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Diatoms as non-native species

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32.1 Introduction

The degree to which diatoms move across the Earth by natural processes is debatable (Finlay *et al.*, 2002; Vyverman *et al.*, 2007), but the inadvertent spread of diatoms in a globalized human society is apparent. In this chapter, we examine documentation of diatom introductions and their implications for aquatic ecosystems. For many organisms, especially larger ones, the ecologic, economic, and social impact of species introductions, or invasions, is relatively well known (Pimental *et al.*, 2000). On the other hand, recognition of the microscopic trespasses of diatom species and their impact on ecosystems in new geographic areas is generally far less noticed.

A species is considered to be "non-native" if it is located in a region outside of its native geographic range. Non-native species are also referred to as introduced, non-indigenous, exotic, alien, or invasive. While some non-native species cause little harm, others cause severe ecosystem damage. The use of terminology, particularly the adoption of military words to describe species geographic distributions, elicits emotional reactions that influence scientific and popular responses (Larson *et al.*, 2005). We recognize that much of the current literature employs these military metaphors, but we seek to promote an ecological perspective.

Even among well-known organisms, such as the common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) growing near Lake Superior, the distinction between native and non-native status may be unclear (Willis and Birks, 2006). The biogeographic distribution of diatoms, and microscopic organisms in general, is currently under debate. One school of thought advocates that microorganisms do not exhibit biogeographic differences (Baas-Becking, 1934; Finlay *et al.*, 2002). Under this hypothesis, vast local populations of microorganisms drive global dispersal and panmixis. As a result, species invasion and extinction are rendered impossible at local and global scales. Within this context, native and non-native species do not exist. An alternate school of thought advocates that microorganisms do, in fact, exhibit biogeography. An increasing body of empirical data supports the biogeography of microorganisms (Martiny *et al.*, 2006) and of diatoms, at least in some regions (Soininen *et al.*, 2003; Telford *et al.*, 2006; Vyverman *et al.* 2007; Vanormelingen *et al.*, 2008). For example, diatom communities in Finland streams showed a strong spatial component that could not be attributed to environmental parameters other than location (Soininen *et al.*, 2003). Likewise, Telford *et al.* (2006) demonstrated that the dispersal of diatoms was limited and timescales of isolation allowed for regional genetic differences to develop and endemic taxa to evolve. In other work, historical factors explained significantly more observed geographic patterns in richness (measured at the genus level) than environmental parameters (Vyverman *et al.*, 2007). In fact, diatom species introductions may help illuminate the biogeographic discussion. The number of taxa with widespread distributions has been suggested to be related to anthropogenic change (Kociolek and Spaulding, 2000), but at the same time, the hypotheses of "everything is everywhere" is challenged by examples of anthropogenic introductions (Vanormelingen *et al.*, 2008).

Determination of the non-native status of diatoms, as a group whose basic biology, taxonomy, biogeography, and genomes are not well known, is possible through the application of long-term floristic studies and paleolimnological reconstruction. The degree to which diatoms are introduced is likely underestimated because the idea of non-native diatoms has been proposed relatively recently and includes efforts to recognize endangered, or red-list diatoms (Lange-Bertalot and Steindorf, 1996; Denys, 2000). The introduction of non-native species, extirpation of native species, and habitat alterations

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that facilitate these two processes are considered biological homogenization (Rahel, 2002). Even when the number of total species increases by species introductions, the enhancement often includes taxa that are already widespread, tolerant of degraded habitats, and considered a nuisance by humans (Pimental *et al.*, 2000). We consider a few case studies of diatom introductions and their ecological implications.

32.2 Case studies of diatom introductions

32.2.1 Laurentian Great Lakes of North America

The Laurentian Great Lakes comprise five major post-glacial lake basins – Lakes Superior, Huron, Michigan, Erie, and Ontario – and contain one-fifth of the world's fresh surface waters (Herdendorf, 1982). Before European colonization of the region, great water depth, oligotrophy, unique physical limnology, geographical barriers, and the geographic extent of the Great Lakes contributed to produce food webs that included endemic fishes (Smith and Todd, 1984) and endemic diatom species such as *Stephanodiscus superiorensis* E. C. Ther. & Stoermer, *Hannaea superiorensis* Bixby & Edlund, and *Cyclotella americana* Fricke (Theriot and Stoermer, 1984; Bixby *et al.*, 2005; Jude *et al.*, 2006). However, the combined effects of overfishing, degradation of tributaries, urbanization, nutrient pollution, and finally the introduction of non-indigenous species at every trophic level irrevocably changed the structure and functioning of biological communities. Through fishing regulations, nutrient reductions, and tributary restoration, strides have been made to improve water quality and fish communities; however, the introduction and establishment of non-native species remains the most serious threat to ecological integrity of the Great Lakes (Jude *et al.*, 2006).

Over 180 non-indigenous species have been purposefully or accidently introduced to the Great Lakes (Mills *et al.*, 1993; Ricciardi, 2006). Early invaders, including the parasitic sea lamprey (*Petromyzon marinus* L.) and the planktivorous alewife (*Alosa pseudoharengus* Wilson), entered the lakes when shipping canals bypassed natural barriers (Jude and Leach, 1999). Others, such as the salmonids, were intentionally introduced to fill ecological voids caused by earlier invaders and revive a sport fishery (Jude and Leach, 1999). More recently, species introduced through ballast water from the Ponto-Caspian and Baltic regions have caused upheaval in the Great Lakes ecosystem (Stoermer *et al.*, 1996; Vanderploeg *et al.*, 2002; Getchell and Bowser, 2006). A number of high-profile invasive species introductions underscore that introduction rate is not declining, even with ballast exchange regulations (Ricciardi, 2006). In fact, species have gained entrance to the Great Lakes at all trophic levels, from viruses and bacteria to higher plants and algae.

Mills *et al.* (1993) listed 24 algae, including 16 diatoms, that were considered non-native to the Great Lakes. Subsequent introductions have added to that list (e.g. Edlund *et al.*, 2000; Lougheed and Stevenson, 2004), which includes freshwater and brackish/marine representatives that are generally found in the plankton. Several of the introduced species had limited temporal establishment or were restricted to waters with elevated conductivity (e.g. *Thalassiosira visurgis*, *Thalassiosira weissflogii* (Grunow) G. A. Fryxell & Hasle, *Pleurosira laevis* (Ehrenb.) Compère, *Terpsinoe musica* Ehrenb.). Other arrivals include widespread freshwater species that responded favorably to increased nutrients (e.g. *Cyclotella pseudostelligera* Hust., *Stephanodiscus subtilis* (Goor) A. Cleve, *Stephanodiscus binderanus* (Kütz.) Krieg.; reviewed in Edlund *et al.*, 2000).

Although monitoring programs were established in the Great Lakes, detecting the introduction of diatoms has been hindered by discontinuous funding, a pelagic focus (many introductions are first recorded nearshore in bays and harbors; Hasle, 1978), limited seasonal sampling, and taxonomic naïvety. Paleolimnological analyses have provided a retrospective on species introductions, the tempo of geographic spread, and clarified the native diatom flora (Stoermer *et al.*, 1993). Most well-dated paleorecords show that non-native diatoms were introduced and well established long before they were reported by routine survey. For example, *Thalassiosira baltica* Grunow is recorded in sediments dated AD 1988 in Lake Ontario, but this taxon was not routinely recorded in the plankton until the late 1990s (Figure 32.1). *Actinocyclus normanii* f. *subsalsa* (Juhl.-Dannf.) Hust. is present in Lake Ontario sediments by AD 1932, spread to Lake Erie by AD 1939 (Figure 32.1), and is present in Lake Huron sediments by the 1940s (Wolin *et al.*, 1988). This diatom was first reported in 1951 as "*Coscinodiscus subtilis* var." or *C. subtilis* var. *radiatus* Hohn (1952) from Lake Ontario and inland New York waterways (Hohn, 1951), but was not reported from lakes Erie and Michigan until 1960 and 1964, respectively (Wujek, 1967; Hohn, 1969; Stoermer and Yang, 1969; as *C. radiatus* Ehrenb. or *C. subsalsa* Juhl.-Dannf.). Similarly, *S. binderanus* can be found in Lake Erie sediments dated AD 1945 and Lake Ontario sediments dated 1952 A.D. (Figure 32.1), but was not reported in surveys until 1955 (Brunel, 1956).

While most non-native diatoms have had little discernable effect on the Great Lakes ecosystem, others induce dramatic impacts. *S. binderanus* blooms caused taste and odor issues in drinking water and clogged water-treatment-plant filters in the lower lakes in the 1950s–1970s (Hohn, 1969). Additional

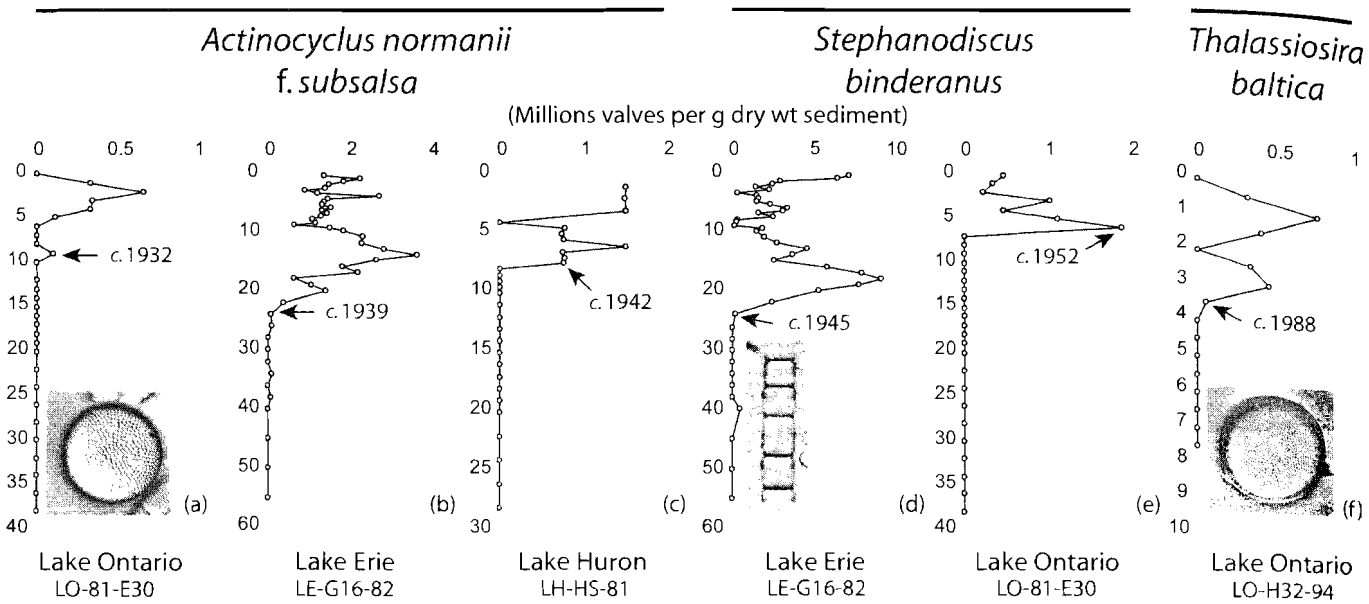

Figure 32.1 Distribution and abundance (millions of valves per g dry sediment) of select non-indigenous diatoms (inset light micrographs) and their dates of introduction (arrows) in Laurentian Great Lakes sediment cores. Depth scales (cm) vary among cores due to differences in sedimentation rates among lakes. Cores were collected in 1981 (Lakes Ontario and Huron), 1982 (Lake Erie), and 1994 (Lake Ontario; LO-H32–94). (a–c) *Actinocyclus normanii* f. *subsalsa* in Lakes Ontario, Erie, and Huron. (d, e) *Stephanodiscus binderanus* in Lakes Erie and Ontario cores. (f) *Thalassiosira baltica* in Lake Ontario sediment. Graphs modified and redrawn from Stoermer *et al.* (1985, 1987), Wolin *et al.* (1988), and Edlund *et al.* (2000).

filtration equipment was installed and monitoring programs were instituted to address problems caused by *S. binderanus* (Vaughn, 1961). Other diatoms had ecosystem-level impacts, specifically *A. normanii* f. *subsalsa*, a heavily silicified species that forms blooms in the summer. Frustule formation depleted dissolved silica from the water column, which subsequently allowed cyanobacteria to out-compete other species and bloom in bays and nearshore waters (Theriot and Stoermer, 1985). A recent invader in the Great Lakes, *T. baltica* (Edlund *et al.*, 2000) may result in a similar disruption of species succession or a decrease in biodiversity. In its native habitat, the Baltic Sea, *T. baltica* blooms control silica dynamics by removing dissolved silica from the water column and then making it inaccessible within the sediments (Olli *et al.*, 2008). Some evidence suggests that introduced species have led to extirpation of native diatoms, because introductions are coincident with such extirpations. In a sediment core from Lake Ontario, introductions of *S. binderanus* and *A. normanii* f. *subsalsa* were concomitant with local extinctions of *Stephanodiscus transilvanicus* Pant., *Cyclotella comta* (Ehrenb.) Kütz., *Cyclotella michiganiana* Skvortsov, *Cyclotella ocellata* Pant., and *Cyclotella stelligera* (Cleve & Grunow) Van Heurck (Stoermer *et al.*, 1985).

32.2.2 Volga River

Long-term floristic studies on the Volga River in Russia (Kiselev, 1948; Slynko *et al.*, 2002; Korneva, 2007) further document diatom introductions associated with anthropogenic and environmental impacts. The Volga River extends for 3530 km from its headwaters north of Moscow to its outlet in the Caspian Sea. Like the Laurentian Great Lakes, several invasive species (including bivalves, crayfish, mysids, and amphipods) were introduced by canal and ship traffic during the eighteenth and nineteenth centuries. The Volga River acted as an invasion corridor, which is a system of waterways connecting previously geographically isolated river and sea basins. As a result, aquatic species expanded beyond their historical ranges by active or passive dispersal (Slynko *et al.*, 2002). Furthermore, the Volga River has been heavily impacted by the construction of dams, which converted a free-flowing river system to a series of reservoirs. These hydrologic changes facilitated the introduction and dispersal of diatoms that favor the stable water column of impoundments. For example, in the 1950s, planktonic species (*Stephanodiscus binderanus*, *Stephanodiscus hantzschii* Grunow, and *Stephanodiscus minutulus* (Kütz.) Cleve and Möller) increased in abundance from the northern extent of the Volga River and spread in a southward direction (Korneva, 2007) until these introduced species came to dominate the spring and summer algal community of the river. In fact, the abundance of *S. binderanus* eventually became several orders of magnitude greater in reservoirs than in the unregulated sections of the

river. Increase in flow of the Volga River has been attributed to climate change and resulted in rising levels of the Caspian Sea (Slynko *et al.*, 2002). With decreases in salinity of the northern basin of the Caspian Sea, brackish species spread northward (Korneva, 2007). *Skeletonema subsalsum* (Cleve-Euler) Bethge was a common species of the Caspian and Azov seas and advanced northward to the reservoirs on the river in the early 1950s. Likewise, *Thalassiosira incerta* Makarova, *Thalassiosira pseudonana* Hasle and Heimdal emend. Hasle, *Thalassiosira guillardii* Hasle, and *T. weissflogii* (Grunow) Fryxell and Hasle spread to the north. The latest advance from the Caspian Sea, in the 1980s, was of *A. normanii* (Gregory ex Greville) Hust. Overall, the total number of diatom species has increased since 1948 (Kiselev, 1948) with the new species tolerant of high electrolyte waters, high organic nutrients, and warmer temperatures. The construction of dams, loss of differences in regional water chemistry, alteration of flow, warming by thermal pollution from power plants, and eutrophication has resulted in a greatly changed river system and a more homogeneous physical environment and diatom community in the Volga River.

32.2.3 French rivers

Long-term studies of diatoms in French rivers have provided documentation of species introductions, and records of species that proliferated rapidly in France, yet were absent from other European rivers (Coste and Ector, 2000). For example, *Gomphoneis minuta* Kociolek and Stoermer, was originally described from North America, but reported in 1991 for the first time in Europe in the Ardèchec River. As in many cases, no clear vector of transport was identified. This diatom subsequently spread throughout southern France to the Loire River. *Eolimna comperei* Ector *et al.*, *Gomphoneis eriense* (Grunow) Skv. & Meyer and *Encyonema triangulum* (Ehrenb.) Kütz. are also considered to be a species introduced from outside Europe. Like the blooms in the Great Lakes and Volga River, many of the non-native diatoms in French rivers reach their greatest abundance during the summer. These include the tropical species *Hydrosera triquetra* Wall., which blooms in estuaries, and *Diadesmis confervacea* Kütz, which thrives in the warm waters of power-plant discharges.

32.2.4 Introductions to New Zealand

32.2.4.1 Asterionella formosa Analysis of sediment cores of 14 lakes in New Zealand provides evidence that *Asterionella formosa* Hass. was introduced with European settlement around 1880 (Harper, 1994). The species is frequently considered a cosmopolitan planktonic species, yet the New Zealand lake sediments showed no trace of *A. formosa* prior to European settlement. This species is now common in New Zealand, found in 45% of lakes with plankton records. The transportation of salmon eggs into New Zealand is considered the most likely vector for the introduction of *A. formosa* (Harper, 1994). Like many non-natives, *A. formosa* is a species that thrives with eutrophication. For example, in high-elevation lakes in Colorado, *A. formosa* was present in pre-settlement sediments in trace amounts and increased in abundance with elevated nitrate (NO_3^-) concentrations (Wolfe *et al.*, 2003). In these lakes, *A. formosa* was environmentally stimulated and maximum abundances occurred concomitantly with elevated nutrients, rather than via species introduction.

32.2.4.2 *Didymosphenia geminata* In many ways, the example of *Didymosphenia geminata* (Lyng.) M. Schmidt provides a different pattern for non-native species than other diatoms. Since the late 1980s, the large, stalked species seems to have undergone a transformation from a relatively rare species found in boreal and mountain regions of the northern hemisphere to a common bloom-forming organism with invasive tendencies. Although there are historical reports of *D. geminata* periodically forming thick benthic mats in its native range (e.g. Skvortzow, 1935; Heuff and Horkan, 1984; Lindstrøm and Skulberg, 2008), persistent blooms in some regions appear to be a new phenomenon.

Individual cells form small nodular colonies attached by mucopolysaccharide stalks to suitable substrates (Figure 32.2). As cell division proceeds, the colonies expand into continuous mats, which may eventually cover kilometers of streams and rivers and reach a thickness of more than 10 cm (Figure 32.2). The mats are composed primarily of stalks and resemble dirty cotton wool or housing insulation. The appearance of wet *D. geminata* mats has earned the species the moniker, "didymo." A remarkable characteristic of *D. geminata* is its ability to form blooms in low-nutrient waters (Kirkwood *et al.*, 2007). Typically, attached algal biomass in such streams is low, but stream food-web structure can be profoundly changed with blooms of *D. geminata* (Kilroy *et al.*, 2009). The species has potential economic impacts such as blocking water intakes and interfering with angling and other recreational activities (e.g. Mundie and Crabtree, 1997; Spaulding and Elwell, 2007).

Didymosphenia geminata is known to have been widespread in the northern hemisphere for at least one hundred years (Blanco and Ector, 2009, Pite *et al.*, 2009). Unusual blooms were reported in the late 1980s in rivers on Vancouver Island, Canada (Sherbot and Bothwell, 1993). Similarly, in the 1990s,

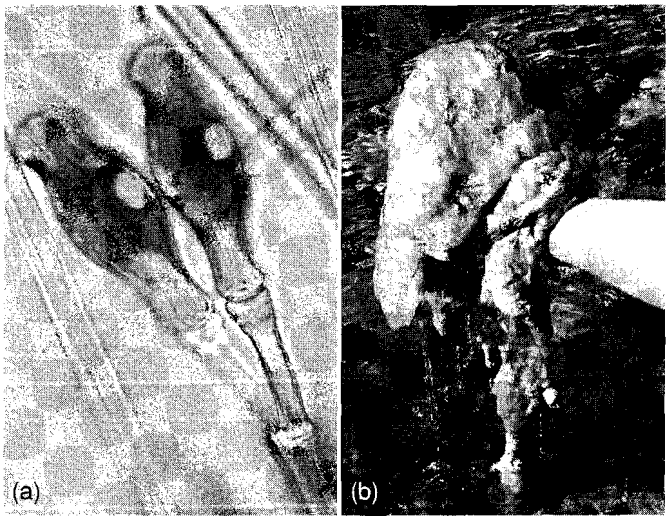

Figure 32.2 (a) A light micrograph of live *Didymosphenia geminata* cells, showing stalk attachment and branching; (b) typical appearance of a well-developed colony, with extensive cover by *D. geminata* of the river bed in the background.

D. geminata blooms were reported across rivers in Iceland (Jonssen *et al.*, 2000), central Europe (Kawecka and Sanecki, 2003), and the United States (Kumar *et al.*, 2009). While of concern to local managers, the blooms were not regarded as invasions, because *D. geminata* was assumed native to these regions. However, the sudden appearance of large blooms of *D. geminata* in rivers of New Zealand in 2004 was a watershed event: it confirmed that this species is an invasive organism and sparked international attention.

The discovery of *D. geminata* in the lower Waiau River, Southland, New Zealand, represented the first finding of the species in a location where it was almost certainly not present previously. A single record of *D. geminata* in North Island, New Zealand, in the 1920s (Cassie, 1984) was discounted as unverifiable and most likely a misidentification (Kilroy, 2004). In addition, failure to record such a distinctive species in over 10 years of sampling in the river where it was first discovered, or from any other New Zealand river, indicated that *D. geminata* was a new arrival. The fact that *D. geminata* was present in bloom proportions raised immediate concerns about its potential effect on the trout-fishing industry and tourism. In late 2004, *D. geminata* was declared an "unwanted organism" in New Zealand and a coordinated response was initiated (Vieglais, 2008). As an aquatic microorganism with unknown impacts, *D. geminata* presented a difficult case. As discussed earlier in this chapter, introductions of freshwater diatoms are rarely recognized, although the diatom flora of a remote region such as New Zealand seems likely to contain other recent arrivals. This species warranted special attention, however, because of its visible effects on streams and rivers. The response therefore included both basic and management-related research, e.g. potential distribution (Kilroy *et al.*, 2008); assessments of social and economic consequences (e.g. Campbell, 2008); ecological effects; methodology to optimize detection (e.g. Cary *et al.*, 2008); survivability of cells, which could indicate potential transport mechanisms (Kilroy, 2008); and possible control methods.

Despite containment efforts, within a year *D. geminata* formed blooms in three other catchments, up to 400 km from the Waiau River. Subsequent surveys tracked the spread over three years, with a gradual dispersal from infected centers and occasional "jumps" to new areas (Figure 32.3). The surveys probably underestimated the presence of *D. geminata*, but were accurate with respect to the number of catchments affected. At the time of writing, some catchments are still free of *D. geminata*, including the North Island, as confirmed using sensitive genomic detection techniques (Cary *et al.*, 2008).

While there is no direct evidence for the mode of spread, the occurrence of initial blooms at sites popular with recreationalists (e.g. anglers, kayakers), frequently visited for monitoring purposes, or downstream of river crossings, strongly suggests inadvertent spread via human activities. Laboratory tests indicated that cells remained viable for weeks if maintained in wet, cool conditions (Kilroy, 2008). Thus, it is feasible that *D. geminata* could spread from catchment to catchment, and indeed from country to country on, for example, damp sports equipment. An important outcome of the *D. geminata* invasion was development by the New Zealand Government of a public education campaign, supported by recommended methods to properly clean gear.

An initial assessment of the ecological susceptibility of New Zealand's rivers to *D. geminata* blooms found the South Island to be at greater risk than the North Island (Kilroy *et al.*, 2008). However, the assessment was thought to greatly underestimate the risk to the North Island because it was based on sparse knowledge of *D. geminata*'s ecological tolerances. In particular, the assessment assumed that *D. geminata* is a cool-water species, an assumption subsequently challenged by its appearance in warm areas of the southern United States (Kumar *et al.*, 2009). Nevertheless, there are no examples to date of blooms of *D. geminata* in locations where the mean air temperature in the coldest month exceeds 5 °C (Kilroy, 2008). Other conditions considered suitable for *D. geminata* blooms included stable substrate, stable flows (in particular lake-fed or dammed rivers), and clear waters (i.e., non-humic and non-glacial) (Kilroy *et al.*,

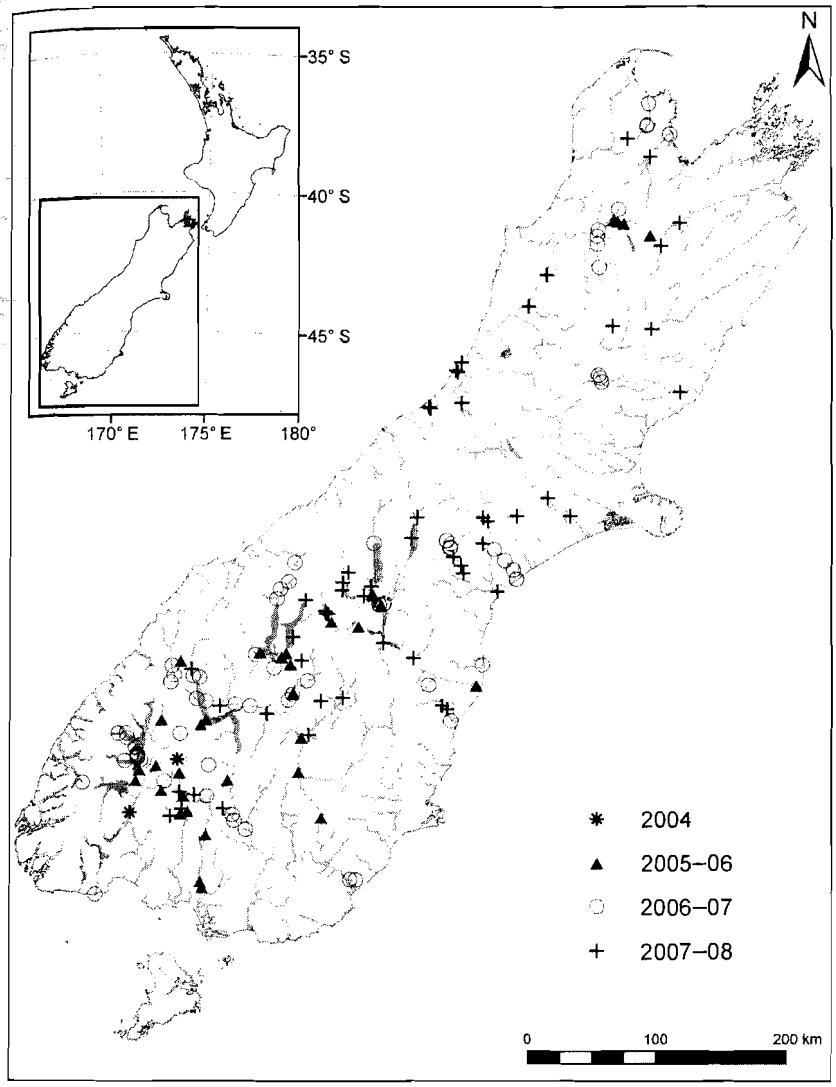

Figure 32.3 Map of *Didymosphenia geminata* distribution in South Island, New Zealand, showing the spread from 2004 to 2008. Stars show the location of the Waiau–Mararoa catchment, which is assumed to be the point of entry of the invasion in October 2004. In September 2005, *D. geminata* was detected in distant catchments and has continued to spread. Triangles: detection September 2005–August 2006; circles, September 2006–August 2007; crosses, September 2007–November 2008.

2008). Flow stability has also been shown to be important in other studies (Dufford *et al.*, 1987; Kirkwood *et al.*, 2007; Kumar *et al.*, 2009). Subsequent modeling in New Zealand has confirmed that *D. geminata* biomass is strongly related to recent hydrologic history (Kilroy, 2008).

Although the precise factors are unresolved, the distribution of *D. geminata* at the scale of river reaches in New Zealand indicates that water chemistry is an important factor determining the species' ability to become established and form blooms. Blooms have been linked to high nitrogen-to-phosphorus ratios (N:P) and high organic-to-inorganic P ratios (Ellwood and Whitton, 2007), consistent with observations of blooms in conditions of very low inorganic P (Kilroy, personal observation).

Understanding the effects of *D. geminata* on river ecosystems in New Zealand remains challenging because the organism has been established for such a short time. However, shifts in community composition, and spatial homogenization of benthic macroinvertebrate communities have been associated with *D. geminata* blooms (Kilroy *et al.*, 2009). Similar effects have been recorded in the benthic algal communities of one river (Figure 32.4). In this case, the algal community composition was determined by listing and identifying taxa in homogenized samples. Each sample was scanned for a standardized time at magnifications up to 400×. Diatom species identifications were verified with reference to permanent voucher slides of

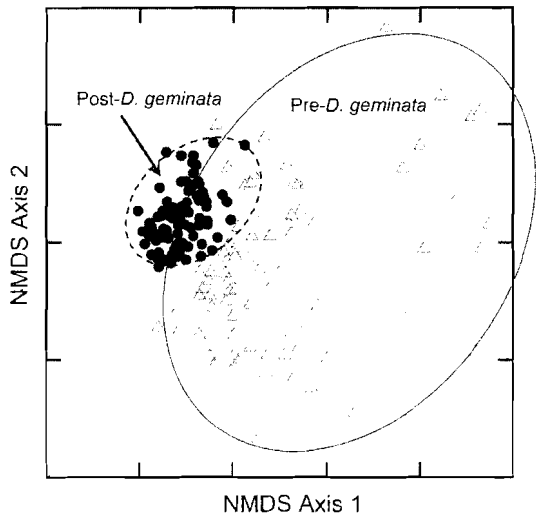

Figure 32.4 Non-metric multidimensional scaling plot (PRIMER v. 6) showing a two-dimensional (2-D) representation of Bray–Curtis similarities among algae samples from the lower Waiau River, Southland, New Zealand, collected annually in 2001, 2002, and 2004, before invasion of the river system by *Didymosphenia geminata* (open triangles) and in 2005, 2006, and 2007, after the invasion (closed circles) (2D stress = 0.23; 3D stress on the same data = 0.16). Each symbol represents the community in a single sample. Kilroy, unpublished data.

diatoms from the same sites, viewed at 1000×. The relative abundance of each taxon was assessed on an eight-point scale, using the method described in Biggs and Smith (2002). *D. geminata* was the dominant alga in all post-invasion samples and was omitted from the analysis to show its effects on other algae. In Figure 32.4, homogenization of communities is indicated by the much smaller ellipse enclosing post-invasion samples. Mean Bray–Curtis similarity among all pre-invasion samples was 27.4, compared to 49.3 for post-invasion samples (t-test, $P < 0.0001$). A general change in community composition is indicated by the separation of samples from the pre- and post-invasion periods (Figure 32.4). The community differences resulted from greatly increased densities of small diatoms (particularly *Achnanthidium minutissimum* (Kütz.) Czarn., which tends to be associated epiphytically with *D. geminata* blooms, and *Encyonema minutum* (Hilse in Rabenhorst) D. G. Mann) and to declines in species that were common prior to the invasion (e.g. *Cymbella kappii* Cholnoky).

Since the arrival of *D. geminata* in New Zealand, there have been reports of unprecedented blooms in the northern hemisphere, including eastern Canada (Simard and Simoneau, 2008), eastern United States (Kumar *et al.* 2009), Italy (Beltrami *et al.* 2008), and Spain (González *et al.*, 2008). It has been suggested that a genetic variant of *D. geminata* may be responsible (Kirkwood *et al.*, 2007), in which case the northern hemisphere may contain a true invader, which is non-indigenous (e.g. Falk-Petersen *et al.*, 2006). However, it remains to be determined if genetic alteration caused the species to abruptly become more competitive in environments where it was not previously able to become established itself or outcompete indigenous species. Bothwell *et al.* (2009) proposed that the worldwide spread of *D. geminata* is linked to the globalization of the recreational river fishing industry. This implies that the success of the species may also be due to the environmental suitability for *D. geminata* of rivers that also support fishable populations of salmonids, but does not explain the novel appearance of blooms in streams known to have supported low populations of *D. geminata* previously.

32.3 Summary

In general, the success of introduced diatoms appears to conform to patterns observed for other aquatic and terrestrial species. Attributes of successful invasive species include wide distribution, broad environmental tolerances, short generation times, rapid growth, a capability for rapid dispersal, and ability to thrive under conditions resulting from anthropogenic activity (Ricciardi and Rasmussen, 1998). The ability to form resting stages (Sicko-Goad *et al.*, 1989) or for vegetative cells to remain viable (Kilroy, 2008) outside of aquatic habitats and to survive transport are also relevant factors. Euryhaline diatoms rank high among successful Great Lakes, Volga River, and some of the European river colonizers; such diatoms are physiologically adapted to survive ballast exchange and tolerate increases in dissolved salts (Hasle and Evensen, 1975; Hasle, 1978; Korneva, 2007). *Didymosphenia geminata*, however, presents the unusual case of a species that blooms in low-nutrient waters. In New Zealand, homogenization of diatom communities in the presence of *D. geminata* has resulted in a reduction of overall aquatic biodiversity and replacement of native species by non-natives (Rahel, 2002). Another phenomenon common to many species invasions is a decline in the abundance and vigor of the invader over time (Simberloff and Gibbons, 2004). This has been observed for *D. geminata* on Vancouver Island, particularly in rivers not controlled by dams (Bothwell *et al.*, 2009) and to some extent in Iceland (Jónssen *et al.*, 2008).

Anthropogenic change not only alters environments in such a way as to favor invasive species, humans may directly deliver non-native species to the newly created habitat. Aquatic invasive species are favored in reservoirs, sites that are not only altered in physical and chemical parameters, but are more accessible to humans and potential introductions than natural

lakes (Johnson *et al.*, 2008). Reservoirs of the Volga River are habitats, in particular, where invasive diatoms thrive. Downstream of reservoirs, the generation of hydroelectric power and the resulting high fluctuations in discharge was found to favor immigration of both large and weakly attached species (Peterson, 1986). The outlets of reservoirs also favor *D. geminata* (Dufford *et al.*, 1987; Kirkwood *et al.*, 2007). Dams have resulted in homogenization of flow regimes for entire regions across the United States (Poff *et al.*, 2007). There is reason to expect that the river regulation that resulted in homogenization of freshwater fish faunas and establishment of non-native and otherwise poorly adapted species also applies to diatoms.

The few studies documented here are likely not representative of the degree to which diatoms have been introduced into new habitats. Even the idea that diatoms have distinct regional distributions continues to be challenged (Kociolek and Spaulding, 2000; Finlay *et al.*, 2002; Vyverman *et al.*, 2007). Paleoecology provides a valuable historical perspective to help interpret diatom distributions and to put anthropogenic change into context.

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