

Chapter 24

Marine Invasions in New Zealand: A History of Complex Supply-Side Dynamics

Barbara J. Hayden, Graeme J. Inglis, and David R. Schiel

24.1 Introduction

New Zealand's recent ecological history is often held up as a textbook example of the havoc that can be wrought by non-native species (Clout and Lowe 2000). The first human inhabitants of New Zealand arrived (by boat) just 800 years ago, and brought with them food crops and dogs. They arrived in a country where, already, many elements of the endemic fauna were in serious decline; an apparent legacy of the introduction of the Polynesian rat (*Rattus exulans*: 'kiore') by transient human visitors, some 1000 years before (Holdaway et al. 2002). In the eighteenth and nineteenth centuries, British immigrants to New Zealand brought with them a wave of new predators, plant pests and grazing animals. When Charles Darwin stopped in NZ on his *Beagle* voyage in 1835, the settled European population in NZ numbered fewer than 2000 but Darwin lamented the rampant spread of "very troublesome" weeds which had already "overrun whole districts" and the loss of native flightless birds, "annihilated" by introduced Norway rats (*Rattus norvegicus*) (Darwin 1889). Now, 170 years later, there are more than 4 million human inhabitants and 25,000 introduced plant species in New Zealand, with established exotics outnumbering native species (Beston 2005; NZ Plant Conservation Network 2006).

Introduced species have significantly altered the natural landscape and ecological functioning of New Zealand's environments. Deliberate and accidental introductions of organisms continue to occur at an alarming rate. In this chapter we discuss the status of marine invasions in NZ, some of the impediments to accurately defining that status and the importance of taking account of "supply-side" dynamics when assessing the risks of new introductions. "Supply-side" ecology is the term introduced into marine ecology in the late 1980s to describe the study of the processes of arrival of new members of populations (see also Johnston et al. this volume). Its importance was to re-emphasise the consequences of variability in the supply of recruits to adult populations. While not new, the concept served to refocus attention on the dynamics of reproductive success, oceanographic influences on dispersal, larval behaviour, the process of settlement, and features of the receiving environment that cause variations in

numbers of recruits from place to place and time to time (Underwood and Fairweather 1989). Supply-side dynamics are also an important part of marine invasions because establishment of new populations of introduced species is contingent on variability in the same processes described above that influence the success of new recruits. However, because human activities spread marine invaders, the supply-side of the equation also encompasses variability in the transport pathways in which the species are carried to new environments. We use data on changing trade patterns in New Zealand to demonstrate the importance of including that aspect of supply-side dynamics into assessments of incursion risk. Other equally important processes that form part of supply-side ecology, such as dispersal of propagules and settlement success, are not discussed in this chapter.

24.2 Status of Marine Invasions in NZ

Non-native species have been introduced by humans into New Zealand's marine environment at least since the arrival of European ships in the mid-1860s, and almost certainly earlier, during the first wave of Maori settlement. Invasion of the Polynesian rat ca. 2000 years ago is thought to have had consequences for New Zealand's marine ecosystems even before settlement. Fossil evidence suggests the kiore was associated with the demise of vast numbers of sea birds, which nested in coastal burrows (Holdaway 1989).

Within a month of Captain James Cook setting foot on New Zealand shores in 1769, he ordered his crew to careen his vessel, the *Endeavour*, and "heel'd and scrubbed both sides of the Ship". The rate of fouling was so great that, just two months later, Cook once again gave the order to careen the ship, where the "barnacles and seaweed" were scraped off. Later, in the early 1800s, whalers and sealers from America, England and other European nations operated in increasing numbers around the coast of New Zealand. They and the other sailing vessels of that era are likely to have brought with them on their hulls a range of fouling organisms that were introduced into a marine biota but had not yet been scientifically described (Cranfield et al. 1998).

Like many other countries, New Zealand has only recently begun to document the extent of invasions in its coastal environments. It is possible that some of the species that arrived on the hulls of early vessels are now so widespread and abundant that they cannot readily be distinguished as non-native. Species that are currently considered "cosmopolitan" or even "native" could well have been spread before any records were made (Cranfield et al. 1998; Ruiz et al. 2000). A few species introduced in the eighteenth and nineteenth centuries characteristically have very limited distributions and are more readily identifiable as adventives. For example, the brown alga *Chnoospora minima* is found in only one location in New Zealand, Port Underwood, where it grows abundantly unattached in about 8 m of water. In the early 1800s, Port Underwood was an

important destination of the southern right whaling fleet arriving from the tropical Pacific where *C. minima* is widespread (Nelson and Duffy 1991). Similarly, the red alga *Chondria harveyana* is known only from Porirua Harbour, and from Tasmania, Australia. In the early nineteenth century, Porirua Harbour contained a whaling station that was regularly supplied from Tasmania (Nelson 1994).

Hayward (1997) and Cranfield et al. (1998) used published and unpublished biological records to compile inventories of the known and suspected introduced marine species that are present in New Zealand. The more comprehensive of these lists, that by Cranfield et al. (1998), tested adventism against nine biogeographic criteria developed by Chapman and Carlton (1991). They identified 139 species that satisfied at least 3 of the criteria and a further 20 species that have been found in New Zealand, but which did not become established. The organisms included macroalgae, estuarine grasses, "Protozoa", Porifera, Cnidaria, Annelida, Mollusca, Arthropoda, Entoprocta, Bryozoa, and Chordata. Most (96%) of these species arrived accidentally, as fouling organisms on vessel hulls (69%), in ballast (6%), or as either fouling or ballast (21%).

Since the inventory was compiled, a further 40 suspected introduced marine species and 27 cryptogenic species (see Chap. 2, Carlton) have been described from New Zealand waters (NIWA and MAF Biosecurity NZ unpublished data). The dramatic increase in the rate of discovery in the intervening nine years coincides with greater awareness and reporting of bioinvasions among the scientific community and general public, and the commencement, in 2001, of national baseline port surveys and targeted surveillance for unwanted marine organisms that have the expressed aim of identifying introduced marine species (Hewitt et al. 2004). Between 2001 and 2003, baseline port surveys were completed of all 13 major commercial ports in New Zealand and the 3 main first-marinas-of-entry for recreational vessels.

24.3 What is Non-native?

Inventories of the type prepared by Cranfield et al. (1998) are subject to several types of unsystematic bias that are difficult to estimate or control (Ruiz et al. 2000; Chap. 2, Carlton; but see Solow and Costello 2004). Perhaps the most significant of these is the variable quality of taxonomic and biogeographic information for many marine groups. "Cryptogenic" species – species which are not demonstrably native or non-native – can comprise up to 30% of some coastal marine assemblages (Ruiz et al. 2000). The patchy status of marine taxonomy, systematics and biogeography continues to provide a significant challenge for discriminating native from non-native species (Gordon 2001). New Zealand has the world's fourth-largest Exclusive Economic Zone (EEZ), which at more than 4 million km² is 15 times the land area (Blezard 1980). Although specimens have been collected from >9000 stations in this zone, sampling of

the biota is estimated to cover less than 2 km² or one five-millionth of the EEZ area (Nelson and Gordon 1997). Since the early 1980s, the rate of discovery of new species and records of marine invertebrates has been approximately three per week, although this estimate is likely to be conservative because not all marine invertebrate groups are being studied in New Zealand. The paucity of specialist taxonomic expertise in New Zealand means that formal descriptions are unable to keep up with the rate of discovery of new species (Nelson and Gordon 1997). For instance, the origin of 160 species detected in New Zealand in the national port baseline surveys since 2000 cannot be determined decisively. Of these, 106 species are thought to be new to science and are yet to be described.

In north-eastern New Zealand, the problem of distinguishing native from non-native species is compounded by occasional natural immigration of subtropical species during warm summers (Dell 1968; Francis et al. 1999; see also Chap. 3, Lonhart). Some of these immigrants manage to establish viable breeding populations and would satisfy at least three of the criteria of Chapman and Carlton (1991) (i.e., sudden appearance, subsequent spread and restricted distribution). Natural arrivals of this type are also a prominent feature of the fossil records in New Zealand. Indeed, New Zealand's extant marine biota represents a blend of species with Indo-Pacific affinities and colder-water Antarctic affinity (Knox 1975). This mix is the product of a long series of incursions and subsequent extinctions of warmer water species that were associated with latitudinal shifts in the position of the subtropical and Antarctic convergences (sharp gradients in water temperature that intersect the New Zealand archipelago).

The prevalence of cryptogenic species (Chap. 2, Carlton) in the marine biota creates an uncertain regulatory environment for managers of marine pests (see also Chap. 19, Hewitt et al.). Eradication and control measures available under The Biosecurity Act, 1993, can be initiated only if the target organism is deemed to be a pest, and authorities are unwilling to take action against native species. Decisions to act, therefore, frequently revolve around the geographic origin of the species. This difficulty was highlighted in 2001, when the harbourmaster of a small harbour in north-eastern New Zealand reported an unusual growth blanketing wharf piles and some boat hulls in the harbour. Subsequent surveys revealed that the organism was a colonial ascidian in the genus *Didemnum*, *D. vexillum* sp. nov (Kott 2002). The species was subsequently recorded in the nearby port of Tauranga, and on a barge in Picton Harbour that had been relocated from Tauranga. Picton Harbour is located in Marlborough Sounds, where NZ's large industry of cultured greenshell mussels is located. Because of its habit of overgrowing other fouling species including mussels, discovery of the ascidian in Marlborough Sounds raised alarm bells in the mussel industry. While facing pressure from the industry to initiate an eradication programme, MAF Biosecurity NZ had to evaluate conflicting opinions from international taxonomists about the likely origin of the organism before they could act. Appearance of the New Zealand didemnid was followed closely by

reports of nuisance species in this genus from the Atlantic coast of the USA, Mediterranean, North Sea and English Channel. Detailed morphological comparison suggests that these are, in fact, different species (Kott 2004). Because *D. vexillum* sp. nov. has not been recorded elsewhere, it is currently assumed to be a native New Zealand species which underwent a sudden unusual bloom in abundance.

24.4 Evidence of the Leaky Border

The large increase in detected incursions in the last nine years is most likely to be a result of increased search effort rather than an increase in introductions. Nevertheless, exotic species continue to arrive, probably at an increasing rate. Visits from merchant vessels discharging ballast water have increased by 10% per annum since 2000 (Hewitt et al. 2004). Although increased vessel speed, faster port turnaround times, and more effective antifouling paints might be expected to make it more difficult for exotic species to reach New Zealand via hull fouling than in the past, Cranfield et al. (1998) observed that the number of introduced species that arrived on hulls and established in New Zealand between 1958 and 1998 was similar to the number that arrived on hulls in the 50 years previous to that period.

Evidence that New Zealand's marine border remains very leaky is illustrated by *Undaria pinnatifida* (Laminariales), the Asian brown alga that was first discovered in New Zealand in 1987 (Hay and Luckens 1988). Thought to have arrived in ballast water or attached to the hull of a ship, *Undaria* was progressively found in 11 other ports and coastal locations in the 10 years following its first discovery. Since 1997, *Undaria* has continued to spread around New Zealand with discoveries at a further six locations. Because it was also found on the hulls of vessels in some of these locations, the vector for the spread was presumed to be the coastal movement of vessels. Fouled vessels are indeed likely to be the main vector of spread from already established populations but a recent study of the genetic diversity of native and introduced populations of *Undaria* worldwide has shown that there have been multiple new introductions of the species to NZ since 1987 (Uwai et al. 2006).

24.5 Reasons Why Introductions Continue

New Zealand's biosecurity system, designed to protect both the terrestrial and aquatic environments from impacts of non-indigenous species, is based around (1) border control, (2) Import Health Standards, (3) post-entry quarantine, (4) surveillance, and (5) management of pests once in New Zealand (Hayden and Whyte 2003; Chap. 19, Hewitt et al.). In the marine realm, this has taken the

form of national baseline surveys of biota in high risk ports, active surveillance for a range of unwanted marine organisms, assessments of fouling on vessel hulls and the efficacy of hull cleaning facilities as discussed in Hewitt et al. (2004). Border and pre-border control is the first line of defence against the introduction of exotic species and inspection by a range of techniques takes place at all entry pathways (passengers, aircraft, mail, personal effects, commercial cargo) except marine. The lack of effective marine border controls is one reason why organisms continue to arrive and establish themselves.

24.6 Most Common Marine Pathways

24.6.1 *Ballast Water*

Marine species are most commonly introduced in ships' ballast water and as fouling assemblages on the hulls of vessels (Carlton 1985; Ruiz et al. 2000; Hewitt et al. 2004; Chap. 6, Hewitt et al.) and submerged structures such as oil platforms (Foster and Willan 1979). Alternative pathways of transfer (Chap.5, Minchin et al.; Chap. 20, Campbell), such as the release of species for fisheries and aquaculture, or escape of aquarium species, account for a much smaller proportion of known establishments in New Zealand (Cranfield et al. 1998).

New Zealand has had voluntary guidelines for the management of ballast water discharges, based on the International Maritime Organisation's Guidelines, since 1992. The voluntary guidelines were transferred into an Import Health Standard (IHS) in 1998 (Ministry of Fisheries 1998) but the IHS lacked a legal framework until the enactment of The Biosecurity Act in 1993. Because it is "reasonable to suspect" that ballast water arriving into New Zealand poses a risk to the flora and fauna already in New Zealand, ballast water is classified as a "risk good" and the powers of the Biosecurity Act can be used to authorise controls. Under the Act, no "risk goods" can be imported into New Zealand unless they have complied with a relevant Import Health Standard (IHS).

The main features of the ballast water IHS are that ballast water should not be discharged within New Zealand if at all possible. If it must be discharged, then it should be ballast that has been exchanged or loaded in the open ocean. Other options include disinfection of the ballast water prior to discharge, discharge into an approved area or to an onshore facility, or to have the ballast tested to show it is not a risk. Effective treatment options are still in the development stage and there are currently no areas approved for ballast dumping nor any onshore discharge or ballast water treatment facilities. Thus, the only practical option available is to exchange the ballast water with oceanic water before the ship arrives in New Zealand's territorial waters, a practice known to be only partially effective at minimising the risk of exotic introductions (Rigby et al. 1993).

No sediment or mud from the cleaning of the holds, ballast tanks or equipment on the vessel can be discharged in New Zealand waters.

24.6.2 Hull Fouling and Sea Chests

Not all vessels that enter New Zealand waters are ballasted merchant vessels. Since the 1970s, many of New Zealand's major fishing companies have chartered foreign vessels on a seasonal basis and increasing numbers of private pleasure craft and passenger cruise liners are also entering New Zealand's waters. Emphasis in the past two decades on ballast water as a primary vector of marine introductions has temporarily diverted attention away from fouling assemblages on the hulls and other external structures of vessels. The shift in focus has in part been based on the assumption that modern antifouling paints, the high speed of merchant vessels and their rapid port turn-around times would minimise the risk of introductions via fouling. However, there is evidence that hull fouling and sea chests remain significant vectors of marine introductions (James and Hayden 2000; Gollasch 2002; Coutts et al. 2003; Coutts and Taylor 2004; Floerl and Inglis 2005; Floerl et al. 2005a, b). An Import Health Standard (IHS) has yet to be established for fouled hulls or sea chests although MAF Biosecurity NZ is currently assessing the risks associated with hull fouling on all vessel types entering New Zealand. This is a comprehensive study that is using a standardized sampling approach to measure the biomass and identity of fouling organisms on the external structures of 450 merchant, fishing, recreational and passenger vessels and towed barges. Data on associated risk factors such as travel and maintenance history of the vessels have also been collected. The challenge to find management options for vessels deemed to be high risk is being addressed by additional MAF Biosecurity NZ projects to evaluate the efficacy of a range of hull cleaning operations.

24.7 The Dynamic Nature of Incursion Risk

Successful establishment of invasive species is likely to be a highly probabilistic outcome that depends on the coincidence between delivery of the species to the new location and suitable conditions for establishment, including the absence of enemies and the availability of resources (see also Chap. 7, Johnston et al.; Chap. 8, Miller and Ruiz; Chap. 12, Olyarnik et al.; Chap. 11, Torchin and Lafferty). Both the supply of colonizing stages of invasive organisms ("propagule supply") and the opportunity for their establishment ("niche opportunity") are likely to be highly variable in space and time. For a range of organisms, the most consistent correlate of invasion success tends to be propagule

supply (Veltman et al. 1996; Forsyth and Duncan 2001; Mack et al. 2000; Kolar and Lodge 2001; Lester 2005; Verling et al. 2005; Wonham et al. 2005; Herborg et al. 2007). However, in marine invasive species research, propagule supply is rarely measured directly because of the difficulty in obtaining representative samples from ballast tanks and the cost of identifying all viable species present. Risk assessments tend to use the most cost-effective proxies available, which are related to the amount, type and frequency of shipping or ballast discharge from different locations (e.g., ACIL 1994; Hilliard and Raaymakers 1997; Clarke et al. 2004). In many cases these are not calibrated against actual propagule transport (i.e., abundance or frequency of delivery of species or species groups) and are static (i.e., cross-sectional) representations of the vector and transport pathway risk. However, historical vessel voyage data from New Zealand indicate that the vector risk is far from static, especially at the scale of individual ports, highlighting the need for more dynamic, quantitative predictors of risk.

24.8 Changes in the Source of Invaders

At a coarse level, the geographic origins of marine invaders tend to be correlated with the predominant shipping routes into and out of a country (e.g. Carlton 1996; Ruiz et al. 2000). This is also true of New Zealand invaders. In Fig. 24.1 we used the putative date of discovery of each introduced species that has established in New Zealand waters to construct four historical time periods with roughly equal numbers of discoveries: 1800 to 1925 ($n = 40$), 1926 to 1960 ($n = 37$), 1961 to 1990 ($n = 37$), 1991 to 2005 ($n = 35$). This allowed changes in the relative proportions of species coming from different regions to be compared with trade from those regions. Several patterns are immediately obvious in these data. First, as we noted earlier, the rate of discovery has quickened over time; the first 40 species were recorded over a 125 year period, the following 37 occurred within 34 years, the next 37 in 29 years, and the final group of 35 discoveries occurred in less than half that time, at a rate of 2.3 per year. As Costello and Solow (2003) point out, this does not necessarily imply an increasing rate of incursion, particularly because it does not account for increasing search effort as scientific knowledge of New Zealand's marine biota has increased and surveys have been specifically tasked with finding introduced species.

Nevertheless, when the presumed origin of these species is considered, the data do reveal a noticeable shift in the regions from which the invaders are arriving. Between 1800 and 1960, more than 90% of the introduced species recorded in New Zealand were thought to have derived from Europe, Australia or North America, or were considered "cosmopolitan". Often these cosmopolitan species were also first described from British and European specimens. Since 1960, the relative proportions of species from Europe and North America have declined and there has been a concomitant rise in the proportion of species

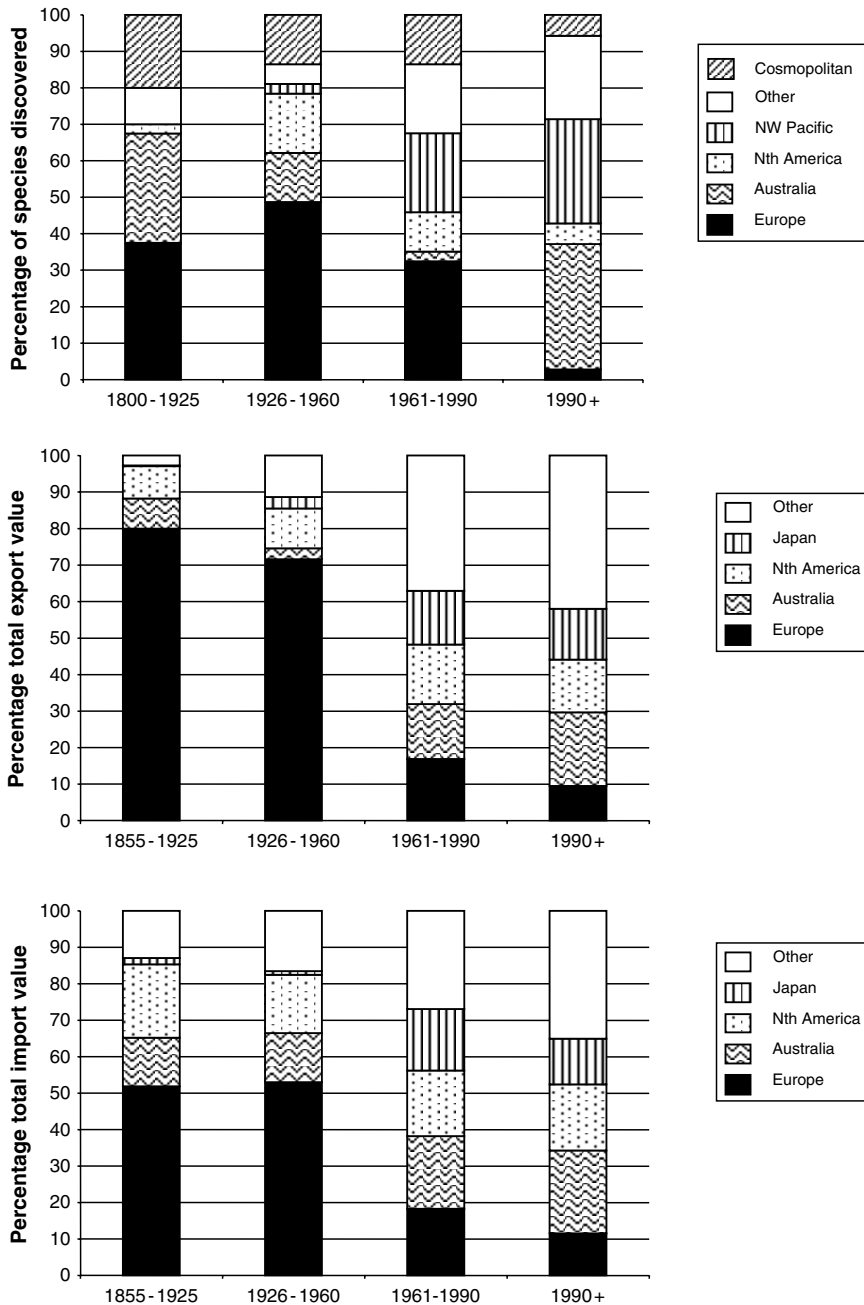


Fig. 24.1 Historical changes in the percentages of introduced marine species (a), exports (b), and imports (c) in New Zealand from different source regions. Roughly equal numbers of introduced species were discovered in each time period (1855–1925 n = 40, 1926–1960 n = 37, 1961–1990 n = 37, 1991–2005 n = 35). (Sources: Cranfield et al. 1998, NIWA & MAF Biosecurity NZ unpublished data, Statistics NZ. Overseas Trade Statistics)

whose biogeographic origins are in the North West Pacific and ‘other’ regions (such as South East Asia, South America, the Indian Ocean and Arabian Seas). This change mirrors long-term shifts in New Zealand’s international trade patterns over the same period (Fig. 24.1).

During the early 1800s, most of New Zealand’s shipping trade was with Australia and the United Kingdom, when New Zealand was administered as part of the New South Wales colony. Following the first refrigerated shipment of meat and dairy products to the United Kingdom in 1882, exports to more distant markets became possible and the economy became increasingly agriculturally based. Trade with North America increased in the mid-1800s with the gold-field discoveries that linked California, Australia, and New Zealand. Later, in the 1940s, the German blockade of allied shipping in the English Channel forced New Zealand shipping and goods to be diverted from the traditional British market to the USA and Canada. Nevertheless, the United Kingdom remained New Zealand’s largest trading partner until the 1970s, when it joined the European Union. Since that time there has been significant diversification of the countries with which New Zealand trades and a decline in the relative importance of the United Kingdom. Japan emerged as a major market for New Zealand exports in the 1960s and 1970s following the first shipments of frozen meat in 1956. Although Australia remains New Zealand’s single largest trading partner, the burgeoning economies of the Northwest Pacific - Japan, Korea, China and Taiwan –accounted for more than 64% of the gross tonnage of New Zealand exports in the period from 1996 to 2004 and, collectively, comprise the largest regional source of discharged ballast water (Hewitt et al. 2004).

24.9 The Complexity of Making Forecasts

Gross national trends such as these overlay more complex patterns of trade with individual ports. It is at this local scale that invasions begin. We are still a long way from developing predictive relationships at this scale between propagule supply and marine invasions. Patterns of global shipping are becoming increasingly complex as faster transit times, increased global demand, and lowering trade restrictions open access to new markets. At the same time, this is offset by globalization of production, so that competition to supply markets is intensifying. These two factors – increased market diversity and global competition – have a major impact on the trade patterns of ports, which can change rapidly over relatively short time periods.

To illustrate this point, in Figs. 24.2 and 24.3 we present data on the changing patterns of trade in forest products in New Zealand ports. Forest products are typically transported in dedicated bulk vessels that discharge large volumes of ballast water in New Zealand ports. Forestry related products have dominated recent bulk export growth in New Zealand and account for around 13% of total

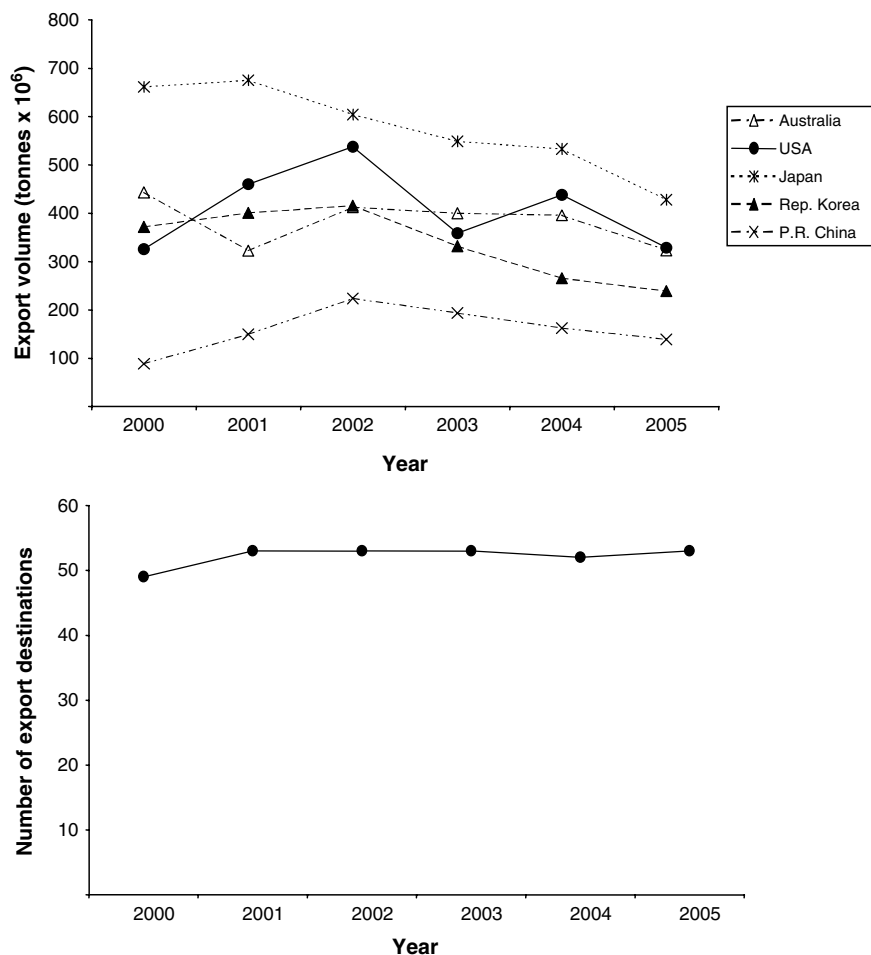


Fig. 24.2 Changes in the gross export volume of wood and wood articles from New Zealand to the top five destinations (a) and the total number of export destinations between 2000 and 2005 (b). (Source: Statistics NZ. Overseas Trade Statistics Merchandise Trade Exports)

exports. Since the early 1980s exports of forest products have more than doubled, with the volume of wood available expected to increase by 74% between 1996 and 2010. Over the past five years, total exports of wood and wood products to New Zealand's principal markets show (1) a doubling in export volumes to China, (2) steady decline in volumes leaving for Japan and Korea, (3) relatively consistent trade with Australia and the USA, and (4) no overall change in the diversity of export destinations (Fig. 24.2). Within individual ports, however, the trading patterns are much more dynamic and diverse (Fig. 24.3). At this level, trade in forest products is driven by local supply (i.e., the maturation of nearby forest plantations), global market demand and competition with other

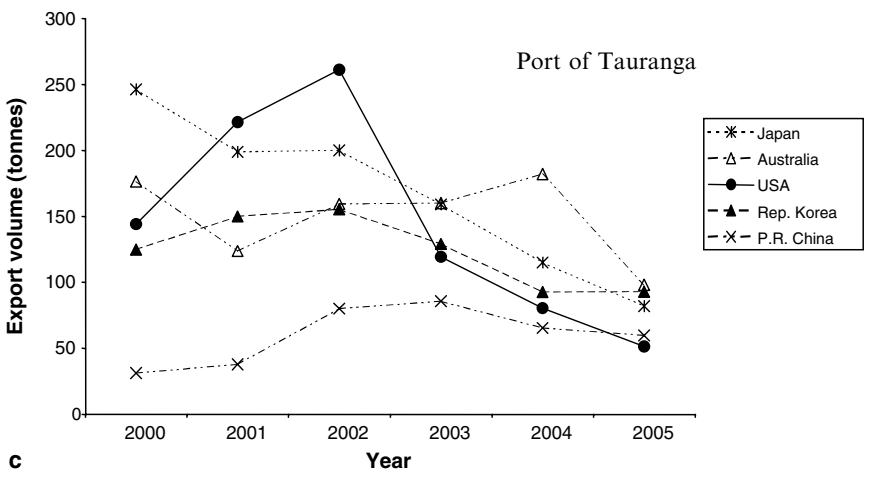
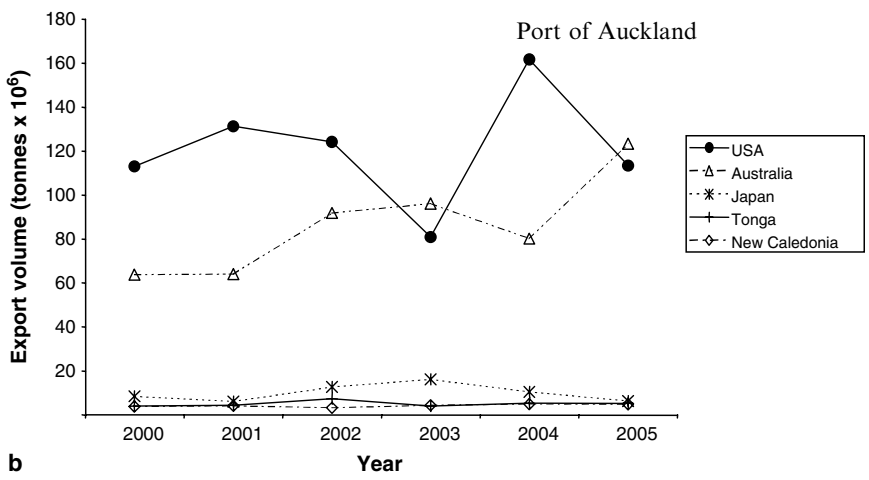
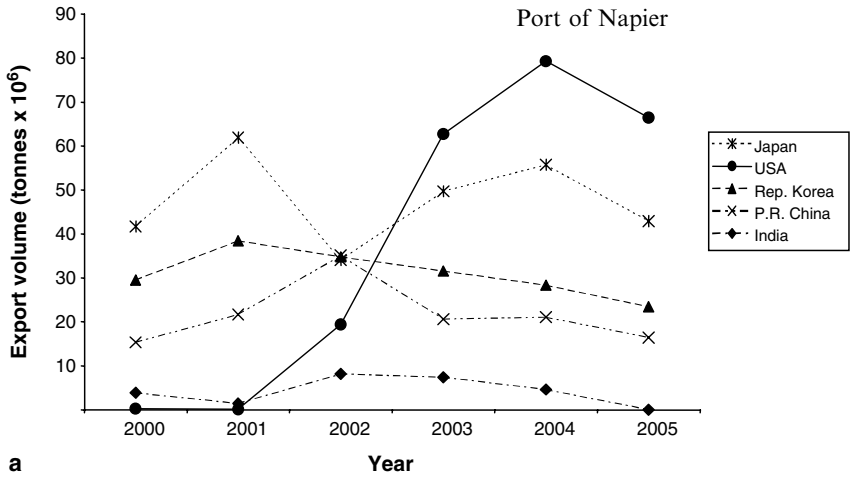


Fig. 24.3 Changes in export of wood and wood articles from three New Zealand ports: **a** Napier; **b** Auckland; **c** Tauranga. (Source: Statistics NZ. Overseas Trade Statistics Merchandise Trade Exports)

suppliers, both national and international. Currently, New Zealand exports bulk forest products to more than 50 countries worldwide, into 13 of the 18 bioregions in the IUCN's marine classification (Kelleher et al. 1995). Individual ports exhibit markedly different patterns of trade with different countries and these individual port dynamics will influence risk assessments over relatively short time-frames.

24.10 Conclusion

Despite the gaps in our taxonomic expertise and the difficulty in determining the origin of cryptogenic species, New Zealand has made major advances in describing the introduced marine biota in high risk entry points over the last decade. Our knowledge of marine invasions that may have occurred outside those entry points is less advanced. Multiple research projects to underpin the development of policy for managing marine invasive pests have also been initiated in the same time period (Hewitt et al. 2004; Chap. 20, Campbell) but positive outcomes from the research that will allow the leaks in the marine border to be plugged are still some way off. Propagule supply will remain a primary focus of incursion management. However, if we are to develop better predictive understanding of propagule supply (and thereby invasion dynamics), study of marine invasions needs to move from being a purely descriptive biological undertaking to an interdisciplinary science that incorporates economic and social drivers of risk, including those that drive changes in shipping patterns. Recent studies of risk factors associated with hull fouling of maritime vessels have revealed a similarly complex mix of social, economic and biological determinants of risk (Floerl et al. 2004, 2005a, b; Floerl and Inglis 2005). To paraphrase Underwood and Keough (2001), we contend that unless unpredictability caused by variations in the supply of introduced species is also included in conceptual understanding of marine invasions, our ability to effectively manage them will be severely limited.

References

- ACIL Economics and Policy Pty Ltd (1994) Bio-economic risk assessment of the potential introduction of exotic organisms through ships' ballast water. Australian Quarantine and Inspection Service, Canberra, 47 pp
- Beston A (2005) Native plants outnumbered. NZ Herald 2 December 2005:A7
- Blezard RH (1980) Calculated sea area of the New Zealand 200 nautical mile Exclusive Economic Zone. N Z J Mar Freshwater Res 14(2):137–138
- Carlton JT (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanogr Mar Biol Annu Rev 23:313–371
- Carlton JT (1996) Pattern, process, and prediction in marine invasion ecology. Biol Conserv 78:97–106

- Chapman JW, Carlton JT (1991) A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). *J Crustacean Biol* 11:386–400
- Clarke C, Hilliard R, Junqueira Ade OR, Neto Ade CL, Polglaze J, Raaymakers S (2004) Ballast water risk assessment, Port of Sepetiba, Federal Republic of Brazil, December 2003: Final Report. GloBallast Monograph Series No 14, IMO, London
- Clout MN, Lowe SJ (2000) Invasive species and environmental changes in New Zealand. In: Invasive species in a changing world. Mooney HA, Hobbs RJ (eds) Island Press, Washington, DC, pp 369–383
- Costello CJ, Solow AR (2003) On the pattern of discovery of introduced species. *Proc Natl Acad Sci* 100:3321–3323
- Coutts ADM, Taylor MD (2004) Variation in fouling patterns between different areas on the hulls of merchant vessels. *N Z J Mar Freshwater Res* 38:215–229
- Coutts ADM, Moore KM, Hewitt CL (2003) Ships' sea-chests: an overlooked transfer mechanism for non-indigenous marine species. *Mar Pollut Bull* 46(11):1510–1512
- Cranfield HJ, Gordon DP, Willan RC, Marshall BA, Battershill CN, Francis MP, Nelson WA, Glasby CJ, Read GB (1998) Adventive marine species in New Zealand. NIWA Tech Rep 34, 48 pp
- Darwin C (1889) *Journal of researches into the natural history and geology of the countries visited during the voyage of the H.M.S. "Beagle" round the world*. Ward, Lock, London, 381 pp
- Dell RK (1968) Composition and distribution of the New Zealand Brachyuran fauna. *Trans R S N Z* 10:225–240
- Floerl O, Inglis GJ (2005) Starting the invasion pathway: the interaction between source populations and human transport vectors. *Biol Invas* 7:589–606
- Floerl O, Pool TK, Inglis GJ (2004) Positive interactions between non-indigenous species facilitate transport by human vectors. *Ecol Appl* 14:1724–1736
- Floerl O, Inglis GJ, Hayden BJ (2005a) A risk-based predictive tool to prevent accidental introductions of nonindigenous marine species. *Environ Manag* 35:765–778
- Floerl O, Inglis GJ, Marsh H (2005b) Selectivity in vector management: an investigation of the effectiveness of measures used to prevent transport of non-indigenous species. *Biol Invas* 7:459–475
- Forsyth DM, Duncan RP (2001) Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. *Am Nat* 157:583–595
- Foster BA, Willan RC (1979) Foreign barnacles transported to New Zealand on an oil platform. *N Z J Mar Freshwater Res* 13:143–149
- Francis MP, Worthington CJ, Saul PJ, Clements KD (1999) New and rare tropical and subtropical fishes from northern New Zealand. *N Z J Mar Freshwater Res* 33:571–586
- Gollasch S (2002) The importance of ship hull fouling as a vector of species introductions into the North Sea. *Biofouling* 18(2):105–121
- Gordon DP (2001) *Marine biodiversity*. Alpha 108. The Royal Society of New Zealand, Wellington, New Zealand
- Hay CH, Luckens PA (1988) The Asian kelp *Undaria pinnatifida* (Phaeophyta: Laminariales) found in a New Zealand harbour. *N Z J Bot* 25(2):329–332
- Hayden BJ, Whyte CF (2003) Invasive species management in New Zealand. In: Ruiz GM, Carlton JT (eds) *Invasive species: vectors and management strategies*. Island Press, Washington, DC, pp 270–291
- Hayward BW (1997) Introduced marine organisms in New Zealand and their impact in the Waitemata Harbour, Auckland. *Tane* 36:197–223
- Herborg L-M, Jerde CL, Lodge DM, Ruiz GM, MacIsaac HJ (2007) Predicting invasion risk using measures of introduction effort and environmental niche models. *Ecol Appl* 17(3):663–674
- Hewitt CL, Willing J, Bauckham A, Cassidy AM, Cox CMS, Jones E, Wotton DM (2004) New Zealand marine biosecurity: delivering outcomes in a fluid environment. *N Z J Mar Freshwater Res* 38:429–438
- Hilliard RW, Raaymakers S (1997) Ballast water risk assessment for twelve warm-water ports in Queensland, Australia. *Proceedings of the Combined Australasian Coastal Engineering and Ports Conference*, Christchurch, pp 717–722
- Holdaway RN (1989) New Zealand's pre-human avifauna and its vulnerability. *N Z J Ecol* 12(Suppl):11–25

- Holdaway RN, Roberts RG, Beavan-Athfield NR, Olley JM, Worthy TH (2002) Optical dating of quartz sediments and accelerator mass spectrometry ^{14}C dating of bone gelatin and moa egg-shell: a comparison of age estimates for non-archaeological deposits in New Zealand. *J R Soc N Z* 32(3):463–505
- James P, Hayden BJ (2000) The potential for the introduction of exotic species by vessel hull fouling: a preliminary study. NIWA Client Rep WGN00/51, 57 pp
- Kelleher G, Bleakeley C, Wells S (1995) A global representative system of marine protected areas. Vols 1–4. Great Barrier Reef Marine Park Authority; The World Conservation Union (IUCN); The World Bank, Washington, DC
- Knox GA (1975) The marine benthic ecology and biogeography. In: Kuschel, G (ed). *Biogeography and ecology in New Zealand*. Dr W. Junk Publishers, The Hague, pp 353–458
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends Ecol Evol* 16:199–204
- Kott P (2002) A complex didemnid ascidian from Whangamata, New Zealand. *J Mar Biol Assoc UK* 82:625–628
- Kott P (2004) A new species of *Didemnum* (Ascidiacea, Tunicata) from the Atlantic coast of North America. *Zootaxa* 732:1–10
- Lester PJ (2005) Determinants for the successful establishment of exotic ants in New Zealand. *Divers Distrib* 11(4):279–288
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Ministry of Fisheries (1998) Import Health Standard (Biosecurity Act 1993) for ships' ballast water from all countries, 3pp. http://www.fish.govt.nz/sustainability/biosecurity/ballast_health.html
- Nelson WA (1994) Marine invaders of New Zealand coasts: Auckland Botanical Society Lucy Cranwell Lecture 6 October 1993, University of Auckland. *Auckland Bot Soc J* 49(1):4–14
- Nelson WA, Duffy CAJ (1991) *Chnoospora minima* (Phaeophyta) in Port Underwood, Marlborough – a curious new algal record for New Zealand. *N Z J Bot* 29:341–344
- Nelson WA, Gordon DP (1997) Assessing New Zealand's marine biological diversity – a challenge for policy makers and systematists. *N Z Sci Rev* 54(3/4):58–66
- NZ Plant Conservation Network (2006) http://www.nzpcn.org.nz/exotic_plant_life_and_weeds/index.asp
- Rigby GR, Steverson IG, Bolch CJ, Hallegraeff GM (1993) The transfer and treatment of shipping ballast waters to reduce the dispersal of toxic marine dinoflagellates. In: Smayda TJ, Shimizu Y (eds) *Toxic phytoplankton blooms in the sea*. Elsevier, pp 169–176
- Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. *Annu Rev Ecol Syst* 31:481–531
- Solow AR, Costello CJ (2004). Estimating the rate of species introductions from the discovery record. *Ecology* 85:1822–1825
- Underwood AJ, Fairweather PG (1989) Supply side ecology and benthic marine assemblages. *TREE* 4:16–20
- Underwood AJ, Keough MJ (2001) Supply-side ecology: the nature and consequences of variations in recruitment of intertidal organisms. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine community ecology*. Sinauer Associates, Sunderland, Maine, pp 183–200
- Uwai S, Nelson W, Neill K, Wang WD, Aguilar-Rosas LE, Boo SM, Kitayama T, Kawai H (2006) Genetic diversity in *Undaria pinnatifida* (Laminariales, Phaeophyceae) deduced from mitochondrial genes – origins and succession of introduced populations. *Phycologia* 45:687–695
- Veltman CJ, Nee S, Crawley MJ (1996) Correlates of introduction success in exotic New Zealand birds. *Am Nat* 147:542–557
- Verling E, Ruiz GM, Smith LD, Galil B, Miller AW, Murphy KR (2005) Supply-side invasion ecology: characterizing propagule pressure in coastal ecosystems. *Proc R Soc B* 272(1569):1249–1256
- Wonham MJ, Lewis MA, MacIsaac HJ (2005) Minimizing invasion risk by reducing propagule pressure: a model for ballast-water exchange. *Front Ecol Environ* 3(9):473–478

