fig. 5 Native large bioregions for *(shaded bars)* introduced and occupied large bioregions *(open bars)* cryptogenic species that have become established in PPB. For more detailed information describing the large bioregions see Kelleher et al. (1995) and Hewitt et al. (1999)



dominance may be real (see below), but may also reflect the markedly different levels of taxonomic knowledge between groups. In some taxa, for example, high degrees of endemicity correlate with low taxonomic resolution (i.e., few species described and named). In these groups, the identification of introduced species is thus problematic. Differences among taxa could also reflect the uneven assignments of species to native, introduced, or cryptogenic status. Although the ten-point criteria of Chapman and Carlton (1991, 1994) were recommended to aid the identification of introduced species, these criteria are not definitive and can be poorly applied (Poore 1996; Hilliard et al. 1997; however, see Cranfield et al. 1998).

Historical patterns, invasion rates, source regions and vectors

The first non-native species recorded from PPB was *Electra pilosa*, a cosmopolitan bryozoan noted as present in 1862 (MacGillivray 1869). Determining the subsequent invasion history of the bay is extremely difficult, given that most of the groups of interest are inconspicuous, subject to substantial taxonomic problems, and have been sampled sporadically.

For the PPB biota, dates at which introduced and cryptogenic species were first reported are conspicuously bi-modal, with one peak of reports in the late 1800s and a second after 1960 (Fig. 4a). This suggests a spate of introductions early in the development of PPB as a trading port, most likely as a result of hull fouling on wooden vessels from Europe, followed by a long period of few new introductions (because the readily transported European species had already invaded?), in turn followed by a modern resurgence of introductions associated with new vectors (e.g., ballast water), increased levels and rates of transport, and new source bioregions. However, the pattern could also reflect differences in survey intensity and frequency (Fig. 4a). Across all taxa, there is a very high correlation between survey frequency in each decade and the number of non-indigenons and potentially non-indigenous species reported (Fig. 4a). This pattern is also very evident in a few speciose phyla, such as the bryozoans, in which a peak of reports of exotic species in the late 1800s reflects research by MacGillivray (1869–1889), who was particularly interested in the group. After MacGillivray's research, there was virtually no local work on the phylum until the post-1960 taxonomic surveys. All four of the groups that dominate the records pre-1920 (bryozoans 12 of 28 species, cnidarians 6, sponges 5, and crustaceans 3) show similar strongly bi-model distributions of reporting years and, we suspect, reflect the same bi-modality in historical taxonomic interest. Of the three crustaceans reported pre-1920, it is noteworthy that two (*Cancer novaezelandiae* and *Carcinus maenas*) are large and conspicuous, and hence would be more likely than most other invaders to be noted by early naturalists.

There are two ways to overcome the confounding effects of sampling intensity. First, for groups such as bryozoans and hydroids, we can compare results of comprehensive work prior to 1900 with subsequent taxonomic studies. Specifically, we can calculate invasion rates for these taxa pre-1900 based on the work of various authors (e.g., MacGillivray, Sonders, Wilson), for the interval between 1900 and about 1970, based on comprehensive faunal surveys of PPB by scientists in the 1950s and 1960s, and since 1970, based on the results of the current study. The number of non-indigenous bryozoan species first reported in those periods are 12, 2 and 5, respectively, which corresponds to mean invasion rates of 0.12, 0.028 and 0.17 species/year. The equivalent numbers for hydroids are 5, 2 and 6, corresponding to invasion rates of 0.05, 0.028 and 0.2 species/year. These numbers suggest that the bi-modal peaks in invasion rate for benthic species, at least, may be real. Second, we can examine those phyla that are conspicuous and that have a high probability of being noted within a few years of an invasion, largely irrespective of specialist taxonomic interest in them. Three taxa fit this description: molluscs, fishes, and echinoderms (Fig. 4b). The first exotic fish in PPB was first noted in 1977; the first echinoderm in 1995 (excluding several very early records of three common cryptogenic species, which may be native), and the first mollusc in 1953. This mollusc was the Pacific oyster (*Crassostrea gigas*), which was deliberately introduced to Australia (Tasmania and Western Australia); the first accidentally introduced mollusc was noted in 1956. The rate of invasion by these conspicuous taxa has increased steadily over the last several decades (Fig. 4b).

Thirteen accidental introductions have occurred since 1956, that is, one new species every 2.3 years, but since 1990, it has been about one new species every 1.3 years. For all taxa, the historical mean rate of invasions is one new species every 64 weeks, based on the 160 species identified in this study. However, the confounding effects of taxonomic uncertainty and irregular effort make even this crude estimate problematic. If the rate of invasion by the relatively well-studied bryozoans and hydroids (which are similar post-1970, at about 1 new species every 8 years) is typical for fouling groups in general, then an invasion rate of one or two fouling species/year is likely to be conservative. If this were representative of all groups, it would suggest that PPB is now being successfully invaded by three or more benthic species every year. Future studies will show if this is indeed so.

The difficulties of accurately identifying a species' place of origin have been discussed elsewhere (e.g., Cohen and Carlton 1998; Coles et al. 1999; Ruiz et al. 2000). Given the long history of trade with Britain and the historic parliamentary limitations on traffic into PPB, the anticipated origin of many species was the North Atlantic (Northeast and Northwest). This was borne out in the results, however the wide number of donor regions from which successful invasions have occurred (Fig. 5) demonstrates the susceptibility of the bay to further invasions. The shift of invasions post 1950 to North Pacific species (Northeast Pacific, 7.5%; Northwest Pacific, 9.5%) is likely to reflect Australia's increased trade with this region. For at least some North Pacific species, introduction into PPB is likely to be a secondary invasion from other infested Southern Hemisphere sites. Genetic data indicate that *Asterias amurensis* in PPB, for example, originated from Tasmania (see papers in Goggin 1998).

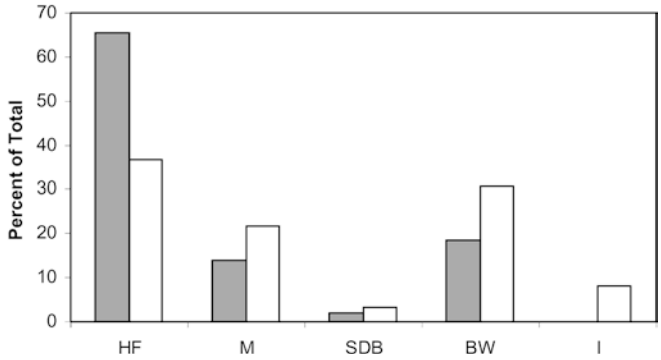


Fig. 6 The proportion of the introduced species in *(shaded bars)* PPB and *(open bars)* San Francisco Bay attributable to each of five broad invasion vectors (see text for methods). Data for San Francisco Bay derived from Cohen and Carlton (1995)

Analysis of likely vectors is also problematical, in part because of distortions due to the taxonomic unevenness of the sampling (as in most similar studies, the phyla we examined are predominantly fouling organisms in the broad sense of the word) and in part because of uncertainty about the vector involved in any given introduction. For example, we have allocated all fish introductions to ballast water on the basis that the "easiest" invasion route appears to be via the planktonic larval stage. However, at least one species is believed to have been originally introduced into Australia in oyster aggregates shipped live from New Zealand. All these species are small, cryptic, and frequently occupy burrows; these characteristics, along with reports of similar kinds of fish in sea chests (Rainer 1995), suggest that other vectors may have been involved. Similarly, the bivalve *Corbula gibba* is also considered a "ballast water" species, but we have also collected it from sea chests (Coutts et al. 2003).

The evaluation of transport vectors, compiled into five groups (hull fouling/boring, mariculture, dry and semi-dry ballast, water ballast, and intentional introduction, following Carlton 1979, 1985; Coles et al. 1999) suggests that both hull fouling (78.3%) and ballast water (19.9%) are both high-risk vectors (Fig. 6). The prominence of hull fouling is not just historical; fouling not only accounts for the first introduced species reported in PPB, but also the most recent, e.g., *Undaria pinnatifida* and *Codium fragile* ssp. *tomentosoides*. Nonetheless, available data suggest that ballast water is the major vector for introductions since 1990, accounting for 8 out of 18 species first reported in that decade (see also Ruiz et al. 2000 and Hewitt 2003).

We can draw three specific conclusions with regard to PPB. First, even given the uncertainties associated with uneven sampling and taxonomic coverage, it is evident that bay marine communities are highly invaded by non-native species. Around 10–15% of the biota in any given taxon is either introduced or not demonstrably native, and in some habitats (e.g., inshore fouling communities), almost all of the conspicuous biota is introduced or significantly affected by introduced species (e.g., Holloway and Keough 2002). Harris et al. (1996) noted that three of the six most abundant benthic species in PPB were introduced, while Currie and Parry (1999) state that five of the ten most abundant species are not native.

Second, non-indigenous marine species, and presumably their impacts, are not uniformly distributed throughout the bay. Areas such as the Port Melbourne are much more heavily invaded than more pristine areas further from industrial development. Nonetheless, no area in the bay is either entirely free of invaders or safe from further invasions.

Third, PPB is threatened by both international and domestic translocations of exotic species. Even though the original source regions for invaders may be overseas, many of the exotic species now found in PPB are likely to be secondary introductions from other areas within Australia (or New Zealand). Additional high profile and very abundant exotic species have invaded the bay from other regions in Australia— *Asterias amurensis* and *Codium fragile* ssp. *tomentosoides*.

Comparison with other regions

The diversity of the introduced biota of PPB reflects, at least in part, the effort expended in documenting the problem. Although data are available for other Australian ports via the National Port Surveys, first indications are that they do not support as diverse an assemblage of exotic species as PPB (see Hewitt 2002). However, there are three points of apparent similarity between PPB and other sites in Australia and New Zealand. First, the total number of actual (99) or potential invasive species detected in this study (160 including cryptogenic species) is similar to the total number reported for New Zealand (148) by Cranfield et al. (1998). Second, the prominence of several taxa (algae, bryozoans, crustaceans, and cnidaria) in the introduced biota of PPB is also evident in the regional assessment of Australian introductions as a whole [difference between PPB and Australia summed (Hewitt, unpublished data), $G_{[12]} = 17.1$, n.s.] and in New Zealand ($G_{[12]} = 17.3$, n.s.). The PPB and whole-of-Australia data sets are not independent, and similarities between Australian and New Zealand patterns of dominance could reflect similar suites of taxonomic expertise and literature. Nonetheless, these similarities could indicate a distinctive pattern for the introduced regional biota. And third, there is consistent evidence of the prominence of hull fouling as a transport vector. For Australia as a whole, the dominant mode of introduction historically is hull fouling, followed by accidental releases associated with mariculture and ballast water at about equal levels, and then dry ballast and intentional releases (Thresher et al.1999; Hewitt 2003). Ballast water accounts for about 20% of introduced marine species identified so far from Australian coastal waters. The prominence of hull fouling and mariculture is independently the case for all Australian states and territories except for the Northern Territory, for which we do not have enough data yet as to justify any conclusions. It also appears to be the case for New Zealand; Cranfield et al. (1998) stated that "most (69%) of the adventive species...arrived in New Zealand as part of hull fouling communities", and only attributed 3% unambiguously to ballast water and another 21% to either fouling or ballast water.

The number of introduced and cryptogenic species we found in PPB is higher than those reported for a comparable body of water anywhere else in the world (Thresher et al. 1999; Hewitt 2003). More non-indigenous species are reported for the Mediterranean Sea, but this figure includes Lessepian migrants and a number of species detected only once, that have apparently not established. Cohen and Carlton's study of the San Francisco Bay and delta region (Cohen and Carlton 1995) also reports a greater richness of non-indigenous species overall, but their study includes estuarine, salt marsh, and freshwater species, which we did not include in the PPB analysis. If the comparison is restricted to only those species in marine and brackish water habitats, PPB has more non-indigenous species than the San Francisco Bay (160 vs 138)(latter figure from Carlton, personal comment).

More meaningful between-area comparisons can be made in relation to invading taxa and introduction vectors. In contrast to the similarity in taxonomic dominance in Australian and New Zealand surveys, the ranking of invasive taxa in Australia differs significantly from those observed in San Francisco Bay ($G_{[12]} = 48.9$, $P < .005$), Coos Bay ($G_{[12]} = 24.2$, $P < .05$), and Pearl Harbor ($G_{[12]} = 67.7$, $P < .005$). Across all sites, the difference is significant for pooled Northern (San Francisco Bay, Coos Bay, and Pearl Harbor) and pooled Southern (Australia and New Zealand) Hemisphere sites ($G_{[12]} = 87.8$, $P < .005$). The difference is due principally to the dominance of crustaceans and molluscs in the introduced biota of the Northern Hemisphere, and their relative sparseness in Southern Hemisphere samples to date. In the San Francisco Bay, crustaceans were the richest introduced taxon (53 species), followed by molluscs and fish (30 and 28 species, respectively) (Cohen and Carlton 1995). Similarly, in Pearl Harbor, molluscs and crustaceans comprised the two richest introduced groups (38, 35 species, respectively) (Coles et al. 1999). In contrast, crustaceans were only the fourth richest invasive taxon (after bryozoans, cnidarians and chordates) in PPB, and molluscs ranked only seventh.

The relative importance of the main groups of vectors also seems to differ between PPB (Australasia in general) and Northern Hemisphere sites. The historical dominance of hull fouling as an introduction vector in Australasia contrasts with the findings of Cohen and Carlton (1998) for San Francisco Bay (Fig. 6), though more similar to that reported for Britain by Eno et al. (1997).

The results of this study provide further evidence that the level of introduced marine species is global, significant and increasing. Although taxonomic difficulties (and often sparse, poorly supported taxonomic expertise) and differences in sampling methods suggest caution in comparing survey results among sites (Coles and Eldredge 2002; Ruiz and Hewitt 2002), there are several robust conclusions that can be drawn from the analyses above.

First, the problem of introduced marine species in the Southern Hemisphere is comparable in magnitude to that in the Northern Hemisphere. The need to cross the equator, and the presumed thermal stresses that temperate species are subjected to while making this crossing, has not protected Southern Hemisphere sites from invasions by North Atlantic and North Pacific species. In many instances, these are the same species that have been successful invaders in the Northern Hemisphere (e.g., *Carcinus maenas*, *Undaria pinnatifida*, *Codium fragile* ssp. *tomentosoides*).

Second, the threat to endemic biota by introduced species is an old one. European species were detected in PPB within a few decades of the port developing, and have likely been present since the first European ships arrived. Thus the biota of PPB has not been fully "natural" since at least that time, irrespective of the effects of other modifications such as port development, urban pollutants, and fishing.

Third, the nature of the threat has changed in recent decades, because of new vectors (notably ballast water) and new source bioregions (notably the North Pacific) (see Carlton 1996b). However, no single vector accounts for all, or even most of the problem. Hull fouling, broadly defined, accounts for most non-indigenous species in PPB and Australasia in general, but the mix and importance of different vectors varies with locality and time.

PPB represents one of Australia's largest receiving trade regions both historically and currently. The long history of invasions, and the broad diversity of introduced species in PPB suggest that this is an ecosystem highly susceptible to invasions. As such, the bay will continue to be invaded given that the dominant vectors and trading regions are shifting and thus presenting new suites of potential invaders through time. The extent to which the ecological resistance of the bay has been significantly altered by previous invaders is unknown, but the evidence posed by community level alterations in the San Francisco Bay in which an accelerating rate of invasions has been observed suggests that an "invasional meltdown" (sensu Simberloff and von Holle 1999) may be occurring, whereby invasions have sufficiently disrupted natural processes sufficient to allow additional invasions to occur.

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