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Chapter 8

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Pathways of Biological  
Invasions of Marine Plants

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Less is known about exotic species and biological invasions in the marine than in the terrestrial environment, particularly for marine plants. The scarcity of information can be explained as follows: (1) There is a lack of historic knowledge of marine flora on most coasts of the world. Most floristic studies on marine vegetation are recent, limiting comparisons of flora composition over time. (2) The sea remains a cryptic medium, where the presence of new species may often go undetected. (3) In most cases, the consequences of marine plant invasions only appear over long periods, sometimes as a result of changes in biological and environmental factors. (4) In general, the direct repercussions of marine plant invasions on human activity are much lower than those of invasions on land or even in freshwater. As a result, interest in the study, evaluation, and control of marine plant invasions has been relatively low.

It is difficult to obtain a clear picture of spatial and temporal patterns for marine plant invasions even though there are many sources of information. Floristic studies have been carried out in many countries and geographical regions (Abbott and Hollenberg 1976, Adams 1994, Lawson and John 1982, Noda 1987, Scagel et al. 1989, South and Tittley 1986, Taylor 1957, 1960, Verlaque 1994, 2001, Womersley 1984, 1987, 1994). Many papers and reports focus on particular exotic species (Boudouresque et al. 1994, Cranfield et al. 1998, Eno et al. 1997, ICES 1981, 1987, 1989, 1991, 1997, Munro et al. 1999, Ribera and Boudouresque 1995, see also reference section). In addition, information is increasingly available through elec-

tronic databases (e.g., Britain [Eno et al. 2000], Hawaii [Anonymous 2000a], United States [Anonymous 2000b, Invasive *Spartina* Project 2002]). However, given limitations associated with the historic record, most floristic studies are not explicit as to whether a species is native or exotic, and there remains a lack of data for many parts of the world.

To present an overview of the known world distribution of nonnative marine plants, I have grouped, compiled, and examined records from the following geographical regions: the Mediterranean Sea, the European Atlantic coast, the North American Atlantic coast, the North American Pacific coast, and the Australian and New Zealand coasts. The exotic species from islands or countries that do not belong to any of the geographic regions cited, such as China, the Canary Islands, the Azores, and the Hawaiian Islands, are grouped as "others." Because of the relative lack of information published about marine plant invasions in Central and South America, these regions are not included in this chapter (although some sporadic information about the use of exotic species for their commercialization does exist). Moreover, this overview considers both long- and short-distance transport—the former allowing a species to colonize a new continent or geographical area; the latter allowing a species, native or introduced, to extend its distribution range to neighboring countries. Therefore, within any one region—for example, the European Atlantic coasts—the total number of introduced species includes both invasions from outside Europe and introductions of species within and between European countries. For example, *Sargassum muticum* is considered an exotic species for the Atlantic and has subsequently colonized the coasts of several European countries via diffusion (natural or not). Likewise, although *Mastocarpus stellatus* is native to the European coastline, it was introduced by scientific experiments to the Helgoland area (one of the North Frisian Islands), where it did not previously occur.

This assessment of marine plants includes 189 exotic species (Fig. 8.1, Appendix 8.1). The list does not include taxa recorded at supraspecific levels or doubtful species. The composition of the known exotic marine flora is as follows: 100 red algae (53%), 42 brown algae (22%), 21 green algae (11%), 15 phytoplanktonic species (8%), and 11 higher plants (6%). All these data are probably underestimates. In the case of macroalgae, the number of invaders in each group (red, brown, and green) is roughly proportional to the total number of species known globally in each category. However, following this line of thought, the number of exotic microalgae is likely to be underestimated with respect to the total number of global taxa (possible reasons for this are discussed on page 188). In contrast, the percentage of successful exotic higher plants is elevated (6%) relative to

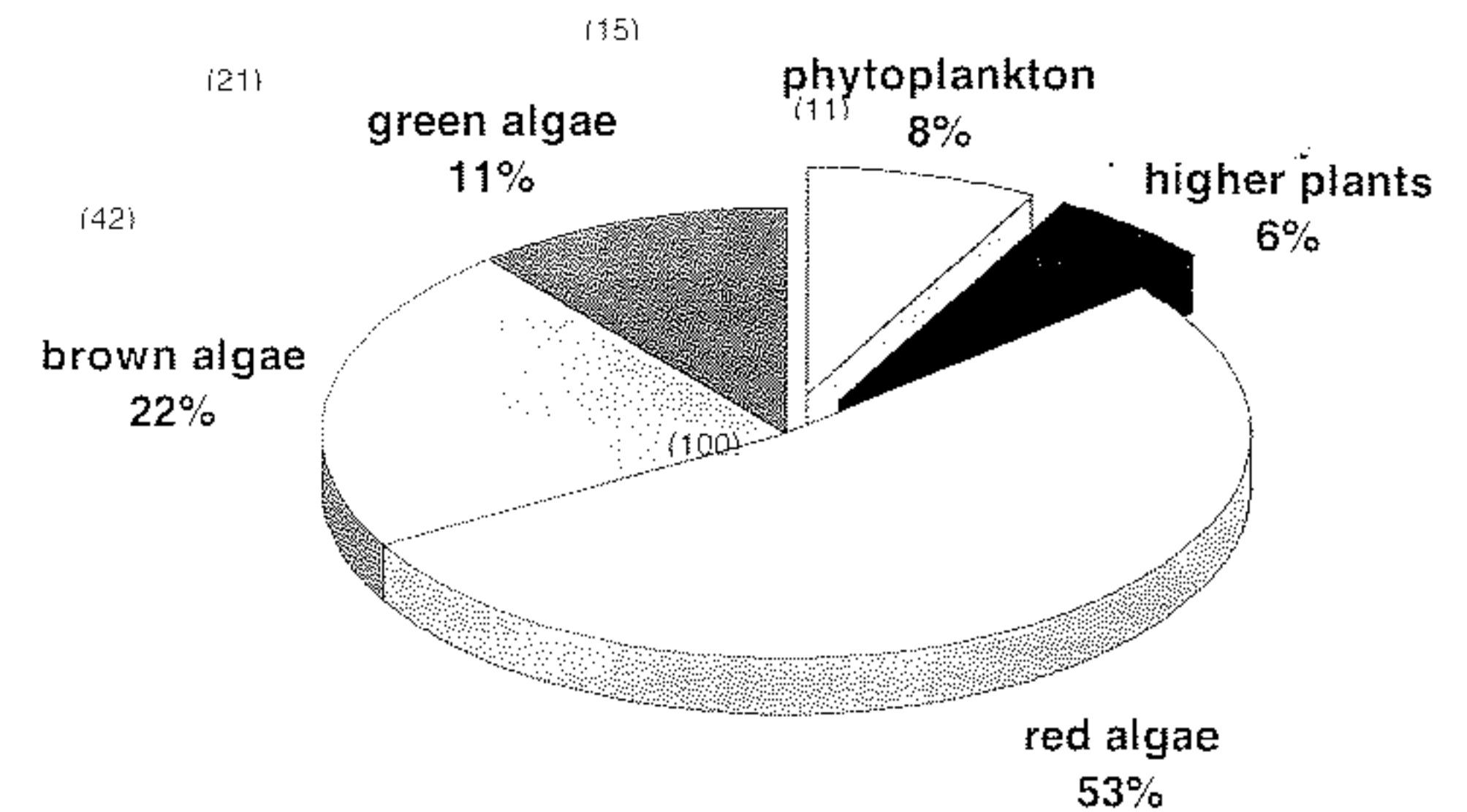


FIGURE 8.1. Number and percentage of nonnative species of marine plants, presented by systematic groups.

the total number of known marine phanerogams in the world. This observation suggests that risk of invasions is relatively great for higher marine plants as a taxonomic group (Ribera and Boudouresque 1995).

The main aim of this chapter is to review the pathways by which species are introduced into different environments, and to relate these pathways to taxa. However, before presenting the results, I wish to emphasize some overarching considerations about the relation between species and pathways, and about interpreting my analyses:

1. It is difficult, and sometimes impossible, to identify the dispersal mechanism (or vector) of exotic marine species. There are few species for which a single vector can be clearly identified. The possible vector is determined on the basis of known associations and life-history characteristics. For instance, ships' hulls are a possible vector for species that (a) appear in a port and (b) are known to occur on ships' hulls in the same port or in nearby waters. The same reasoning can be used for ships' ballast water as a vector. Of course, finding a species on a ship's hull does not exclude it from ballast water transport, and vice versa. For some species, many transfer mechanisms are possible and the likelihood of any one is difficult to estimate; I have considered the pathway of these species (55 total) to be uncertain at the present time.
2. The same taxon may also be involved in various pathways among regions. For example, depending on the region, invasion by *Codium fragile* subsp. *tomentosoides* has been associated with ships' deballasting, transfer by oysters, packing materials used for baits, fishing nets,

ships' hulls, and ships' propeller shafts. Given that one of the main points of interest here is the relationship between the transport systems of different species, it is important to emphasize and adequately reflect the possible occurrence of multiple pathways for the same species. In the analyses (see Conclusions section, p. 202), this explains why the total number of nonnative species distributed in distinct pathways is always greater than the total number of nonnative species, and also why some species are cited more than once in Appendix 8.1.

3. For most species it is very difficult to define species-specific relationships with particular pathways or vectors. Most of the main pathways are not usually highly selective, making it impossible to draw up a profile of risk organisms for each one. Instead, factors such as the propagule supply (pressure) from a particular region, resulting from the extent and frequency of maritime transport and the abundance of a species in a given source region, are likely to determine the dispersal vector from that region.

## DESCRIPTION OF MAIN PATHWAYS

The following review of the patterns of invasion for marine plants associated with particular pathways is based on my synthesis and analyses of records for focal geographic regions. This summary excludes species records for which the pathway is considered uncertain (55 total).

### Maritime Transport

Transport by vessels (ships) may be the greatest mechanism of global dispersal of marine organisms. This vector includes both the intentional and accidental transport of organisms both outside and inside the vessel (Carlton 1994). Intentional transport aboard ships mostly concerns animals, so the focus here is only on unintentional pathways. Marine macrophytes (including higher plants, red algae, brown algae, and green algae) have been detected most frequently on the outside of vessels, on or in various structures or parts of the ship, such as hulls, rudders, propeller shafts, and anchors. These organisms are usually sessile—that is, fixed on the surface of these structures (fouling)—but they can also be vagile species (clinging) or species that live in holes (boring) (Zibrowius 1991). Inside the vessel, organisms can be found in seawater pipe systems, in the anchor chain locker, and in other places, but in general these “habitats” do not provide suitable survival conditions for marine plants; in contrast, animals and

unicellular plants (phytoplankton) are more abundant in the ballast tanks of vessels (Carlton 1994).

### Transport on Ships' Hulls

Dispersal of at least 39 marine plants is attributed to hull fouling (Fig. 8.2), and a high number of those nonnative species considered to have an uncertain pathway may also have been transported via this vector (Ribera and Boudouresque 1995). Of these 39 species, most (31) were red algae, and it is interesting to note that higher plants are not involved in this pathway (Appendix 8.1).

Species transported by fouling usually correspond to small specimens that have a flexible and filamentous vegetative structure and a high growth rate, such as species belonging to Acrochaetiales, Ceramiaceae, Ectocarpales, and *Cladophora*. Furthermore, very large sporophytes of the big brown alga *Undaria pinnatifida*, which measure more than a meter, have been observed on the hull of a boat in a New Zealand harbor after sailing hundreds of kilometers (Hay 1990). Therefore, this species may have reached New Zealand through the fishing fleets of Korea and Japan (Adams 1994). In addition, this vector may disseminate large plants whose life cycles include a microscopic stage, such as the microscopic gametophytes of *U. pinnatifida*. Fletcher and Manfredi (1995) predicted that coastal traffic would be responsible for the significant spread of *U. pinnatifida* in northern European waters. Equally, species with a wide range of ecological requirements can survive successive submersion in waters with

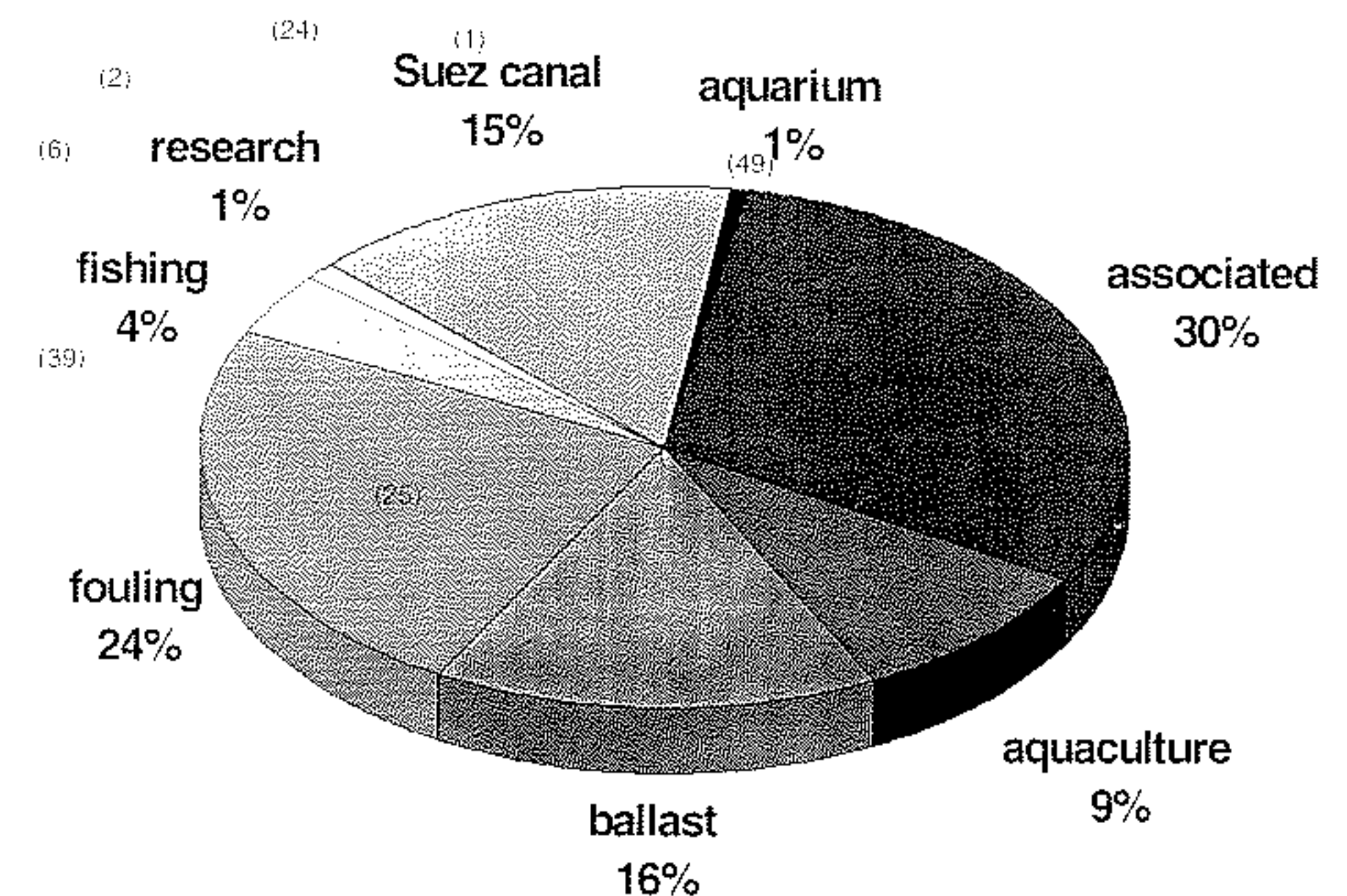


FIGURE 8.2. Number and percentage of nonnative species of marine plants introduced by each pathway.

different physical and chemical characteristics, especially temperature and salinity. In some cases these differences may act as biological barriers, impeding the introduction of species into a new area. This is the case of the Baltic Sea, where the water is virtually fresh (Leppäkoski 1994).

In the Mediterranean Sea, many established exotic plant species belong to the group Ceramiaceae, such as *Acrothamnion preissii*, *Antithamnion amphigeneum*, or *Antithamnionella spirographidis*. Most of these species produce blooms in the initial naturalization phase or periodically, depending on the environmental conditions. These fouling species have sometimes become dominant in invaded communities. For example, in the northwestern Mediterranean Sea, *Asparagopsis armata* covers as much as 100 percent of the available hard substratum in winter but virtually disappears for the rest of the year (Ribera and Boudouresque 1995). In addition, *Polysiphonia harveyi* is now the dominant small seaweed during much of the year at many locations on the North Sea; it has a wide range of biological features that have given it an advantage as an immigrant (Maggs and Stegenga 1999).

The transport of fouling organisms on ships' hulls is the most probable mechanism of transoceanic dispersal of *Codium fragile* subsp. *tomentosoides* (Carlton and Scanlon 1985). The direct observations of this species on the hulls of vessels traveling from Europe to North America (Loosanoff 1975) lend strong support to the hypothesis that the population of this Asian species on North American coasts originated in Europe. Similarly, Hillson (1976) suggested that this species might have been transported to Virginia on a ship's hull. However, according to Carlton and Scanlon (1985), other mechanisms may have contributed to the movement of *C. fragile* subsp. *tomentosoides* along the Atlantic coast of North America.

### Transport through Ships' Ballast

Ships' ballast may also make a significant contribution to the transfer of marine plants. The volume of ballast water transported globally is immense; it is estimated that 79 million metric tons of ballast water are released annually into U.S. waters (Carlton et al. 1995) and up to 3,000 million tons worldwide (Gollash 1996). Ballast water frequently contains sediment, which is an ideal medium for the transport of certain organisms. In a survey of 343 cargo vessels, Hallegraeff and Bolch (1992) found that 65 percent contained ballast tank sediments.

I attribute the colonization of at least 25 nonnative marine plants to this vector (Fig. 8.2). Most (16) of these species are phytoplankton (Appendix 8.1). I believe these data are underestimates, as the scarcity of floristic studies on the ballast water of commercial vessels and the numerous

problems in the taxonomy of planktonic microalgae make it difficult to detect nonnative species. Recognition of the presence of a new species is often restricted to the appearance of algae blooms (red tides), suggesting that many rare species may go undetected. Improved methods used in taxonomic analyses, especially on dinoflagellates, based on new techniques of ultrastructural chemical composition and genetic molecular analysis should increase understanding in these areas and allow detection of new species. For example, the reports of *Gymnodinium catenatum* in northern European waters do not refer to a recently introduced exotic species but constitute a misidentification of a native overlooked in these waters: *G. nolleri* (Elbrächter 1999). This author refers to this kind of species as pseudoexotic species.

The percentage (20%) of higher plants that have colonized new areas in this way is surprising; this may be attributable to the production of fruits or seeds that are adapted to survive for long periods under constant humidity (water or sediment) and low light.

Carlton and Geller (1993) note that ships' ballast is among the least selective means of species transfer, from an ecological and taxonomic point of view. As an example, they pointed out that 317 species were recorded in the ballast of Japanese ships on arrival in Oregon (USA). In spite of this complexity, I can attempt to identify the characteristics of plants that are susceptible to this mode of transport:

1. Planktonic species. Ballast is probably the most feasible method of transport for microscopic organisms living free in a mass of water.
2. Plants that can develop structures of resistance during their life cycle, such as cysts, zygotes, spores of resistance, or fruits. This strategy can be present in both micro- and macrophytes, and can guarantee survival in ballast tanks (normally in sediment ballast), and especially viability in later life in the new area. Thus diatoms, with their siliceous frustule, and dinoflagellates, with their cysts, may be best adapted to ballast water or sediments. One single ballast tank was estimated to contain more than 300 million dinoflagellate cysts, which could germinate into confirmed toxic cultures (Hallegraeff and Bolch 1991).
3. Plants with vegetative reproduction. Ballast can be the pathway for macrospecies that form specific propagules or fragments of plants, like cuttings. Some large brown algae, such as *Sargassum muticum*, fragment easily and can even form large floating masses; these fragments could easily withstand ballast tank conditions for several days. The red alga *Furcellaria lumbricalis* and the brown alga *Fucus serratus* were probably introduced to the area of the Gulf of St. Lawrence (Canadian

Atlantic coast) in the late nineteenth century, and ships' ballast has been suggested as the likely mechanism (Novaczek and McLachlan 1989).

Ballast introductions are dependent on the survival of organisms during transit; the specific conditions in ballast tanks may be a barrier to invasion for some organisms or may enhance the survival of others (Galil and Hülsmann 1997). The darkness of ballast tanks, combined with continued zooplankton grazing pressure, result in a considerable decrease in algal densities, thereby precipitating a decline in the light-driven food web (Galil and Hülsmann 1997). A study of ballast carried by cargo vessels entering Australian ports reported that 50 percent of sediment samples contained dinoflagellate cysts and 5 percent were cysts of the toxic dinoflagellates *Alexandrium catenella* and *A. tamarensis* (Hallegraeff and Bolch 1992). Similarly, MacDonald and Davidson (1998) detected *Alexandrium* cysts (including *A. minutum* and *A. tamarensis*) in 17 percent of the ships arriving in Scottish ports (European Atlantic coast) after short voyages through regional European seas. In contrast, no cysts of potentially harmful dinoflagellates were detected in a study of ballast tanks of vessels on the Mediterranean coast of Israel (Galil and Hülsmann 1997).

These microalgae, whether they are naturalized (i.e., established for a relatively long period of time) or recent arrivals, can give rise to blooms that have a large impact on the environment or the human population. For example, the introduction of the diatom *Coscinodiscus wailesii* to the North Sea has caused the clogging of fishing nets by extensive mucus production (Boalch and Harbour 1977). The dispersal of toxic dinoflagellates can be more dangerous because they pose a serious threat to aquaculture and public health. The human illness Paralytic Shellfish Poisoning (PSP) results from the consumption of products contaminated with alkaloid toxins from any of 11 species of planktonic dinoflagellates (Hallegraeff et al. 1995), such as *Alexandrium catenella*, *A. minutum*, *A. tamarensis*, and *Gymnodinium catenatum*. Although in a strict sense PSP is a natural phenomenon, well known to native North American Indian tribes, until 1970 poisoning records were confined to temperate waters of Europe, North America, and Japan (Hallegraeff 1993). However, by 1990, PSP outbreaks were documented throughout the Southern Hemisphere, including South Africa, Australia, New Zealand, and Papua New Guinea, and the Northern Hemisphere, including India, Thailand, and the Philippines (Hallegraeff 1998). The introduction of Southeast Asian dinoflagellates of the genera *Gymnodinium* and *Alexandrium* into Australian waters in the 1980s caused PSP, and as a result there was a ban on the sale of cultured and wild

shellfish, mussels, oysters, and scallops, which had a catastrophic economic impact (Pollard and Hutchings 1990). Similarly, blooms of *Gymnodinium catenatum* were first recognized in waters of southern Tasmania in late 1985 (Hallegraeff and Summer 1986). The most likely vector of this introduction is ballast water discharge either from northeast Asian ports or, less likely, from European ports (McMinn et al. 1997).

### Transport by Other Parts of a Ship

There are other means of plant transfer by maritime transport, for example, adhesion to the propeller or anchor. This kind of vector may be more important in marginal rather than remote dispersal of marine species. The dissemination of *Caulerpa taxifolia* across the Mediterranean was probably caused by successive anchorage, often over long distances, by pleasure boats plying between the French coast and the Balearic Islands or the Italian coast (Meinesz 1992). By following the most frequent pleasure routes in the Mediterranean (Meinesz et al. 1998), I can reconstruct the progress of *C. taxifolia* from the French Mediterranean coast. Ecophysiological studies on *C. taxifolia* confirm that this species survives long periods in the prevailing conditions of an anchor locker (Sant et al. 1996). Therefore, Knoepffler-Péguy et al. (1985) suggested that small boats caused the expansion of *Sargassum muticum* outside the Thau Lagoon (France). Species transported by this method develop rapidly and can regenerate from vegetative fragments. Moreover, if the species are tolerant to desiccation, a wide range of temperatures, and the dark, their potential survival in new areas is enhanced.

### Aquaculture Activities

The introduction of 64 exotic marine plant species has been associated with aquaculture, accounting for 39 percent of the total (Fig. 8.2, Appendix 8.1). Aquaculture activities are comprised of three separate pathways: the controlled culture of algae (deliberate pathway); the unintentional escape of individuals from controlled cultures; and the transfer of marine plants associated with imported aquaculture species (unintentional pathway).

#### RELEASE OF NONNATIVE SPECIES INTO THE OPEN SEA FOR AQUACULTURE PURPOSES

At present, 15 nonnative species of marine plants (11 red algae, 4 brown algae) are used in aquaculture as experimental cultures or as exploited resources (Fig. 8.2). Only red and brown algae are transported by this pathway, since the greatest economic profit to be obtained from algae

today is from their use as raw material for the extraction of colloids (alginates from brown algae, and agar and carrageenan from red algae). These two groups are also the algae most extensively used in the food industry.

*Laminaria japonica* is the alga used most frequently in marine aquaculture throughout the world, with a global production of 3,521,108 tons fresh weight in 1993 (Perez 1997). China, where the alga was intentionally introduced in 1925, is now the world's largest producer of *L. japonica*, estimated in 1996 as 3,900,000 tons fresh weight (Perez 1997). This species has also been introduced for the same purpose in Korea (Perez 1997). *Undaria pinnatifida* was also deliberately introduced for farming to the coast of Brittany (French Atlantic coasts) from the Thau Lagoon (French Mediterranean Sea), where it had been accidentally introduced with Japanese oysters (Perez et al. 1984).

In an attempt to produce more economically viable species, the introduction of exotic species in close proximity to natives is very common. For example, since the 1980s *Porphyra yezoensis* has been one of the nonnative species with better prospects for industrial cultivation off the coasts of Canada and the United States (ICES 1997). Numerous studies have been done on its biology and the impact of natural populations on indigenous communities.

By crossing small geographical barriers, sometimes a nonnative species is imported from neighboring countries, where the species is native. This may modify natural distribution. Equally, the transfer of species within a country with a long coastline means new introductions: although a species is included in the national floristic lists, a native species should be considered nonnative in a geographical region where it did not exist previously. In Chile, for example, the transfer of *Gracilaria* species from one region to another for aquaculture activity has altered the geographical range of this genus (Santelices 1989). Finally, the transfer of individuals of a native species (potentially representing a distinct genome) from a different geographical area must also be considered an introduction. For example, strains of *Hypnea musciformis* from Senegal were cultured in Corsica (Mediterranean Sea) in the 1980s, because they appeared to be more productive than the Mediterranean strains (Mollion 1984). The introduction of geographically isolated strains of the same species or of close relatives to the native ones may lead to a new kind of biological contamination, genetic mixing, the consequences of which are unpredictable (Ribera and Boudouresque 1995).

Most countries have no legislation on the management of introduction and transfer of marine plants. Normally the importation, control, and

quarantine measures of these organisms are governed by regulations on agriculture or fisheries. Consequently, in most cases, aquaculture projects in the open sea, which do not have sufficient knowledge of the species or the appropriate measures for control, are permitted.

#### ESCAPES FROM CONTROLLED CULTURES

Most nonindigenous cultured species do not reach reproductive maturity and, therefore, do not complete their life cycle in the new territory. To control the culture of nonnative species, the presence of naturalized individuals of these species is searched for in neighboring areas. Of all the exotic species cultivated in Europe, only *Undaria pinnatifida* has colonized regions near its farming site on the French Atlantic and Mediterranean coasts (ICES 1987). When this species was introduced in Brittany (France) in 1984, experts claimed that it was not possible for the gametophytes to mature and produce sporophytes in situ because of the water temperature prevailing in this region (these claims are noted by Wallentinus 1994). But the full life cycle of this species could be completed (Floc'h et al. 1991) and at present *U. pinnatifida* forms wild populations along the French Atlantic coast (Castric-Frey et al. 1993, 1999). This escape started a controversy about whether cultivation should be allowed to continue, but after several evaluations of the risks, these were considered too small to stop further development of other farms (ICES 1989). However, not all countries have applied the same criteria. For example, proposals to introduce the farming of this species in Ireland were rejected (Eno et al. 1997).

Attempts to profit from naturalized nonindigenous species are habitual, and sometimes even used as a possible way to control spread. However, if economic benefits are optimal, this may lead not only to exploitation of natural populations but also to their culture and spread. These cases could be considered marginal dispersal pathways. For example, *Laminaria japonica* and *Undaria pinnatifida*, naturalized in the interior of the Thau Lagoon in the French Mediterranean Sea, are now cultivated in the open sea along the nearest coasts (Perez et al. 1984).

In the industrial production of algae, certain phases of development (or a whole generation) may be attained in controlled cultivation conditions away from the open sea. This method is often used because many plants cannot complete their life cycle with an economically viable growth rate in the open sea. Many decisions about whether to import exotic species for cultivation are based on this premise of containment. However, for some species this is not always true, and they escape to form natural populations.

All projects to cultivate nonnative species, whether contained or open cultivation, should first evaluate formally the opportunities for escape, the viability in situ, and the possible consequences of target species and associated organisms. The results of these studies may not support the establishment of cultures. For example, ICES did not allow continuation of the culture of the brown alga *Macrocystis pyrifera*, started in the 1970s off the Atlantic coast of France, because young sporophytes were allowed to grow for about seven months to 13 meters, and they reached the fertile stage with sporangia.

In 1981 specimens of the red alga *Eucheuma spinosum* from the Philippines were immersed in the open sea in the French Antilles (Guadeloupe), forty-eight hours after being collected, to compare their growth rate with native specimens of the same species. No quarantine measures were applied. Two months later the introduced specimens were all dead, victims of necroses that the authors of the experiment attributed to a disease known in southern Asia as ice-ice (Barbaroux et al. 1984). The authors noted that the indigenous plants were resistant to this disease, and therefore assumed that they might have introduced the ice-ice disease in the Caribbean Sea.

Further, the literature contains several examples of unsuccessful experiments of algal culture. *Gracilaria tenuistipata* from China was cultivated in land-based fishponds on the Baltic Sea coast (1989–90) where it did not survive a water temperature below 7°C (Haglund and Pedersen 1992). Growth experiments with *Alaria esculenta* have been carried out along the Helgoland coast, which is within its range of distribution in European waters, but where the species does not grow naturally because of the high summer temperatures (Munda and Lüning 1977).

#### ASSOCIATED SPECIES WITH AQUACULTURE SPECIES TRANSFER

The accidental transport of epibiont or endobiont organisms associated with the intentional transport of target species is one of the main introduction pathways for marine plants nowadays, especially in association with the importation of oyster spat (seed) for aquaculture. Further, transfers of the Japanese oyster *Crassostrea gigas* have been the most important, both for the volume of imports and for its impact. This species has been progressively transferred to several global regions, including Canada, the United States, Tasmania, New Zealand, Europe, and China (Grizel 1994).

This “associated” pathway is the largest single pathway for naturalized (established) populations, both within aquaculture activities (49 of 64 species) and among all pathways (30% of 189 species considered here; Fig. 8.2). Among these, red algae predominate with 29 species (59%). However,

brown algae, with 14 species (29%), have exhibited the most invasive behavior, in terms of the spread, abundance, and negative impacts. For example, *Sargassum muticum* has colonized the Atlantic coasts of Europe (Scandinavia, the Netherlands, Belgium, Britain, France, Spain), the Mediterranean Sea (France), and the Pacific (Canada, the United States, Mexico, China, Japan, Korea, Philippines, Russia) (Critchley et al. 1990). It was first discovered in European waters off the Isle of Wight (Britain) in 1973 (Farnham et al. 1973) and has spread extensively in European waters from Portugal to Scandinavia, and even into the Mediterranean. Since its introduction this species has become dominant in many lower littoral areas with standing waters and in the sublittoral fringe, covering a broad range of conditions and habitats (Farnham 1994). In some cases it has formed large masses of floating algae, thanks to its air vesicles, which have had serious impacts on marine transport, especially in the English Channel. According to Farnham (1994), *S. muticum* has generally performed as an opportunist “gap-grabber,” without significantly displacing or outcompeting native benthic plants, as had originally been feared. Although new small populations still appear, the clearly invasive aspect of its initial spread has declined more recently, and some initial populations (which survived for several years) have disappeared. This species has been the object of many eradication and evaluation studies, although these have been undertaken on a limited spatial scale (Belsher 1991).

History demonstrates that sites of shellfish culture carry a high risk, as locations of shellfish farming are often “hot spots” in terms of the number of exotic species. For example, the Thau Lagoon at Sète on the French Mediterranean coast is an area of very active shellfish cultivation where up to 45 nonnative species have been identified, 43 of them from the Pacific region (Verlaque 2001). Other aquaculture sites in the Mediterranean Sea are now developing, such as the Venice Lagoon in the Adriatic, where the number of nonnative marine plants is increasing and includes *Sargassum muticum*, *Undaria pinnatifida*, and *Grateloupia doryphora* (Verlaque 1994). These aquaculture farms may be potent sources of infection (spread) to new areas for two reasons:

1. Once established, naturalized species can increase their distributions in the region by other vectors, such as maritime transport activities (sometimes in close proximity to aquaculture) or by natural dispersion. Some nonnative species in the Thau Lagoon, such as *Porphyra yezoensis*, *Solieria chordalis*, *Leathesia difformis*, *Lomentaria hako-datensis*, *Undaria pinnatifida*, and *Sargassum muticum*, have colonized part of the open sea (Verlaque 1994).

2. From these sites, spat or adult shellfish are transferred to other aquaculture farms. This occurs not only with Japanese oysters but also with other bivalves, such as the oysters *Crassostrea virginica* and *Ostrea edulis*, which can become another vector for these exotic plant species. In the Thau Lagoon, for example, exotic species, such as *Cladosiphon zosterae*, *Agardhiella subulata*, and *Chondria coerulescens*, may have been introduced along with oyster transfers from Atlantic farms (Verlaque 2001). Similarly, the worldwide distribution kinetics of the *Sargassum muticum* follow the routes of oyster importation (Ribera and Boudouresque 1995).

Outside the European coast, other cases of nonnative species carried by this vector are known. The transport on shells of commercial oysters moved along the coast for relocation may be responsible for the initial establishment of *Codium fragile* subsp. *tomentosoides* on the south shore of Cape Cod and Boothbay Harbor on the eastern coast of North America (Malinowski and Ramus 1973). In 1996 *C. fragile* subsp. *tomentosoides* was detected in Canadian Atlantic waters and was believed introduced with shellfish from the United States (Campbell 1997). The presence of *Polysiphonia subtilissima* seems to be associated with oyster and mussel farms in New Zealand (Ribera and Boudouresque 1995).

To date, no microalgae are involved in this vector. A unicellular alga that has recently been reported on the Atlantic coast of France, *Fibrocapsa japonica* (Raphidophyceae), may have arrived with ballast water rather than with the spat of the oyster *Crassostrea gigas*, as Billard (1992) had hypothesized. Within this group we can include the endobionts of the oysters, which are less visible but very dangerous if they are toxic. The faeces and digestive tracts of bivalves can be loaded with viable *Alexandrium* cells (Bricelj et al. 1991) and can also contain resistant resting cysts (Hallegraeff 1993).

This vector also transported a higher plant. The sea grass *Zostera japonica* was first reported in 1957 from the state of Washington (North American Pacific coast) probably carried by imported Japanese oysters (Harrison and Bigley 1982). Its later occurrence to the north and south of Washington State may have the same origin or result from spread (natural or human-aided) along the northern Pacific coast (Munro et al. 1999).

### Research Activities

Scientific research has been an uncommon pathway for introduced marine plants. We have recorded only two species associated with this pathway

(Fig. 8.2), but nonnative species or strains are increasingly being used in ecological and physiological studies. I am aware of numerous laboratory experiments on exotic marine plants in the past and present, but in most cases we do not know whether they are still in use. For example, *Gracilaria lemaneiformis* from Florida, *G. verrucosa* from Puerto Rico, and *G. tenuistipitata* from China were used for laboratory tests to produce protoplasts in Sweden (Björk et al. 1990).

### Escapes from Laboratories

Normally, research is carried out with specimens maintained in controlled conditions in laboratory tanks, and their use is usually temporary. In most cases, the behavior and potential ecological impacts of these exotic species (if they became naturalized in a new environment) is not known. Protective measures are usually taken to prevent the escape of these species from their cultures to the environment. Although no case of exotic marine plant species having escaped from laboratories has been reported to date, the risk of this is very high in research centers having an open seawater system; therefore, any drainage network for wastewater can be a mode of transport to the sea. Nowadays, the threat is increasing because research with toxic species is being carried out.

### Accidental Release of Discards

In most cases, previous knowledge of the ecological requirements of the species is sufficient to establish the means by which to safely dispose of live material. The main problem occurs with the fate of the individuals of a species at the end of studies. A total destruction of the material is always advisable, and waste should never be allowed to enter the main drains, as these always lead to the sea.

According to Koch (1951), the populations of the red alga *Bonnemaisonia hamifera* on Helgoland (European Atlantic coast) may have originated from discarded material sampled on scientific expeditions to Norway. However, its presence along other Atlantic coasts in Europe, such as in England, can be related to shellfish cultures (Tittley, pers. comm.; Eno et al. 1997).

Scientific Equipment (diving suits, objects installed in the water for a period of time)

There is no evidence that this vector is the specific cause of the naturalization of any marine plant, but it may play a role in marginal dispersion. How many times have small traces of algae appeared on diving suits? Therefore, all scientific equipment used in environmental research should



be thoroughly cleaned, decontaminated, and dried. Fixed installations in the sea for an extended time act as artificial reefs, which allow the rapid colonization of opportunist algae.

### Release of Nonnative Species into the Environment

Scientists carry out ecophysiological studies with nonindigenous species in the environment to compare them with native species or for their possible exploitation. Only one case of naturalized species by this vector is known. In the late 1970s, as an experiment, the red alga *Mastocarpus stellatus* was transplanted onto a rock on the island of Helgoland in Germany, on which it does not grow naturally. By the early 1990s it had colonized the whole western coast of the island (Munro et al. 1999). In this case, naturalization was predictable because this intertidal species is widely distributed along North Atlantic coasts.

In some cases, if the plants transferred to the open sea showed signs of adapting to the new environment in order to complete their life cycle, researchers have removed them. For example, hybridization experiments between the European brown alga *Laminaria saccharina*, the Canadian *L. longicuris* from British Columbia, and the Japanese *L. ochotensis* were carried out at Helgoland. The hybrids were cultivated in the sea but removed before they became fertile (Bolton et al. 1983).

### Aquarium Trade

The aquarium industry involves the constant and uncontrolled commerce of exotic species, both animals and plants. This activity could be regulated by national legislation and also by the Washington Convention (CITES), but the latter does not include plants. For example, in 1993 the Europrix Company catalogs offered 102 seaweed species, natives or otherwise, which included *Caulerpa taxifolia* and *Sargassum muticum* (Boudouresque and Ribera 1994). Since the invasion of *C. taxifolia*, some Mediterranean countries (France, Italy, and Spain) have national or regional legislation that prohibits the transport, trade, and possession of these species (Boudouresque et al. 1996).

To date, in contrast to freshwater plants, relatively few nonnative marine plants are associated with this pathway. There is one clear example (Appendix 8.1, Fig. 8.2). Despite the low signal, the impacts associated with this one case have been extreme (see below).

### Escapes from Public or Private Aquaria

Many public aquaria have water supply systems that run on an open cir-

treatment of these waters is incomplete (Ribera and Boudouresque 1995). Under these conditions the risk of species escaping from an aquarium is high, but there has been only one known example that involves marine vegetation.

In the Mediterranean Sea, the tropical alga *Caulerpa taxifolia* has been one of the most spectacular marine invasions and was probably introduced via this vector. Its presence in the Mediterranean has been on record since 1984 on the coasts of Monaco, and it probably escaped from an aquarium at the Oceanographic Centre (Meinesz and Hesse 1991). The Mediterranean population has different morphological and physiological characteristics from the tropical populations, exhibiting more invasive behavior such as rapid spread and overgrowth of other species (Boudouresque et al. 1996). Today *C. taxifolia* is found along the coasts of five countries in the northern Mediterranean (Monaco, France, Italy, Spain, and Croatia) and about 6,000 hectares have been affected by this invasion (Meinesz et al. 1998). Sixteen years after the appearance of this alga, it is still advancing with the same vitality and shows no sign of decline. Recently, a new population of this species has been detected on the Tunisian coast in the southern Mediterranean (Langar et al. 2000).

Genetic-molecular studies have been used to confirm the aquarium origin of the Mediterranean population of *C. taxifolia*. The individuals of this species used in private or public aquaria in Europe seem to have the same origin: the Wilhelma Zoologisch-Botanischer Garden of Stuttgart (Germany). At the beginning of the 1980s, this strain was given to the Tropical Aquarium of Nancy (French Atlantic coast) and from here to the Aquarium of Monaco (Mediterranean coast) (Meinesz and Boudouresque 1996). *Caulerpa taxifolia* individuals from several European aquaria and Mediterranean populations belong to a single strain, based on DNA sequence identity (Jousson et al. 1998).

During the spring of 2000, new settlements of *C. taxifolia* were discovered in the Pacific and Atlantic Oceans:

1. *Caulerpa taxifolia* was reported on the east coasts of Australia, about 30 kilometers south of Sydney (A. Miller, pers. comm., Algae-L [Algae-Listserver is a "Forum for marine, freshwater, and terrestrial algae"], May 30, 2000). Although the species grows naturally in some islands in the Tasman and Coral Seas, it was apparently new to this area.
2. Similarly, the species was reported in southern Florida, in the Atlantic Ocean (E. C. Oliveira, pers. comm., Algae-L, May 31, 2000). Oliveira proposed two theories about this new species: either the invasive strain of *C. taxifolia* from the Mediterranean was introduced into Florida, or the local strain of *C. taxifolia* (native in the Caribbean) is

blooming because pollution in the area is decreasing. Carlton (pers. comm.) pointed out that the Florida population of *C. taxifolia* is now considered the native stock of pantropical *C. taxifolia*.

3. In the Pacific Ocean, two populations of this species have been detected on the California coast, one in the San Diego Lagoon (Agua Hedionda) and the other in Huntington Harbor near Los Angeles (Kaiser 2000).

### Deliberate Release of Aquarium Content

The presence in nature of freshwater exotic species from the release of the content of private aquariums is well documented (Welcomme 1992). In contrast, this method of introduction is very uncommon for marine plants. This pathway could explain the appearance of *Caulerpa taxifolia* in Les Lecques Harbor on the coast of Var (French Mediterranean). The presence of a few blocks of tropical coral reef just beside the population of *C. taxifolia* suggests that the content of a personal aquarium had been emptied into the sea (Laborel 1992). Similarly, Hoffmann (in Colmer, pers. comm., Algae-L, July 6, 2000) believes that the presence of this species in the San Diego Lagoon is the result of emptying the contents of a private aquarium into a storm drain or directly into the lagoon. The release of the contents of private aquaria to the environment most likely results from (the avoidable) limited public information about associated risks and possible safeguards. Alternatively, in the case of *C. taxifolia* it may be the reaction to the fear of having a dangerous or illegal species at home.

### Fishing Activities

This group includes activities as diverse as the use of plants as packing for bait, fish, and shellfish, and the transport by fishing nets. While packing is a long-distance transport pathway, transport by fishing nets is more common as a marginal dispersion system. This pathway involves 6 species (2 Rhodophyceae, 2 Phaeophyceae, 1 Chlorophyceae, 1 higher plant), 5 of which have shown invasive behavior (Fig. 8.2).

### Unintentional Release of Packing Material

Marine plants are often used as packing materials to keep marine animals (used for bait, direct human consumption, or aquaculture) cool and damp during transport. These plants are usually medium-sized, branched or foliaceous, with a fleshy consistency, and they can retain humidity for a long time.

Seaweeds used for packing bait are routinely released into aquatic envi-

ronments, where they can naturalize. Two examples are known in the Mediterranean Sea. The Atlantic brown alga *Fucus spiralis* forms a small population in the Gruissan Lagoon (Sancholle 1988), and the red alga *Polysiphonia nigrescens* in the Prévost Lagoon (Verlaque and Riouall 1989); both sites are in the French Mediterranean Sea. Along the Atlantic coast of the United States the use of the green alga *Codium fragile* subsp. *tomentosoides* to wrap fishing baits has probably contributed to its spread. Carlton and Scanlon (1985) suggested that this species may have been transported to the Delaware–Maryland–Virginia region with shipments of the furoid alga *Ascophyllum nodosum*, which are sent to that region from Massachusetts with bait worms and are then discarded.

Various species are used for packing fish and shellfish, but only two examples of plants established in a new area by this pathway are known. The sea grass *Zostera japonica* was first reported in Willapa Bay in Washington State, and from then it continued to spread along the coasts (Harrison and Bigley 1982). This sea grass also occurs along the U.S. coast from Oregon to British Columbia. Although *Z. japonica* has not replaced the native *Z. marina*, largely because the former occurs higher in the intertidal zone, the previously barren mudflats in those areas are drastically changed by its spread (Posey 1988).

### Transport by Nets

The production of very extensive biomass, either floating or easily detachable, of nonnative plants may permit their interfacing with other dispersal mechanisms, such as fishing nets. Nets have played a key role in the transport of filamentous algae such as *Womersleyella setacea* and *Acrothamnion preissii*. The filamentous red algae (*W. setacea*), introduced by ship fouling, is spreading in the Mediterranean Sea and produces temporal blooms, which clog up fishing nets (Verlaque 1989). In this case, nets may be the most direct cause (vector) of range expansion for this species. The same is true of *A. preissii*, which Italian fishermen refer to as *pelo* in the Liguria area (Cinelli et al. 1984). On the Atlantic coast of the United States, Carlton and Scanlon (1985) reported that vessels sailed from Nantucket Sound to the fishing grounds north of Cape Cod with *Codium fragile* subsp. *tomentosoides* in their nets, possibly promoting its spread.

### Opening Maritime Canals

The best example of this pathway is the opening in 1869 of the Suez Canal, linking two biogeographical marine provinces that had been separated for

several million years: the Mediterranean Sea and the Red Sea. The presence of highly saline lakes along the course of the canal had been an obstacle to the transfer of species for many years. Today, progressive desalination of these lakes has permitted the exchange of organisms between the two seas. According to Por (1990), an estimated 200–300 species from the Red Sea have colonized the Mediterranean. Sometimes called Lessepsian immigrants, in reference to the engineer Ferdinand de Lesseps who designed the canal, Por (1989) further considered this wholesale transfer of species to be the largest biogeographic phenomenon witnessed in contemporary oceans. To date, there are 24 known Lessepsian marine plants in the Mediterranean (15 red algae, 4 brown algae, 4 green algae, 1 higher plant) (Fig. 8.2).

Most of the Lessepsian immigrants are localized in the eastern Mediterranean (Boudouresque 1994), a region referred to by Por (1990) as the Lessepsian province. Few of these species reach the occidental basin. Examples include the higher plant *Halophila stipulacea* and the red alga *Sarconema filiforme*, located respectively on the coasts of Italy and France (Ribera 1994). Dispersal of most of the Lessepsian plants from the mouth of the Suez Canal has likely resulted from natural dispersal, as suggested by the linear progression spread. Although spread of some species is multidirectional, as in the simultaneous northern and southern spread of the brown alga *Styopodium schimperi* (Verlaque and Boudouresque 1991), range expansions most frequently follow the dominant anticlockwise current into the eastern basin (Ribera 1994).

In contrast, the Panama Canal, which links the Pacific and the Atlantic Oceans, has resulted in the passage of a very limited number of euryhaline marine species, and there is no evidence that any plant is involved (Por 1978). The primary barrier to successful transport and colonization of the Caribbean species may not be the freshwater lakes, which could disrupt some transfers, but herbivore activity and the lack of reef-generated refuge areas on the Pacific coast (Hay and Gaines 1984).

## CONCLUSIONS

### *Importance and Geographical Distribution of the Different Pathways*

On a worldwide scale, shellfish transport is the main dispersal pathway for exotic species (49 species, 30%). This is followed by ship fouling (39 species, 24%), after which the following vectors are, in order of importance, ballast (25 species, 16%), the Suez Canal (24 species, 15%), and

importation for aquaculture activity (15 species, 9%) (Fig. 8.2). The other vectors (scientific research, fishing, aquaria) represent 6 percent of the total. Overall, maritime transport accounts for 40 percent (including ship fouling and ship ballast), and the combination of intentional and unintentional transfers associated with aquaculture activities accounts for 39 percent (Fig. 8.2). Intentional (partially aquaculture and partially research) and accidental vectors account for 10 percent and 90 percent of marine plant invasions, respectively. As noted earlier, these estimates exclude cases in which vector was considered uncertain.

The high number of exotic plant species involved with shellfish transfers is determined almost exclusively by the importance of this vector in the Mediterranean and European Atlantic coasts (Fig. 8.3A). This result may reflect partially the frequency of studies on the aquaculture installations in Europe, but it also reflects the present-day increase in the number of aquaculture farms in European countries. A quarter of the marine plant invasions of Europe are associated with oyster transfer. In some countries this proportion is greater: half the nonnative marine algae found in Britain are believed introduced via this pathway (Eno et al. 1997).

In the other geographic regions, fewer marine plant invasions are associated with shellfish transfers, but it should be emphasized that aquaculture still leads to important invasions around the world, such as *Sargassum muticum*, *Grateloupia doryphora*, and *Codium fragile* subsp. *tomentosoides*. Moreover, I wish to emphasize that almost all species dispersed by shellfish transport on the North American coasts are also found on the European coasts, introduced by the same vector (Appendix 8.1). This underscores that aquaculture installations are often points of dispersal of exotic species. Thus, although most of the exotic species came directly from the Pacific or Indian Oceans at the beginning of the development of this kind of industry, the Mediterranean and the European Atlantic have now become exporters of Indo-Pacific species.

The transport of fixed organisms on ships' hulls can be considered the oldest transport vector of marine plants. This vector is undoubtedly partly responsible for the present-day distribution of many species of algae, some of which have a worldwide distribution. The data in the literature are clearly incomplete since there are very few references of species dispersed by this pathway on North American coasts. Genetic studies may help resolve cryptic invasions. For example, studies of DNA hybridization in the genus *Cladophora* (van den Hoek et al. 1990) on both sides of the Atlantic showed that populations of *C. albida* have only recently diverged, and those of *C. sericea* are identical. In both cases a transfer by fouling across the Atlantic in one direction or another is suggested (Ribera and

Boudouresque 1995). My data show that transport on ships' hulls is most important in New Zealand (19 species), followed by the Mediterranean Sea (12 species) and the European Atlantic coast (8 species) (Fig. 8.3B). The reduced number of Australian exotic species involved in this vector could be an artifact, since the high number of species with an uncertain pathway may correspond to this vector.

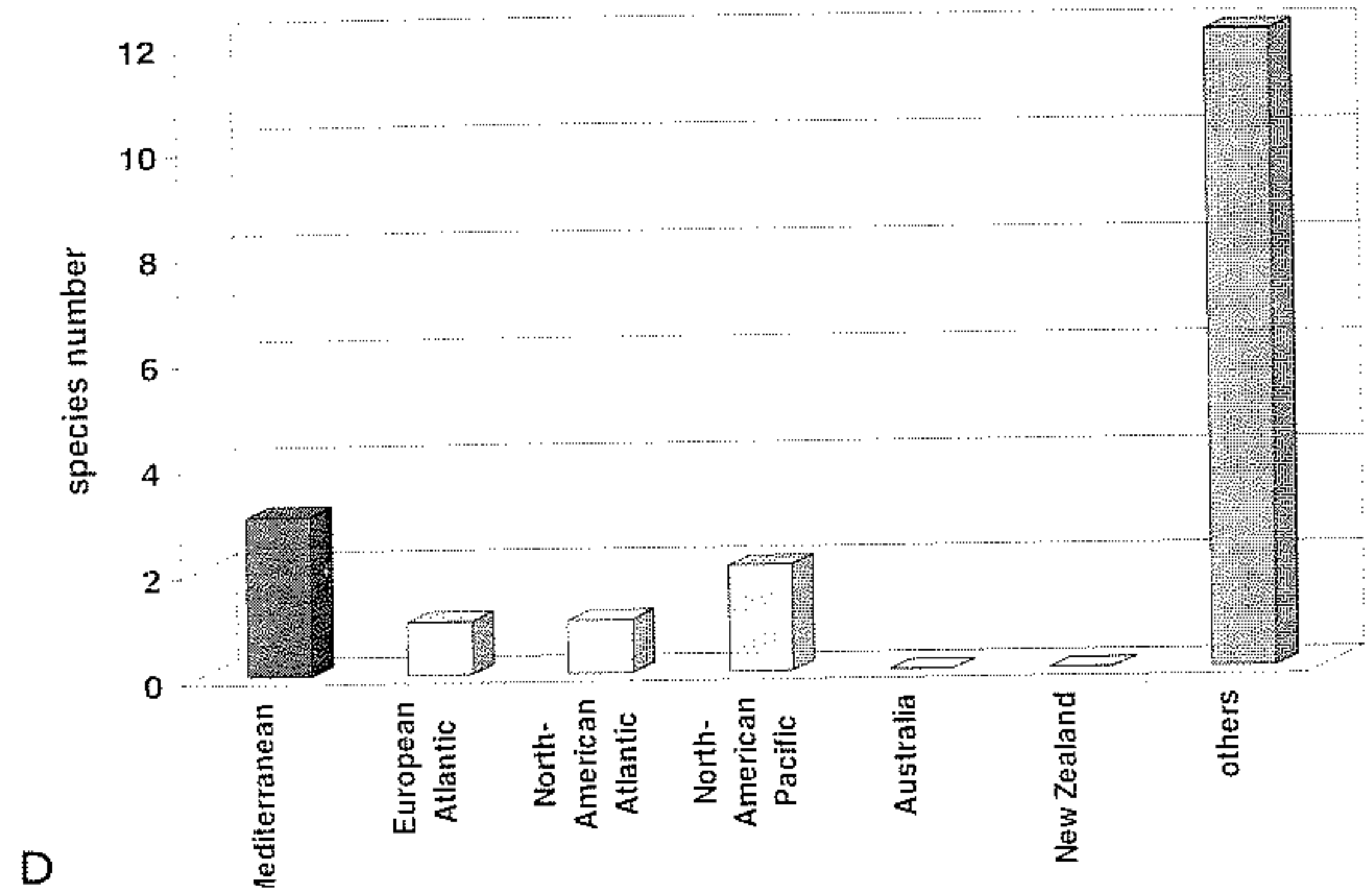
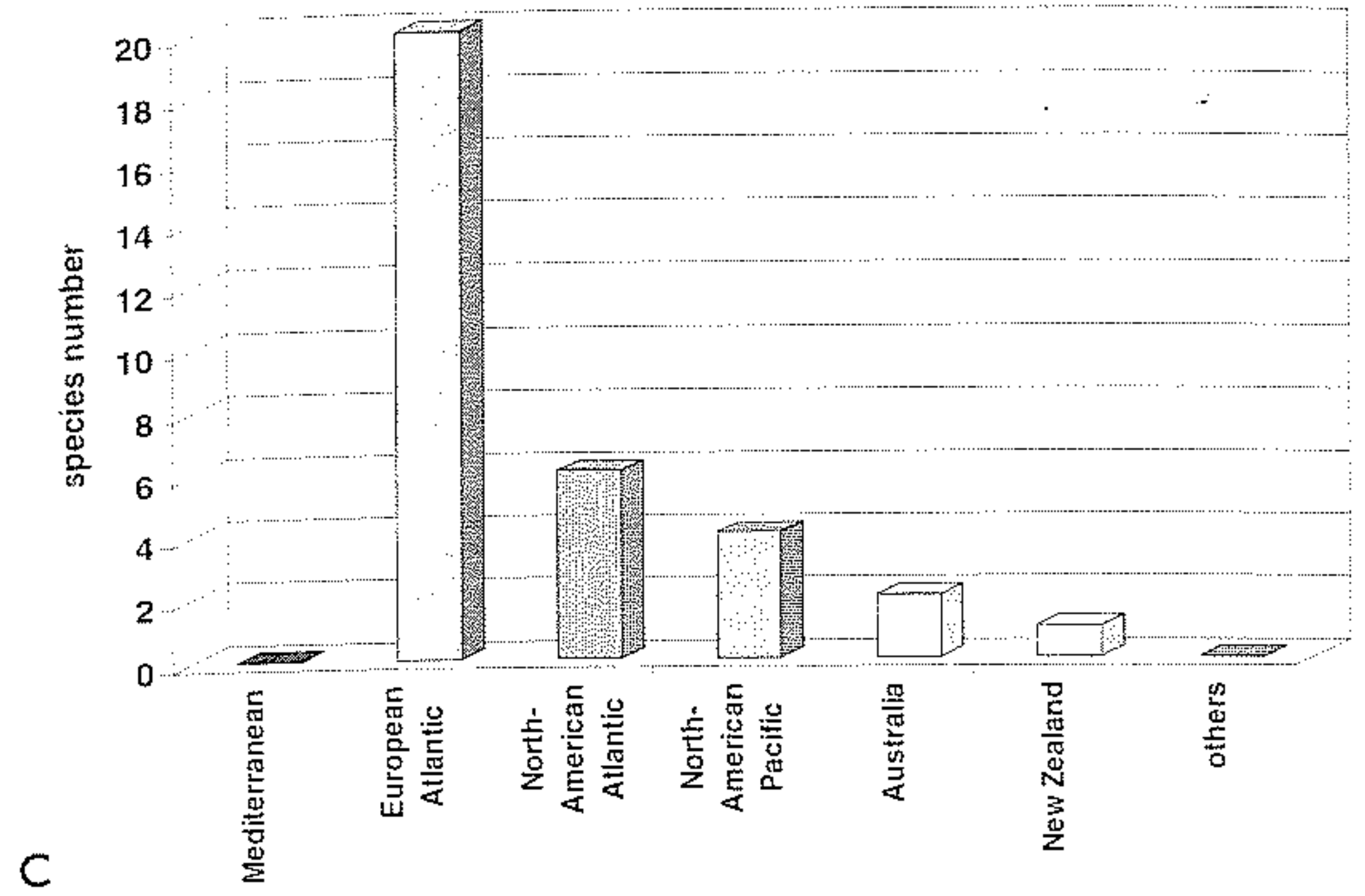
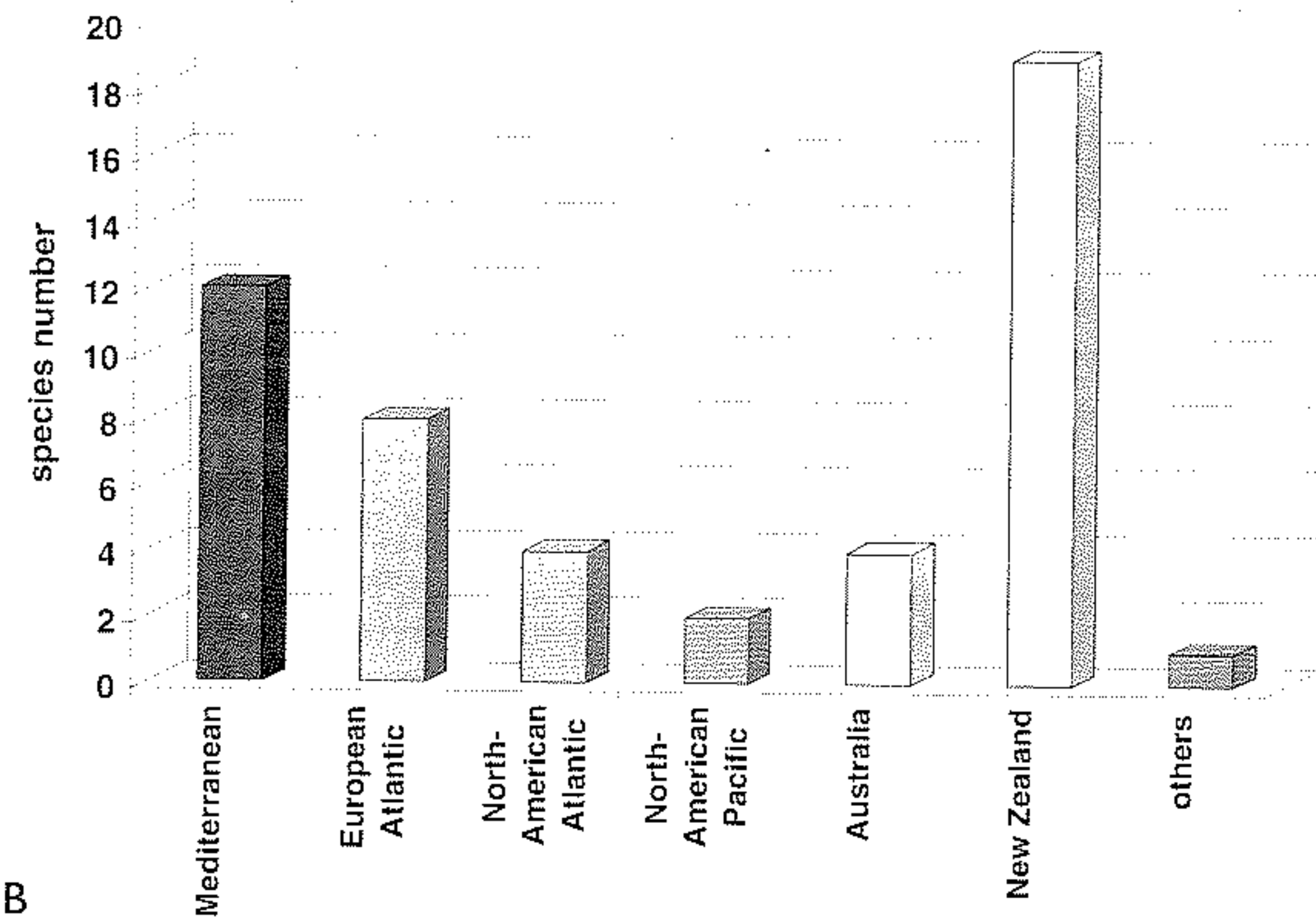
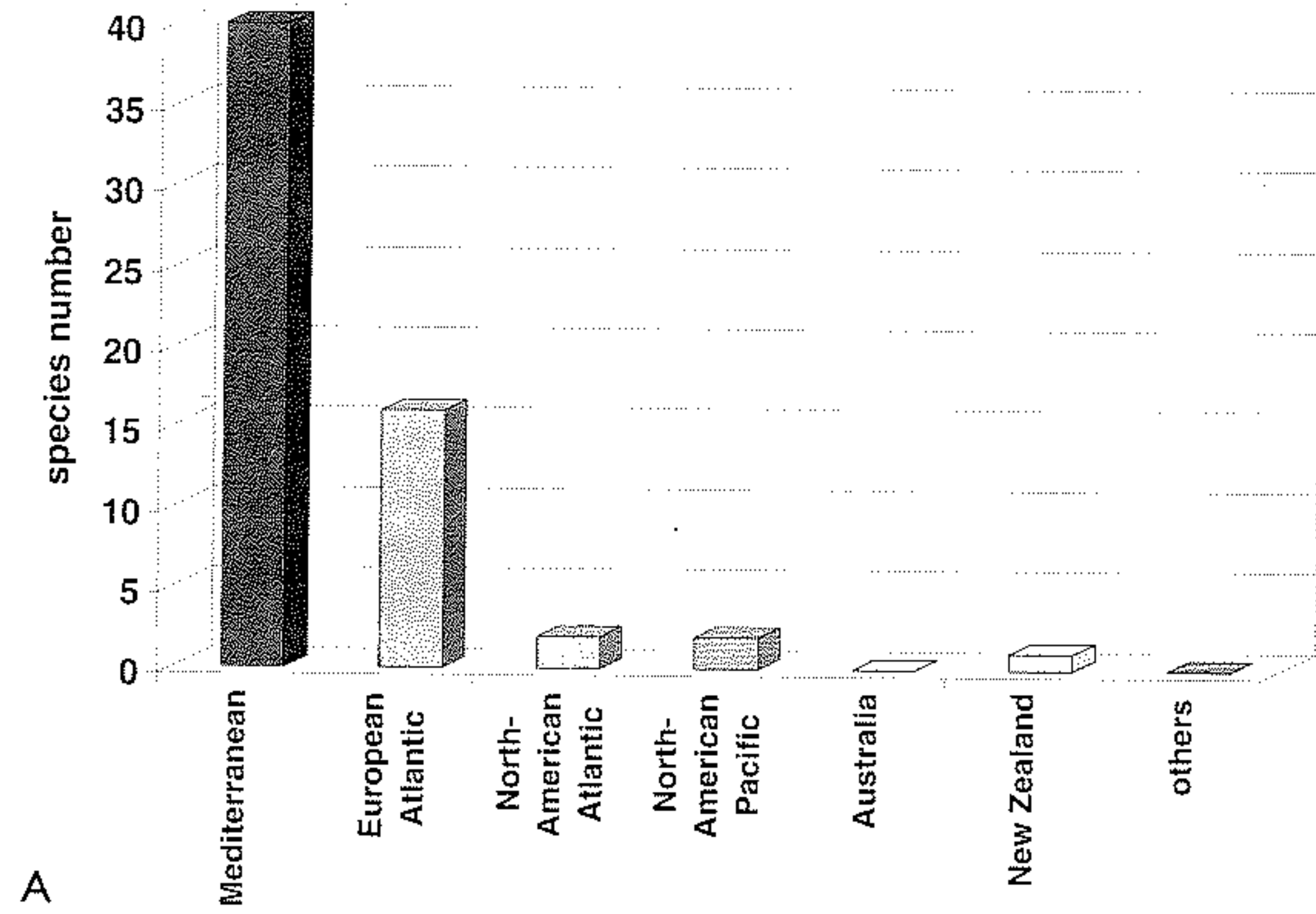


FIGURE 8.3. Importance of different pathways in the introduction of nonnative marine plant species in each geographical area. (A) Oyster transfers. (B) Ships' hulls. (C) Ships' ballast. (D) Aquaculture purposes.

Ships' ballast is the dominant pathway in the European Atlantic coast (20 species), making a relatively small contribution on the Atlantic (6 species) and Pacific coasts of America (4 species) (Fig. 8.3C). As suggested earlier, these data likely reflect the lack of knowledge about nonnative microalgae species, which are among the most common organisms in ballast tanks. For example, in the Mediterranean Sea, where maritime traffic is intense, no nonnative planktonic species have been cited. Occasional or periodic blooms of some dinoflagellates, both toxic and nontoxic forms, are known in the Mediterranean, but there are very few studies available to evaluate adequately any association to nonindigenous species. Similarly, in areas like Australia, New Zealand, and the Hawaiian Islands, the number of exotic species involved in this pathway could be expected to be higher because there is a large amount of maritime traffic. It is perhaps particularly surprising that there are so few nonnative plant species recognized as ballast introductions in Australia, where this vector has had a strong ecological and economic impact on the shellfish farms.

The cultivation of nonnative species of seaweed is not common at the moment for the geographical areas studied, except Hawaii (Fig. 8.3D in others). Nine species, most of them red algae of the genera *Gracilaria*, *Kappaphycus*, and *Eucheuma*, have been introduced to this region for commercial purposes, especially to obtain different classes of carrageenan (Russell 1992) (Appendix 8.1). In contrast, the three species introduced to China for aquaculture, used for the production of alginates and as a food source, are the large brown algae *Laminaria japonica*, *Macrocystis integrifolia*, and *Macrocystis pyrifera* (Appendix 8.1). As mentioned before, some of the nonnative species used now in European aquaculture were introduced earlier by other vectors.

The introduction of species as a result of fishing is known only from the Mediterranean Sea (3 species) and from Atlantic (2 species) and Pacific (2 species) waters of North America. Although the examples of introductions with packed baits may be well documented, marginal dispersion by nets has not been studied in depth and may therefore be underestimated.

Discharges (intentional or accidental) from aquaria, although responsible for the presence of a large number of exotic species (especially animals) in freshwaters have contributed <1 percent of the plant species introduced to marine waters. However, the biological invasion of *Caulerpa taxifolia* in the Mediterranean Sea underscores the potential risks associated with any species and the ability of certain organisms to adapt to the artificial or novel conditions found in aquaria. In such cases, the strain that best adapts may be a unique, genetically modified strain that may not survive in nature. Alternatively, genetic modifications may occur in the pop-

ulations subjected to stress. In addition, in this environment, plants usually reproduce only vegetatively, which can give rise to a clone that spreads by fragmentation. To date, the common origin of various populations of *C. taxifolia* in the Mediterranean has been identified with those of the Stuttgart Center. If the same origin is confirmed for the new populations from the Pacific and Atlantic coasts of the United States, we will be facing a new biological invasion at a worldwide scale with a single origin, similar to the *Sargassum muticum* spread.

### Presence of Exotic Species in the Different Geographical Regions of the World

The comparison of geographical areas shows that the Mediterranean Sea contains the highest number of reported exotic marine plant species (83 species), followed by the European Atlantic coast with 49 species (Fig. 8.4). The other areas have fewer reported exotic species, having roughly similar numbers among regions: 26 species on the Australian coast, 21 on the New Zealand coast, 19 on the North American Pacific coast, 17 on the North American Atlantic coast, and 22 on the coasts of the other regions considered (Hawaii, China, Canary Islands, the Azores) (Fig. 8.4). Therefore, the Mediterranean appears to be an exceptional nucleus, or hot spot, for nonnative species of marine plants.

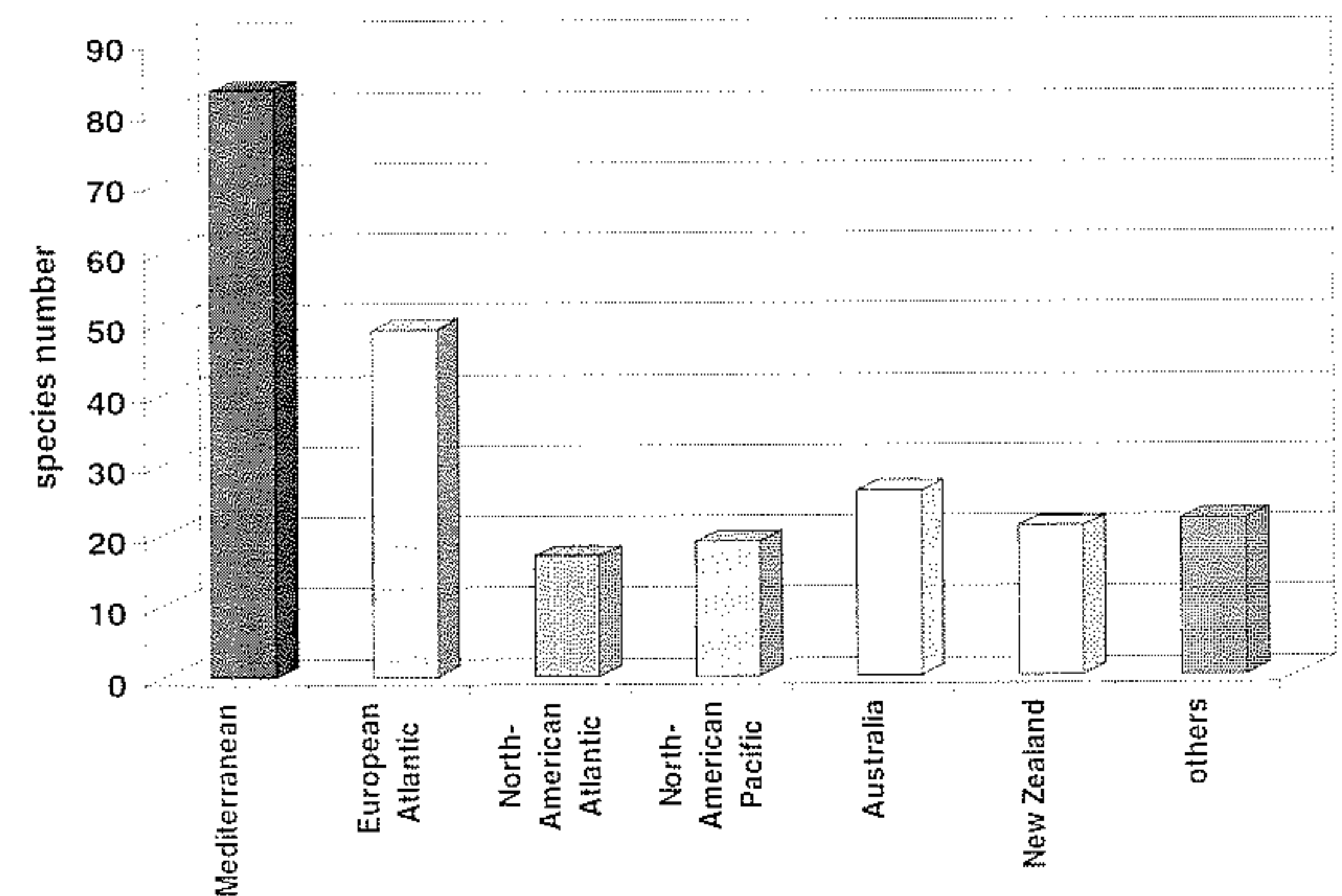


FIGURE 8.4. Diversity of nonnative species of marine plants in each geographical area.

Multiple mechanisms, operating alone or in combination, may explain the observed geographic pattern, and especially the extent of invasions in the Mediterranean. The number of pathways in the area, and their activity level (e.g., number of ships, amount of oyster movement, etc.), may be relatively great in this region. Alternatively, environmental and biological characteristics of the area may influence invasion patterns. Other regions referred to as Mediterranean-like, such as California, Chile, South Africa, and South Australia, are often thought to have climatic conditions that favor colonization of exotic species. Moreover, other features in the Mediterranean may enhance opportunities for colonization, relative to other regions, including (a) a wide range of water temperatures, allowing the acclimation of both cold-adapted and tropical species, (b) a great variety of biotopes, and (c) a scarcity of both large perennial algae and herbivores.

In the Mediterranean Sea the dominant vector is shellfish transfer (40 species) followed by the Suez Canal (24 species) (Fig. 8.3). The other pathways are of limited importance in terms of the number of species. Although a minor contribution to the overall number, it is noteworthy that the unintentional release from a public aquarium of *Caulerpa taxifolia* has had arguably the greatest ecological impact among biological invasions in the Mediterranean Sea. As mentioned before, the absence of species related to ballast transfer might be attributable to the lack of studies on this subject in the Mediterranean area.

The transport of nonnative species by the Suez Canal, which until the beginning of the 1990s was the largest for both flora and fauna in the Mediterranean (Ribera 1994), has now been relegated to second place, at least for flora, because of the alarming growth of species related to the importation of *Crassostrea gigas*. And in this sea, France is the leading importer of exotic species (Ribera and Boudouresque 1995), perhaps because the relevant legislation is deficient and not fully enforced. In particular, especially in the last twenty years, a giant shellfish farm has been developed in the Thau Lagoon. This French lagoon is quickly becoming the most important site of introduction for macroalgae, not only in the Mediterranean Sea but also in European waters (Verlaque 2001). Thus, weighted heavily by oyster imports, and Lessepsian immigrants, the Indo-Pacific Ocean has been the main source of nonnative species found in the Mediterranean.

On the European Atlantic coasts the dominant vector is ballast (20 species), closely followed by oyster transfer (16 species) (Fig. 8.3). France may be considered the country that has imported the largest number of species associated with shellfish aquaculture (Ribera and Boudouresque

ported by ballast (Reise et al. 1999). As occurs in other geographic areas, the nonnative species classified as having an uncertain pathway could correspond to transport by ships' hulls, since the role of the fouling in these European coasts may be underestimated (see below).

On both the Atlantic and Pacific coasts of North America, the number and relative contribution of the different pathways are similar (Fig. 8.3). I emphasize that in these two regions, in contrast to the other areas, all the main pathways have contributed a comparable number of species, including aquaculture (including associated species), ballast, fouling, and fishing. These two areas also have a relatively high number of species with uncertain pathways that, as mentioned above, may correspond to ship fouling (Appendix 8.1). It is interesting to point out that only 5 species are found on both coasts of North America. Among the exotic species with the widest distribution, I can highlight the absence of *Grateloupia doryphora* from the North American Pacific coast, while *Sargassum muticum* is not reported on the North American Atlantic coast (Appendix 8.1). If we compare the exotic species on both the eastern and western Atlantic coasts, the number of common species is equally low (6 species). Concerning the nonnative marine flora on the coasts of Australia and New Zealand, my data only permit me to point out that fouling seems to be the most important vector, with 19 species for New Zealand and 4 species in Australia; again, the relatively high number of species with uncertain pathways for Australia (20 species) may obscure the importance of ship fouling. There is a need for deeper studies to determine the contribution of deballasting of ships and the species associated with species transfers in aquaculture for these regions.

### *Rate and Prediction of the Different Pathways*

In general, it can be argued that the rates of both intentional and accidental introduction of marine plants may be increasing, owing to the growing importance of marine products for human activities, along with the increasing volume of marine trade and transport. To assess the rate of introductions, it is necessary to identify the date of arrival of each species, which is sometimes difficult or even impossible. The results presented here should be interpreted with caution because there could be many artifacts related to the information. It is clear, for example, that the data for the last century and the beginning of this one are underestimations. It should also be borne in mind that the date of the first report of an exotic species could in some cases be much later than the date of arrival.

The rate of reported introductions for nonnative marine plants appears

Europe, including Atlantic and Mediterranean coasts (in this case), as an illustrative example, because (a) I am most familiar with records from this region and (b) it includes the largest number of species for any geographic region. This graph reveals three periods in the rate of increase: up to the beginning of the 1900s, from 1920 to 1960, and from 1970 to the present. In the first two periods the increase is linear, although the number of species in the second period is double that in the first. In contrast, in the third period, the increase is exponential. This increase may be due to greater interest in the subject, to increased pressures to document invasions, or of course to actual increased numbers of invasions. However, this increase does not appear to occur at the same rate in different geographic areas. Since little has been published on the subject, it is very difficult to identify where rates of introductions are increasing and where they are decreasing. Among the European coasts, for example, the exotic species number presents a linear increase in Britain, whereas in the Mediterranean this increase is exponential.

The rate of new introductions does not follow the same pattern for each pathway. The Suez Canal, for instance, is a vector that is likely to lose force in the Mediterranean as long as environmental conditions are not modified, but in any case the eastern Mediterranean is still a very receptive area for new introductions, owing to its biological characteristics.

In contrast, aquaculture activities (and especially the marine culture industry for algae, as well as other organisms) are flourishing for two major reasons. First, demand for algae products is increasing as a result of (a) an increase of Oriental populations and foods in Europe and North

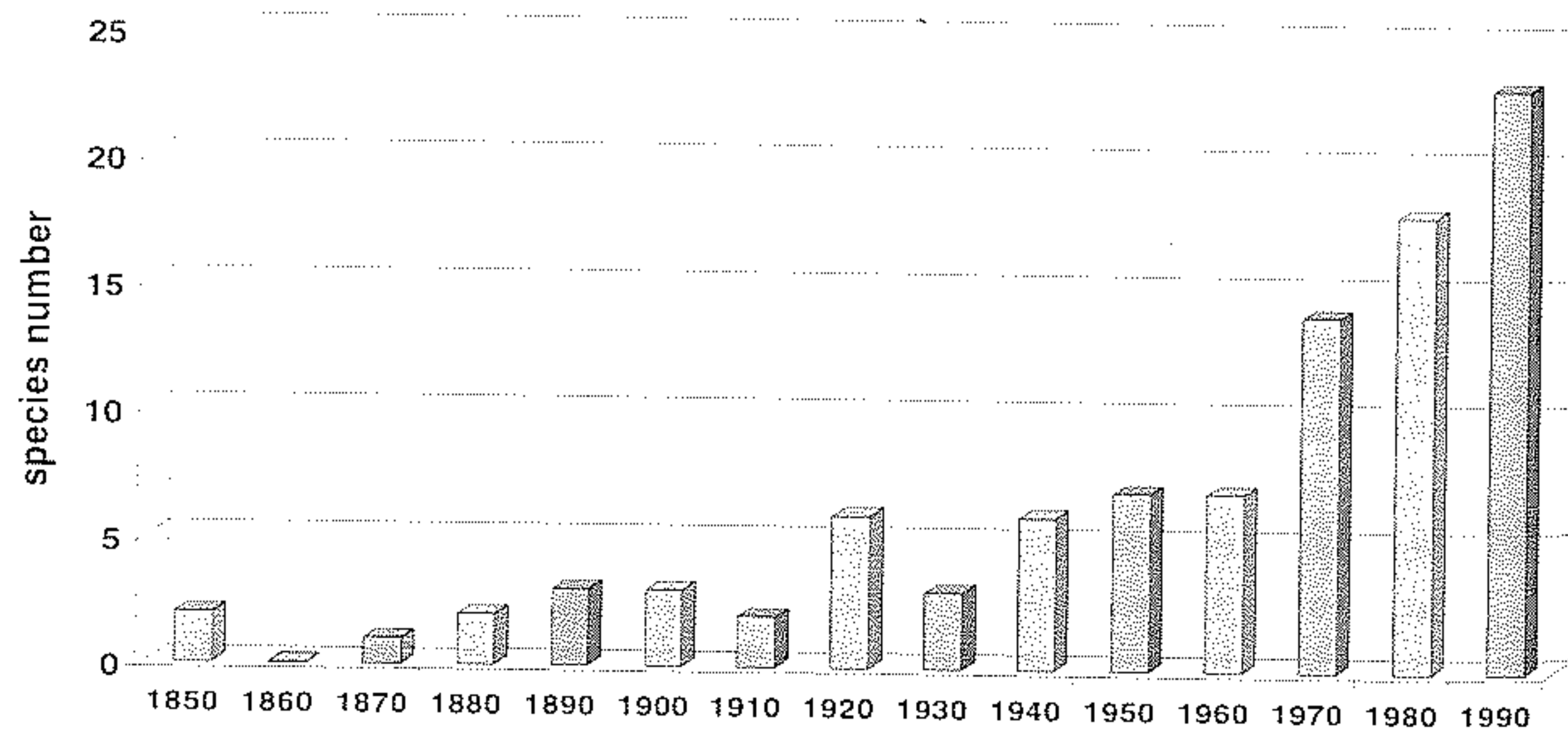


FIGURE 8.5. Number of nonnative marine plant species that were newly reported on the European coast in each decade (noncumulative data).

America, and (b) increased use of natural products for cosmetics, medicines, and diet foods (Perez 1997). Second, additional countries are entering the market to emulate the profitable algal colloids industries developed in China, Japan, and Korea. Both factors promote the importation and naturalization of the most economically competitive algal species despite their geographical origin.

Likewise, the development of fish and shellfish cultures is causing an indiscriminate transport of associated species that may be increasing. The arrival of exotic species associated with shellfish aquaculture on the European coast over time shows a marked increase since the 1970s; in the last ten years the number of exotic algae involved in this pathway has increased fivefold (Fig. 8.6A). According to Eno et al. (1997), before 1960 there were substantial introductions of marine species in association with imports for aquaculture; however, since then quarantine regulations have halted this method of entry into Britain. These measures do not seem to have the same effect in all countries. Verlaque (2001) indicates that failure in decontamination processes and/or quarantine of these authorized or nonauthorized imports has resulted in an increasing number of species introductions to Thau Lagoon. In general, we can argue that the current development of fish and shellfish farming will produce a dramatic increase in the range of species that are cultivated and consequently in the number of introductions (Ribera and Boudouresque 1995).

The temporal pattern of marine plant invasions associated with ships is less clear. For example, the frequency of toxic algae blooms on the Atlantic coasts of Canada has tripled over the past fifteen years, to which ship-mediated invasions may have contributed, but a definitive connection with ballast release has yet to be established (Smith and Kerr 1992, Subba Rao et al. 1994). The level of risk of introductions also remains to be quantified (Forbes 1994). Explanations for the apparent global increase of toxic dinoflagellate blooms include increased scientific awareness caused by the developing aquaculture industry and stimulation of dinoflagellate blooms by increased coastal eutrophication. However, in a limited number of cases, dispersal of nonindigenous estuarine dinoflagellate species across oceanic boundaries—via either ships' ballast water or transport of shellfish products—is more probable (Hallegraeff and Bolch 1991).

On the other hand, the quantity of transoceanic shipping has increased greatly, and the tendency of modern vessels to move faster through the water may increase the survival of both fouling species and those carried in ballast (Eno et al. 1997). Consequently, despite the data on fouling for the European coast suggesting relatively few recent plant introductions associated with ships (Fig. 8.6B), I predict that maritime transport will be

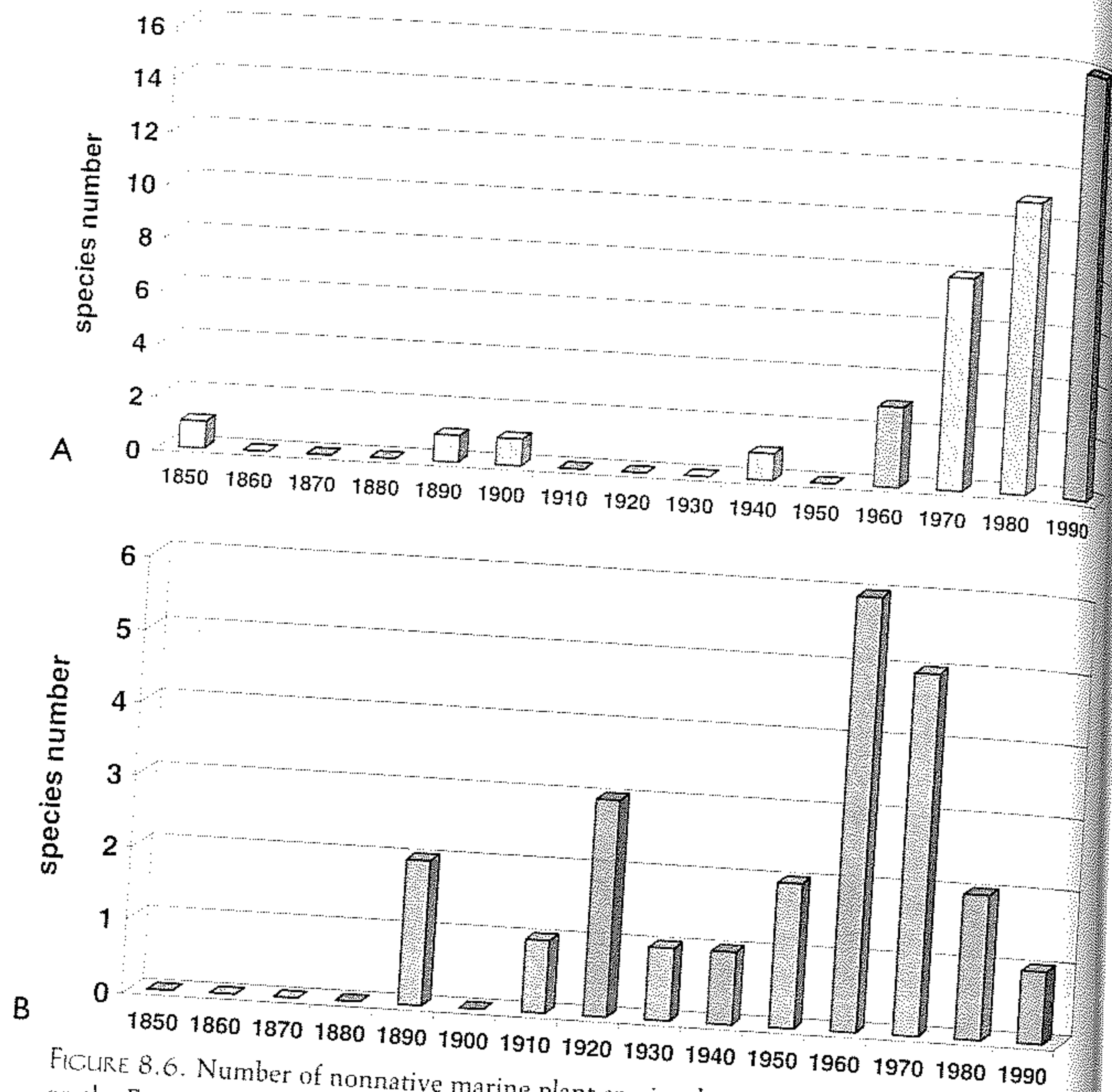


FIGURE 8.6. Number of nonnative marine plant species that were newly reported on the European coast by decade, according to different pathways (noncumulative data). (A) Nonnative species associated with shellfish transfer. (B) Nonnative species introduced on ships' hulls.

one of the main vectors of exotic species introductions in the future. Moreover, we should not forget that any change in marine transport routes could lead to the arrival of new species, like a change in the location of the fishing grounds, or a new tourist industry on a small island that previously had few visitors.

We have seen that the intensity of each pathway (as number of introduced nonnative species) is different for each country and geographical region. The temporal sequence and development of pathways may also depend on the region. For example, the same pathways shown for the European coast can operate at different times.

of the major risks associated with isolated regions that are undergoing, or will undergo, rapid economic development, which can swiftly shift or increase human activities known to transfer organisms. Islands, and small developing states, may be especially vulnerable to such rapid change.

The conclusion, realistic and pessimistic, is that the increasing rate of species introductions is linked, directly or indirectly, to economic interests. These may be in conflict with other economic interests (introduction of diseases or parasites, competition with commercially exploited indigenous species, nuisances, other uses of coastal areas) and also with ethical values that are difficult to evaluate in economic terms (Boudouresque 1994).

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SPECIES	GROUP	PATHWAY	GEOGRAPHICAL DISTRIBUTION				
<i>Corvophloea umbellata</i> (C. Agardh) Kütz.	P	ASSO	Eu A				
<i>Coscinodiscus walsbyi</i> Gran et Angst	B	BA	Eu A				
<i>Cottoniella fusiformis</i> Boergesen	R	???		NA P	NA A		
<i>Cryptonemia hibernica</i> Guiry et L. M. Irvine	R	???	Eu A			AUS	
<i>Cryptonemia seminervis</i> (C. Agardh) J. Agardh	R	???	Eu A				
<i>Cutleria multifida</i> (Sm.) Grev.	P	FO				N ZEA	
<i>Dasya baillouviana</i> (S. G. Gmel.) Mont.	R	FO	Eu A				
<i>Dasya baillouviana</i> (S. G. Gmel.) Mont.	R	FO	Eu A				
<i>Derbesia rhizophora</i> Yamada	C	ASSO	Eu A				
<i>Derbesia tenuissima</i> (De Not.) P. Crouan et H. Crouan	C	ASSO				MED	
<i>Desmarexia viridis</i> O. F. Müll.	P	???				AUS	
<i>Desmarexia viridis</i> O. F. Müll.	P	???				MED	
<i>Dipterosiphonia dendritica</i> (C. Agardh) F. Schmitz	P	ASSO				MED	
<i>Discosporangium mesarthrocarpum</i> (Menegh.) Hauck	R	???				MED	
<i>Elachista orbicularis</i> (Ohta) Skinner	P	???				AUS	
<i>Elodea canadensis</i> Michx.	P	???				AUS	
<i>Eucheuma denticulatum</i> (Burman) Collins et Herv.	HP	BA	Eu A				
<i>Eucheuma isiforme</i> (C. Agardh) J. Agardh	R	AQUA					
<i>Fibrocapsa japonica</i> Toriumi et Takano	Rh	AQUA				HAW	
<i>Fucus evanescens</i> C. Agardh	P	BA	Eu A			HAW	
<i>Fucus serratus</i> L.	P	???	Eu A				
<i>Fucus spiralis</i> L.	P	BA			NA A		
<i>Furcellaria limbricalis</i> (Huds.) Lamour.	P	FIS				MED	
<i>Gelidium vagum</i> Okamura	R	BA			NA A		
<i>Gracilaria armata</i> (C. Agardh) Grev.	R	???			NA P		
<i>Gracilaria disticha</i> (J. Agardh) J. Agardh	R	SUEZ				MED	
<i>Gracilaria epilippisora</i> M. D. Hoyle	R	SUEZ				MED	
<i>Gracilaria eucheumatoides</i> Harv.	R	AQUA					
<i>Gracilaria salicornia</i> (C. Agardh) Dawson	R	AQUA				HAW	
<i>Gracilaria tikvahiae</i> McLachlan	R	AQUA				HAW	
<i>Grateloupia cf. turaturoi</i> Yamada	R	AQUA				HAW	
<i>Grateloupia doryphora</i> (Mont.) Howe	R	AQUA				HAW	
<i>Grateloupia doryphora</i> (Mont.) Howe	R	ASSO					
<i>Grateloupia doryphora</i> (Mont.) Howe	R	ASSO	Eu A			MED	
<i>Grateloupia filicina</i> var. <i>luxurians</i> A. Gepp et E. Gepp	R	FO			NA A		
	R	ASSO	Eu A			MED	

<i>Griffithsia corallinoides</i> (L.) Trevisan	R	ASSO							
<i>Griffithsia crassiuscula</i> C. Agardh	R	FO							
<i>Gymnodinium catenatum</i> Graham	D	BA	Eu A						N ZEA
<i>Gyrodinium aureolum</i> Hulburt	D	BA	Eu A			NA A			
<i>Halophala stipitata</i> (Kütz.) Reinke	HP	SUEZ							
<i>Halothrix limbricalis</i> (Kütz.) Reinke	P	ASSO							
<i>Halymenia actinophylla</i> Howe	R	???				NA P			
<i>Herposiphonia parva</i> Setchell	R	ASSO							
<i>Heterosigma akashiwo</i> (Hada) Hada ex Sourmia	B	BA	Eu A						
<i>Hydroclathrus clathratus</i> (Bory ex C. Agardh) Howe	P	FO							N ZEA
<i>Hypnea cervicornis</i> J. Agardh	R	???							
<i>Hypnea cornuta</i> (Kütz.) J. Agardh	R	SUEZ							
<i>Hypnea esperi</i> auctorum	R	SUEZ							
<i>Hypnea musciformis</i> (Wulfen) Lamour	R	???				NA P			HAW
<i>Hypnea nidifica</i> J. Agardh	R	SUEZ							
<i>Hypnea spicifera</i> (Suhr) Harv.	R	SUEZ							
<i>Hypnea valentiae</i> (Turner) Mont.	R	SUEZ							
<i>Hypnea valentiae</i> (Turner) Mont.	R	FO							
<i>Hypnea valentiae</i> (Turner) Mont.	R	ASSO							
<i>Hypnea valentiae</i> (Turner) Mont.	R	SUEZ							
<i>Ishige isiforme</i> Yendo	P	BA				NA P			
<i>Kappaphycus alvarezii</i> (Doty) Doty ex P. C. Silva	R	AQUA							
<i>Kappaphycus striatum</i> (F. Schmitz) Doty ex P. C. Silva	R	AQUA							HAW
<i>Laminaria japonica</i> Aresch.	P	AQUA							HAW
<i>Laminaria japonica</i> Aresch.	P	ASSO							CHI
<i>Laurencia brongiartii</i> J. Agardh	R	ASSO	Eu A						
<i>Laurencia japonica</i> Yamada	R	ASSO							
<i>Laurencia microcladia</i> Kütz.	R	???							
<i>Laurencia okamurai</i> Yamada	R	ASSO							
<i>Leathesia difformis</i> (L.) Areschoug	P	ASSO							
<i>Lithophyllum yessoense</i> Foslie	R	ASSO							
<i>Lomentaria clavellosa</i> (Turner) Gaitlion	R	???				NA A			
<i>Lomentaria hakodatensis</i> Yendo	R	ASSO	Eu A			NA P			
<i>Lomentaria orcadensis</i> (Harv.) Collins et W. R. Taylor	R	???				NA A			
<i>Lophocladia lallemandii</i> (Mont.) F. Schmitz	R	SUEZ							
<i>Macrocytis integrifolia</i> Bory	P	AQUA				NA P			CHI



SPECIES	GROUP	PATHWAY	Eu A	MED	AUS	N ZEA	NA P N A A	NA P N A A	N A A	GEOGRAPHICAL DISTRIBUTION
<i>Thalassiosira tealata</i> Takano	B	BA	Eu A							
<i>Ulva pertusa</i> Kjellm.	C	ASSO		MED						
<i>Undaria pinnatifida</i> (Harv.) Suringar	P	BA			AUS					
<i>Undaria pinnatifida</i> (Harv.) Suringar	P	AQUA	Eu A	MED						
<i>Undaria pinnatifida</i> (Harv.) Suringar	P	FO				N ZEA				
<i>Undaria pinnatifida</i> (Harv.) Suringar	P	ASSO	Eu A	MED						
<i>Womersleyella setacea</i> (Hollenb.) R. E. Norris	R	FIS		MED						
<i>Womersleyella setacea</i> (Hollenb.) R. E. Norris	R	FO		MED						
<i>Wrangelia bicuspidata</i> Boergesen	R	???								HAW
<i>Zostera japonica</i> Asch. et Graebn.	HP	BA					NA P N A A			
<i>Zostera japonica</i> Asch. et Graebn.	HP	FIS					NA P N A A			
<i>Zostera japonica</i> Asch. et Graebn.	HP	ASSO						N A A		

## Chapter 9

# Spatial and Temporal Analysis of Transoceanic Shipping Vectors to the Great Lakes

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Anthropogenic introductions of nonindigenous species (NIS) are predicted to impact biodiversity of lakes more than any other major ecosystem type over the coming century (Sala et al. 2000). Freshwater ecosystems are highly vulnerable to invasions by NIS because of their close association with human activity, including exploitative uses for municipal and industrial water supplies, natural resource development (e.g., fishing, aquaculture), and commercial navigation and recreation. These varied uses provide countless invasion opportunities for NIS throughout the world. Consequences of these invasions have become well characterized, as many of the world's large lakes have been colonized by infamous nuisance invaders such as Nile perch (*Lates niloticus*), zebra mussels (*Dreissena polymorpha*), water hyacinth (*Eichhornia crassipes*), and hydrilla macrophytes (*Hydrilla verticillata*). Profound changes to the physical, chemical, and biological properties of lakes have followed invasions by these and other species of invertebrate and vertebrate animals, and micro- and macroscopic plants (e.g., Zaret and Paine 1973, Oliver 1993, Spencer et al. 1999, Kete-laars et al. 1999, MacIsaac 1999, Vander Zanden et al. 1999, Hall and Mills 2000, Lodge et al. 2000, Donald et al. 2001, Dick and Platvoet 2000, Schindler et al. 2001, Vanderploeg et al. 2002).

NIS are introduced to lakes through both intentional and inadvertent