

Effects of eutrophication and snails on Eurasian watermilfoil (*Myriophyllum spicatum*) invasion

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Abstract

Exotic species can invade and establish new habitats both as a result of their own traits, and as a result of the characteristics of the environment they invade. Here, we show that the abundance of the invasive submerged aquatic plant, *Myriophyllum spicatum* (Eurasian watermilfoil) is highly dependent on the conditions of the environment in a mesocosm experiment. *M. spicatum* is allelopathic towards epiphytic algae, and in the absence of algivorous snails, we found that the abundance of both algae and *M. spicatum* significantly increased with experimentally increased nutrient loading, while the abundance of native submerged macrophytes declined. However, when snails were present, snail biomass increased with increasing nutrient loading, and *M. spicatum* biomass was consistently low while native submerged macrophyte biomass was consistently high. Our results stress the importance of the interaction between species traits and environmental conditions when considering the invasiveness of certain exotic species and the invasibility of certain environments.

Introduction

Understanding the factors that allow exotic species to invade new communities, displace native species, and alter ecosystem functioning would improve our ability to eradicate exotic species and restore habitats (Williamson 1996, Sakai et al. 2001). Exotic species are more likely to successfully invade habitats that have altered environmental conditions such as increased disturbances (e.g., Hobbs and Huenneke 1992), increased resources (e.g., Davis et al. 2000), or decreased local species diversity (Levine and D'Antonio 1999). Further, the traits of the exotic species itself may determine whether or not it can invade a habitat. For example, Callaway and Ridenour (2004) suggested that some exotic species have 'novel weapons' that allow them to

displace native species. However, in many cases, both the state of the habitat and the traits of the exotic species may interact to determine whether or not a species can invade and impact a community (Shea and Chesson 2002, Daehler 2003, MacDougall and Turkington 2005).

Freshwater ecosystems are strongly influenced by nutrient (i.e., phosphorus and nitrogen) runoff, which causes eutrophication. Eutrophication has a myriad of negative consequences, including algal blooms, loss of dissolved oxygen, and loss of biodiversity (Carpenter et al. 1998). In addition, freshwater ecosystems seem to be particularly vulnerable to invasion by exotic species (Rahel 2002). While those interested in lake conservation and restoration generally have assessed eutrophication and invasive species as isolated problems, these are probably linked.

In this study we examine the link between eutrophication and the invasion of *Myriophyllum spicatum* (Eurasian watermilfoil). *M. spicatum* is native to Eurasia and is now found over much of North America (Couch and Nelson 1985). *M. spicatum* has many negative impacts, including displacement of native vegetation (Madsen et al. 1991), providing poor habitat for wildlife (Newroth 1985, Engel 1987, Lillie and Budd 1992, Madsen 1997), altering water quality (Bates et al. 1985, Madsen 1997), interfering with recreational activities (Newroth 1985), and blocking irrigation pumps (Bates et al. 1985, Eiswerth et al. 2000). As a result, millions of U.S. dollars are spent annually on their control (Eiswerth et al. 2000).

In a survey of 102 lakes, Madsen (1998) found that the relative abundance of *M. spicatum* was positively correlated with nutrient status. We suggest that lake eutrophication may facilitate *M. spicatum* as a result of a cascade of interactions. First, *M. spicatum* possesses polyphenols that render it allelopathic towards a wide variety of epiphytic algae (Gross et al. 1996, Nakai et al. 1999, Gross 2000, Leu et al. 2002), which compete with native submerged macrophytes (Sand-Jensen and Sondergaard 1981, Sand-Jensen and Borum 1991). As a result, when algae are common, as would be the case in eutrophic conditions, *M. spicatum* has a competitive advantage over native macrophytes that are not allelopathic. However, polyphenols can account for as much as 10% of *M. spicatum*'s dry weight (Gross et al. 1996, Leu et al. 2002), suggesting a potentially costly investment, which could cause reduced competitive ability when algae are less abundant.

We further hypothesize that the presence of epiphytic algal consumers, of which freshwater snails are among the most important (Brönmark 1989), may reduce the competitive advantage of *M. spicatum*. The presence of snails curtails algal blooms that would otherwise result from nutrient inputs (e.g., Chase 2003) and facilitate the abundance of native submerged plants by reducing the detrimental effects of shading and nutrient competition with epiphytic algae (Brönmark 1989). Because of *M. spicatum*'s allelopathy towards epiphytic algae, it should not be similarly advantaged by snails. Herein, we present the results from a mesocosm experiment in which we manipulated nutrient levels and the presence of snails.

Methods

Establishment of mesocosms

To test the separate and interactive roles of nutrients and snails on the abundance of *Myriophyllum spicatum*, epiphytic algae and native macrophytes (and macroalgae), we established a factorial experiment in ~1000-1 outdoor mesocosms. The experiment included 3 levels of nutrients (low, medium, and high) and 2 levels of snails (present and absent). Each treatment was replicated 5 times for a total of 30 mesocosms.

Mesocosms were placed in a grid in an old field at the Tyson Research Center, a field station owned by Washington University in St. Louis. The edges of the mesocosm grid were > 30 m from the nearest trees so that all of the mesocosms would receive approximately the same amount of light. In July 2002, we filled each mesocosm with 4–5 cm of a 50:50 mixture of sand and topsoil purchased from a local quarry and nutrient-poor well water.

After mesocosms were filled, we introduced a variety of microbes, plants, and animals that occurred naturally in ponds and lakes throughout the region. Specifically, we inoculated microbes, algae, and zooplankton by collecting large quantities of sediment and water from 10 nearby ponds, concentrating it, and introducing 5-l aliquots to each mesocosm (after carefully checking to avoid any inadvertent introductions of snails or other benthic algal consumers). We also collected several species of attached blue-green algae (e.g., *Microcystis*, *Anabanea*) and green algae (e.g., *Oedogonium*, *Spirogyra*, *Zygnema*, *Cladophora*) from natural ponds, combined them with ~5 l of well water, blended them in a blender to homogenize the inoculation, and introduced 50 ml of the resulting homogenate into each mesocosm.

Along with *M. spicatum*, we introduced several native, co-occurring macrophytes into our mesocosms. These species, *Ceratophyllum demersum*, *Elodea canadensis*, *Najas guadalupensis*, *Potamogeton foliosus*, *Potamogeton pusillus*, and the native macrophyte-like algae *Chara vulgaris*, differ in their mechanisms of nutrient acquisition and in their architecture, and therefore may differ in the way they compete with *M. spicatum* for

nutrients. However, because we were primarily interested in the invasion of *M. spicatum* into an entire community, we focused on general community-level patterns, rather than the specific mechanisms of competitive interactions among the macrophyte species.

We introduced ~10 g damp weight of each of the aforementioned species into each mesocosm. Cuttings of each plant were haphazardly planted into the soil of the bottom of each mesocosm. Native plants were collected from ponds at the Tyson Research Center and other nearby localities. *M. spicatum* was collected from a slow moving section of the Meramec River adjacent to the Tyson Research Center. Each species of plant was monitored for one month to ensure that cuttings survived the initial transplant. For the few (<5 cuttings of all species) that did not survive, we reintroduced individuals of another cutting.

Snails are typically among the most important consumers of attached algae in freshwater systems (Brönmark 1989). Thus, in order to alter the amount of algal consumption, we experimentally manipulated snail presence in mesocosms. Treatments were randomly assigned to mesocosms, and in late July of 2002, 10 individuals of each of the two most common pond dwelling snails in the region, *Physella gyrina* and *Helisoma trivolvis*, were introduced into mesocosms designated to receive snails. This density was sufficient to establish populations of these species, and none went extinct.

Several species other than those specifically manipulated were also present in these communities, including zooplankton, a variety of insects, and tadpoles of the gray treefrog (*Hyla versicolor*). None of these insects (e.g., Odonates) were significant snail predators. Some insects (e.g., Chironomids) and the treefrog tadpoles are known to consume epiphytic algae, and thus could have influenced the results. However, these species did not appear to vary among the treatments (unpublished data), and are typically much weaker consumers of epiphytic algae than snails (e.g., *H. versicolor* eats a considerable amount of phytoplankton rather than epiphyton).

Following the introduction of all plant species and snails, we initiated nutrient treatments in one of three levels. Low nutrient treatments received no added nutrients, and had initial water column

levels typical of naturally nutrient-poor waters – 10 (± 2 standard deviation) $\mu\text{g/l}$ phosphorus (P) and 200 (± 27 standard deviation) $\mu\text{g/l}$ nitrogen (N). Medium nutrient treatments were augmented to 50 $\mu\text{g/l}$ P and 1000 $\mu\text{g/l}$ N, and high nutrient treatments were augmented to 100 g/l P and 2000 $\mu\text{g/l}$ N. N and P were added in the form of solid NaNO_3 and NaPO_4 respectively to the medium and high nutrient treatments. Each spring of the following 2 years, one tenth of these levels were added to each mesocosm in order to account for nutrients lost (e.g., in organisms that emerged from the mesocosm).

Sampling

Macrophytes and algae were sampled non-destructively in August each year for 3 years. The approximate percentage of the volume of the mesocosm filled by each plant species was estimated visually by the same observer (JMC) for all mesocosms (Madsen 1998). Epiphytic and filamentous algae were estimated in a similar manner. Such visual estimation is typical of community-level experiments in both aquatic and terrestrial ecosystems, and is essential in order to be non-destructive. Furthermore, these data were collected blindly with respect to the nutrient treatments so as to minimize any biases with this visual estimation. Finally, percent volume estimates of each plant species were converted to dry-weight biomass estimates taken from a destructively sampled experiment on the same plant species at this site. This methodology of visual estimation correlates strongly with destructive sampling (JMC, unpublished data).

Snails were categorized according to species and size class and counted in quadrats comprising 20% of the total surface area of the mesocosm. Individuals were converted into dry-weight biomass estimates using species and size-specific conversions (JMC, unpublished data), and values were then multiplied by 5 to obtain estimates for the entire mesocosm.

Statistical analyses

After an initial year of rapid growth of snails, algae, and macrophytes, mesocosms appeared to level off without significant change in the relative

abundance of species (we did not find a significant time by treatment interaction). Thus, we simply provide data for the final year of censuses here. We compared snail biomass among the different nutrient treatments using one-way ANOVA. We conducted MANOVA to determine if nutrients, snail presence or their interaction affected producer biomass (algae, *M. spicatum*, and all native plant species). Following a significant MANOVA, we present univariate analyses for attached algae, *M. spicatum*, and native macrophyte biomass. All biomass estimates were cube-root transformed prior to analyses in order to normalize the data. All analyses were performed using Systat 7.0 for Windows.

Results

Snail biomass was strongly influenced by nutrients ($N=15$; $df = 2$; $F=24.8$; $P<0.001$). Specifically, snail biomass (in g dry-weight per tank ± 1 standard error) was 11.6 (3.5), 34.0 (4.7), and 66.9 (7.5) for the low, medium and high nutrient levels, respectively.

MANOVA indicated that the nutrient treatment, presence of snails and their interaction affected the biomass of producers (macrophytes and algae) in our experimental mesocosms (Table 1). The biomass of epiphytic and filamentous algae was higher in higher nutrient treatments and lower in the presence of snails. There was a significant interaction; algae biomass increased dramatically with nutrients when snails were absent but less so when snails were present (Table 2, Figure 1). The biomass of the invasive species, *M. spicatum* showed a similar pattern to that of algae (Table 2, Figure 1). The biomass of native macrophytes was lower in higher nutrient

treatments and higher in the presence of snails. There was a significant interaction; native macrophyte biomass decreased with nutrients when snails were absent but not when snails were present (Table 2, Figure 1).

Discussion

Our results demonstrate that *M. spicatum* thrives in habitats with high nutrient inputs and few algivorous consumers (e.g., snails). In the absence of snails, both *M. spicatum* and epiphytic and filamentous algae achieve greater biomass at higher levels of nutrient inputs. However, in the presence of snails, increasing levels of nutrients had little effect on the biomass of epiphytic and filamentous algae, *M. spicatum*, or native macrophytes, but large increases in the biomass of snails.

These results could be because *M. spicatum*'s allelopathy allows it to outcompete native macrophytes in environments with abundant algae. Its allelopathy enables it to reduce algae on its leaves, even when the algae are abundant in the immediate vicinity (Gross et al. 1996, Gross 2000, Leu et al. 2002). Thus, *M. spicatum* may not be a superior competitor *per se* over other native macrophytes (Valley and Newman 1998), but instead can dominate only in eutrophied waters as a result of indirect interactions with algae. Alternatively, other mechanisms may account for the patterns we observed. For example, *M. spicatum* may be a better competitor for light in the presence of algae, but a poorer competitor for nutrients in the absence of algae.

Our results are further supported by Madsen's (1998) observations that *M. spicatum* was most prevalent in eutrophic lakes. However, the majority of natural lakes have snails and other algivorous species which our results suggest should limit the competitive ability of *M. spicatum*. In natural lakes, there are many natural snail predators, such as fish (e.g., pumpkinseed sunfish [*Lepomis gibbosus*], redear sunfish [*Lepomis microlophus*]) (e.g., Osenberg 1989, Brönmark et al. 1992, Huckins 1997, Huckins et al. 2000) and crayfish (e.g., *Orconectes* spp.) (Lodge et al. 1994, Dorn and Wojdak 2004). Molluscivory (snail consumption) may help

Table 1. MANOVA of biomass per tank of epiphytic algae, *Myriophyllum spicatum*, *Ceratophyllum demersum*, *Elodea canadensis*, *Najas guadalupensis*, *Potamogeton foliosus*, and *Potamogeton pusillus* and *Chara vulgaris*. All response variables were cube-root transformed prior to analyses.

	Wilks' Lambda	F	df	P
Nutrients	0.035	9.235	16	<0.001
Snails	0.051	39.183	8	<0.001
Nutrients \times Snails	0.104	4.476	16	<0.001

Table 2. Univariate analyses of the effects of nutrients and snail presence on biomass of algae and submerged plant species. All response variables were cube-root transformed prior to analyses.

Source	df	Sum of squares	F	P
(a) Epiphytic algae biomass $R^2=0.882$; $N=30$				
Nutrients	2	10.460	31.477	< 0.001
Snails	1	15.861	95.466	< 0.001
Nutrients \times Snails	2	3.496	10.522	0.001
Error	24	3.987		
(b) <i>Myriophyllum spicatum</i> biomass $R^2=0.767$; $N=30$				
Nutrients	2	28.343	23.592	< 0.001
Snails	1	9.020	15.017	0.001
Nutrients \times Snails	2	10.145	8.444	0.002
Error	24	14.416		
(c) Native submerged plant biomass $R^2=0.847$; $N=30$				
Nutrients	2	3.999	19.209	< 0.001
Snails	1	6.500	62.450	< 0.001
Nutrients \times Snails	2	3.307	15.8865	< 0.001
Error	24	2.498		

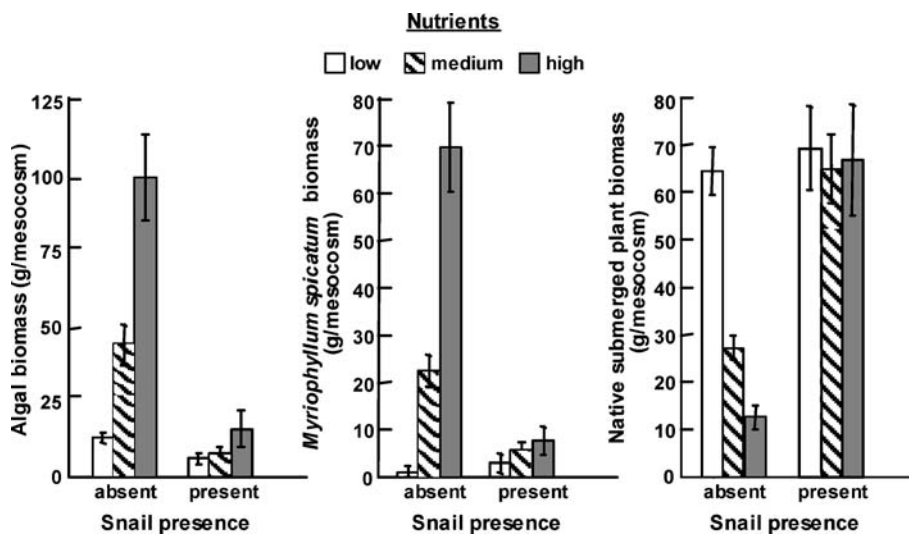


Figure 1. Mean biomass ± 1 standard error of epiphytic algae (left figure), the invasive macrophyte *Myriophyllum spicatum* (middle figure), and native macrophytes (right figure) in experimental mesocosms containing low, medium or high levels of nutrients and snail presence or absence.

explain why snails may not be able to consume enough algae to reduce the invasion by *M. spicatum*.

Anthropogenic use of lakes may increase molluscivore biomass, and thus facilitate invasion of *M. spicatum* when nutrient loading is high. First, intense sportfishing may often result in the reduction of top predators (e.g., bass, pike) (Drenner and Hambright 2002, Mehner et al. 2004) that are important consumers of molluscivorous fish

(Bolding et al. 1998, Huskey and Turingan 2001) and crayfish (Dorn and Mittelbach 1999). Second, humans have deliberately and accidentally introduced many species of molluscivorous predators outside of their native range, which also reduce snail abundances (Strayer 1999). For example, molluscivorous redear sunfishes (*Lepomis microlophus*), native to the southeastern part of North America have been introduced to

northern and western North American, often greatly reducing snail abundances (Huckins 1997, Huckins et al. 2000). Similarly, several exotic crayfishes have been introduced throughout North America, and some are less susceptible to native predators and thus can attain higher abundances and have higher levels of molluscivory (Lodge et al. 1994, Hill and Lodge 1999). Thus, it is possible that the invasion of *M. spicatum* into some lakes in North America may have been facilitated by 'invasional meltdown' (sensu Simberloff and Von Holle 1999) caused by the introduction of exotic molluscivorous fish and crayfish.

Our results are specific to the invasion of *M. spicatum*, because they included a complex interaction between nutrient inputs, the traits of native and the exotic species, and food web interactions. Specifically, the allelopathic nature of the invasive *M. spicatum* may allow it to invade eutrophic systems with abundant algae. When algal consumers reduce algal abundance, *M. spicatum* is not able to invade communities nearly as well. However, our experimental results emphasize the more general importance of knowing both the traits that the species possesses (allelopathy in this case) and the context of the community (eutrophication in this case) in order to fully understand the processes that allow a species to invade a natural system.

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References

- Bates AL, Burns ER and Webb DH (1985) Eurasian water-milfoil (*Myriophyllum spicatum* L.) in the Tennessee-valley: an update on biology and control. In: Proceedings First International Symposium on Water-milfoil and Related Haloragaceae Species, Aquatic Plant Management Society, Vancouver British Columbia
- Bolding B, Bonar SA and Divens M. (1998) Walleye diet in a shallow impoundment: relative importance of pumpkinseed sunfish and yellow perch. *Journal of Freshwater Ecology* 13: 9–14
- Brönmark C (1989) Interactions between epiphytes, macrophytes and freshwater snails – A review. *Journal of Molluscan Studies* 55: 299–311
- Brönmark C, Klosiewski SP and Stein RA (1992) Indirect effects of predation in a fresh-water, benthic food-chain. *Ecology* 73: 1662–1674
- Callaway RM and Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2: 436–443
- Carpenter S, Caraco N, Correll DL, Howarth RW, Sharpley AN and Smith VH (1998) Nonpoint Pollution of Surface Waters with Phosphorus and Nitrogen. *Issues in Ecology* No. 3
- Chase JM (2003) Experimental evidence for alternative stable equilibria in pond food webs. *Ecology Letters* 6: 733–741
- Couch R and Nelson E (1985) *Myriophyllum spicatum* in North America. In: Proceedings First International Symposium on Water-milfoil and Related Haloragaceae Species. Aquatic Plant Management Society, Vancouver British Columbia
- Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics* 34: 183–211
- Davis MA, Grime JP and Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528–534
- Dorn NJ and Mittelbach GG (1999) More than predator and prey: a review of interactions between fish and crayfish. *Vie et Millieu* 49: 229–237
- Dorn NJ and Wojdak JM (2004) The role of omnivorous crayfish in littoral communities. *Oecologia* 140: 150–159
- Drenner RW and Hambright KD (2002) Piscivores, trophic cascades, and lake management. *Scientific World Journal* 2: 284–307
- Eiswerth ME, Donaldson SG and Johnson WS (2000) Potential environmental impacts and economic damages of Eurasian watermilfoil (*Myriophyllum spicatum*) in western Nevada and northeastern California. *Weed Technology* 14: 511–518
- Engel S (1987) The impact of submerged macrophytes on largemouth bass and bluegills. *Lake and Reservoir Management* 3: 227–234
- Gross EM, Meyer H and Schilling G (1996) Release and ecological impact of algalicidal hydrolysable polyphenols in *Myriophyllum spicatum*. *Phytochemistry* 41: 133–138
- Gross EM (2000) Seasonal and spatial dynamics of allelochemicals in the submersed macrophyte *Myriophyllum spicatum* L. *Verhulst International Limnology* 27: 2116–2119
- Hill AM and Lodge DM (1999) Replacement of resident crayfishes by an exotic crayfish: the roles of competition and predation. *Ecological Applications* 9: 678–690
- Hobbs RJ and Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6: 324–337

- Huckins CJF (1997) Functional linkages among morphology, feeding performance, diet, and competitive ability in molluscivorous sunfish. *Ecology* 78: 2401–2414
- Huckins CJF, Osenberg CW and Mittelbach GG (2000) Species introductions and their ecological consequences: an example with congeneric sunfish. *Ecological Applications* 10: 612–625
- Huskey SH, Turingan and RG (2001) Variation in prey-resource utilization and oral jaw gape between two populations of largemouth bass, *Micropterus salmoides*. *Environmental Biology of Fishes* 61: 185–194
- Leu E, Krieger-Liszkay A and Goussias C et al., (2002) Polyphenolic allelochemicals from the aquatic angiosperm *Myriophyllum spicatum* L. inhibit photosystem II. *Plant Physiology* 130: 2011–2018
- Levine JM and D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87: 15–26
- Lillie RA and Budd J (1992) Habitat architecture of *Myriophyllum spicatum* as an index to habitat quality for fish and macroinvertebrates. *Journal of Freshwater Ecology* 7: 113–125
- Lodge DM, Kershner MW and Aloï JE et al., (1994) Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food-web. *Ecology* 75: 1265–1281
- MacDougall AS and Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems. *Ecology* 86: 42–55
- Madsen JD (1997) Methods for management of nonindigenous aquatic plants. In: Luken JO and Thieret JW (eds) *Assessment and Management of Plant Invasions*, pp 145–171. Springer-Verlag, New York
- Madsen JD, Sutherland JW and Bloomfield JA et al., (1991) The decline of native vegetation under dense Eurasian watermilfoil canopies. *Journal of Aquatic Plant Management* 29: 94–99
- Madsen JD (1998) Predicting invasion success of Eurasian watermilfoil. *Journal of Aquatic Plant Management* 36: 28–32
- Mehner T, Arlinghaus R, Berg S, Dörner H, Jacobsen L, Kasprzak P, Koschel R, Schulze T, Skov C, Wolter C and Wysujack K (2004) How to link biomanipulation and sustainable fisheries management: a step-by-step guideline for lakes of the European temperate zone. *Fisheries Management and Ecology* 11: 261
- Nakai S, Inoue Y, Hosomi M and Murakami A (1999) Growth inhibition of blue-green algae by allelopathic effects of macrophyte. *Water Science and Technology* 39: 47–53
- Newroth PR (1985) A review of Eurasian water milfoil impacts and management in British Columbia. In: *Proceedings First International Symposium on Water-milfoil and Related Haloragaceae Species*. Aquatic Plant Management Society, Vancouver, British Columbia
- Osenberg CW (1989) Resource limitation, competition and the influence of life history in a freshwater snail community. *Oecologia* 79: 512–519
- Rahel FJ (2002) Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics* 33: 291–315
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller and SG (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305–332
- Sand-Jensen K and Borum J (1991) Interactions among phytoplankton, periphyton and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany* 41: 137–175
- Sand-Jensen K and Søndergaard M (1981) Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. *Internationale Revue der Gesamten Hydrobiologie* 66: 529–552
- Shea K and Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17: 170–176
- Simberloff D and Von Holle M (1999) Synergistic interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1: 21–32
- Strayer DL (1999) Effects of alien species on freshwater mollusks in North America. *Journal of the North American Benthological Society* 18: 74–98
- Valley RD and Newman RM (1998) Competitive interactions between Eurasian watermilfoil and northern watermilfoil in experimental tanks. *Journal of Aquatic Plant Management* 36: 121–126
- Williamson M. (1996) *Biological Invasions*. Chapman & Hall, London