Hydrobiologia (2012) 684:1–14
DOI 10.1007/s10750-011-0978-8

REVIEW PAPER

Effects of invasive macrophytes on freshwater fish and macroinvertebrate communities: the role of invasive plant traits

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Received: 16 June 2011 / Revised: 19 November 2011 / Accepted: 3 December 2011 / Published online: 22 December 2011

Abstract Biological invasions of aquatic plants (i.e., macrophytes) are a worldwide phenomenon, and within the last 15 years researchers have started to focus on the influence of these species on aquatic communities and ecosystem dynamics. We reviewed current literature to identify how invasive macrophyte species impact fishes and macroinvertebrates, explore how these mechanisms deviate (or not) from the accepted model of plant–fish interactions, and assess how traits that enable macrophytes to invade are linked to effects on fish and macroinvertebrate communities. We found that in certain instances, invasive macrophytes increased habitat complexity, hypoxia, allelopathic chemicals, facilitation of other exotic species, and inferior food quality leading to a decrease in abundance of native fish and macroinvertebrate species. However, mechanisms underlying invasive macrophyte impacts on fish and macroinvertebrate communities (i.e., biomass production, photosynthesis, decomposition, and substrate stabilization) were not fundamentally different than those of native macrophytes. We identified three invasive traits largely responsible for negative effects on fish and macroinvertebrate communities: increased growth rate, allelopathic chemical production, and phenotypic plasticity allowing for greater adaptation to environmental conditions than native species. We suggest that information on invasive macrophytes (including invasive traits) along with environmental data could be used to create models to better predict impacts of macrophyte invasion. However, effects of invasive macrophytes on trophic dynamics are less well-known and more research is essential to define system level processes.

Keywords Allelopathy · Phytophilous fauna · Periphytic invertebrates · Habitat complexity

Handling editor: Sidinei Magela Thomaz

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Introduction

There has been considerable research on interactions between aquatic plants (hereafter macrophytes) and fish due to the importance of fisheries to society and structure and food macrophytes provide to aquatic habitats. A primary linkage between plants and fish are macroinvertebrates, many of which are associated with plants and a source of food for numerous fish species. Motivated by widespread biological invasions occurring in aquatic systems, researchers have begun studying ecological effects of invasive macrophytes on aquatic communities. They have found that invasive species (including macrophytes) are the second greatest threat to imperiled fish species in Canada and the United States after habitat loss and impact 63–70% of the listed species (Lassuy, 1995; Dextrase & Mandrak, 2006). Because native macrophytes typically have positive effects on fish and macroinvertebrate communities, this finding begs the question, "If invasive macrophytes are affecting fish and macroinvertebrate communities differently than native macrophytes, *how* are they doing it?" To address this question, we must first define accepted models of ecological dynamics in communities with native macrophytes.

In general, vegetated habitats have greater densities of fish than unvegetated habitats. Within vegetated habitats, structural variation influences fish community composition, density, behavior, and population dynamics (see review by Dibble et al., 1996). Fisheries researchers indicate that intermediate densities of macrophytes tend to support the greatest species richness of fish and the greatest growth and survival rates (e.g., Savino & Stein, 1989; Ferrer & Dibble, 2005; Strakosh et al., 2009). However, due to variability in size and feeding behavior among fish, response to vegetated habitats is species dependent. For example, certain fishes prefer areas of fairly dense macrophytes (e.g., *Lepomis macrochirus* Rafinesque) and others prefer areas with sparser vegetation (e.g., *Micropterus salmoides* Lacepede) (Johnson et al., 1988). Response of macroinvertebrates to macrophyte density is generally less varied than fish response and tends to increase linearly with macrophyte density (e.g., Cyr & Downing, 1988). Researchers have emphasized how macrophyte structure affects fishes and macroinvertebrates; however, macrophytes play other key roles such as providing food and influencing the aquatic environment physiologically (for a review on submerged macrophyte effects on ecosystem processes, see Carpenter & Lodge, 1986).

Based on the afore-mentioned relationships among native macrophytes, macrointerebrates, and fish, an increase in plant density within aquatic habitats due to an invasion would be expected to increase macroinvertebrate density, decrease fish foraging efficiency, and influence community composition. Due to the multitude of ways plants influence aquatic food webs, environmental conditions, etc., there are likely other ways that invasive species could influence fish and macroinvertebrate communities. Invasive species have specific traits that facilitate their invasion such as high growth rates, defense strategies (i.e., allelopathy), and adaptations to a broad range of environmental conditions (see review by Ren & Zhang, 2009). We posit that if invasive species affect fish and macroinvertebrate communities differently than natives, it is due to traits that enable them to invade because they are responsible for changes to aquatic environments. Furthermore, certain traits will have different effects on the aquatic community than others. If supported by evidence, knowing this information would allow us to better predict impacts of invasive macrophytes on fish and macroinvertebrate communities.

Our review has four primary aims: identify mechanisms by which invasive macrophytes affect fish and macroinvertebrate communities, summarize effects of invasive macrophytes on macroinvertebrates and fish, assess how invasive species traits are connected with how invasive macrophytes affect macroinvertebrates and fish, and specify areas for future research. Dibble et al. (1996) and Petr (2000) reviewed interactions of macrophytes and fish within inland systems extensively, and we will address numerous advances in knowledge since 1997, specifically focused on impacts of invasive macrophytes on fish and macroinvertebrate communities. Our use of the term *invasion* refers to the following definition, "a biological invasion consists of a species' acquiring a competitive advantage following the disappearance of natural obstacles to its proliferation, which allows it to spread rapidly and to conquer novel areas within recipient ecosystems in which it becomes a dominant population" (sensu Valéry et al., 2008). An *invasive macrophyte* is thus the aquatic plant species (floating, submerged, or emergent) referred to in the preceding definition. The definition we used is not limited to non-native species; therefore, we made an explicit effort not to exclude native species from the invasive species included in this review. We excluded certain macrophyte–fish interactions from this publication to either avoid overlap with recent reviews on a topic (i.e., grass carp; Dibble & Kovalenko, 2009) or to limit the scope to freshwater systems and to exclude aquaculture.

Mechanisms driving invasive macrophytes impact on fish and macroinvertebrate communities

Invasive macrophytes affect aquatic communities through biomass production, photosynthesis, decomposition, and substrate stabilization (Fig. 1). Here, we detail various mechanisms driving invasive species effects on biotic and abiotic factors and resulting impacts on fish and macroinvertebrate communities (see Table 1 for a species-specific description of invasive macrophytes and their effects on fish, macroinvertebrates, and native vegetation).

Effects of invasive macrophytes on plant biomass volume and habitat complexity

Invasive macrophytes can form dense monotypic stands, which can change macroinvertebrate and fish densities and community structure as well as interactions between macroinvertebrates and fish (Dibble et al., 1996). Many studies focused on aquatic community response to structural changes as a result of macrophyte invasion; therefore, we have organized this section to address specific responses of macroinvertebrates and fish.

Macroinvertebrate abundance/density

Macroinvertebrate density tends to increase only when both plant biomass and habitat complexity increases, as was the case with invasive species with highly dissected leaves or roots (e.g., *Hydrilla verticillata* (L. f.) Royle, Thorp et al., 1997; *Myriophyllum spicatum* L., Balci & Kennedy 2003; *Trapa natans* L., Strayer et al., 2003; *Lagarosiphon major* (Ridley) Moss, Kelly & Hawes, 2005; *Cabomba caroliniana* A. Gray, Hogsden et al., 2007). For instance, researchers in New Zealand found that beds of invasive *L. major* had 300% greater plant biomass and 113% greater macroinvertebrate densities compared with native vegetation (Kelly & Hawes, 2005). In contrast to the above-mentioned species, an invasion by *Hymenachne amplexicaulis* (Rudge) Nees resulted in 30 times greater plant biomass; however, because it replaced native submerged macrophytes with highly dissected leaves, habitat complexity was reduced (Houston & Duivenvoorden, 2002). Native vegetation had 2.7 times greater macroinvertebrate abundance than invaded areas (Houston & Duivenvoorden, 2002).

Despite an increase in habitat complexity due to invasion of certain macrophytes, investigators have found macroinvertebrate densities decreased

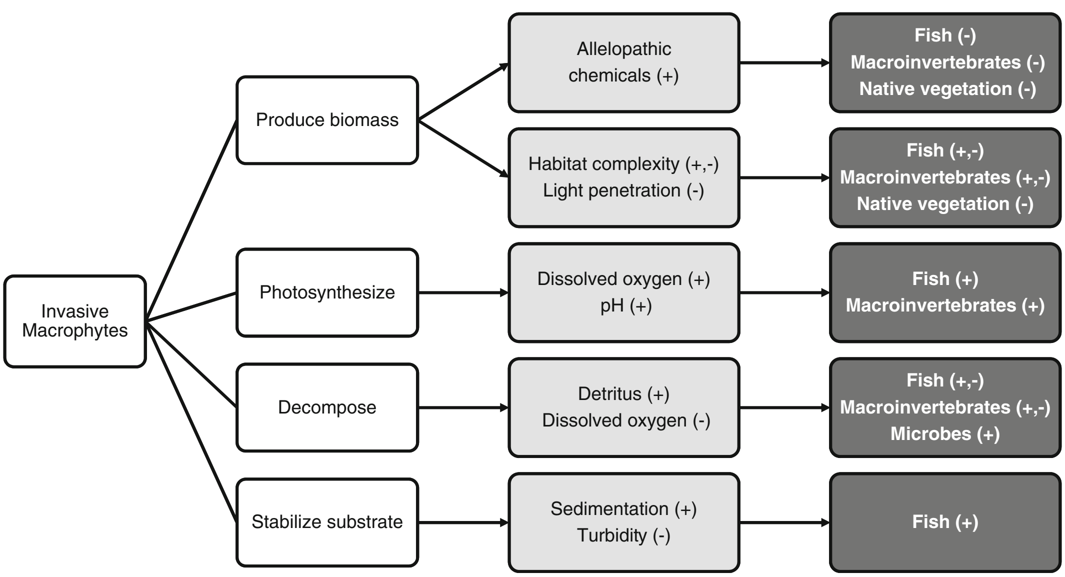

Fig. 1 Effects of invasive macrophytes on the ecosystem. Plant functions (*white*) and associated effects on abiotic (*light gray*) and biotic (*dark gray*) factors are shown. The plus (+) and minus (−) signs indicate the positive or negative response of the variable to an increase in the invasive macrophyte, respectively. In certain cases, the biotic response is unimodal instead of linear (as in the response of fish to habitat complexity), therefore both signs are used to depict the relationship

Table 1 Invasive macrophytes and their interactions with macroinvertebrates and fish

Species	Structure	Range	Invasive trait(s)	Impact on native communities	References
Eichhornia crassipes	Floating	Native to Amazon basin—invaded range is worldwide except for Europe	NW, High GRR, PP_{ET}	Outcompetes native vegetation, decreases dissolved oxygen levels, leads to shift in macroinvertebrate communities and fish diets and fosters non-indigenous amphipods	Masifwa et al. (2001), Brendonck et al. (2003), Toft et al. (2003), Njiru et al. (2004), Greenfield et al. (2007), Troutman et al. (2007), Villamagna & Murphy (2010), Kouame et al. (2010)
Hydrocotyle ranunculoides	Floating	Native to North and South America, invaded range includes Australia and Europe	High GRR, PP_{ET}	Outcompetes native plants for resources, decreases food source availability and quality for macroinvertebrates	Hussner (2008), Stiers et al. (2011)
Ludwigia grandiflora	Floating	Native to South America, invaded range includes the U.S. and Europe	High GRR, NW, PP_{ET}	Outcompetes native plants for resources, decreases food source availability and quality for macroinvertebrates	Dandelot et al. (2008), Hussner (2008), Stiers et al. (2011)
Trapa natans	Floating	Native to warm temperate Eurasia—invaded range is Australia, Burkina Faso, northeastern U.S., and Canada	High GRR	Decreases dissolved oxygen levels, can increase macroinvertebrate density	Cattaneo et al. (1998), Caraco & Cole (2002), Strayer et al. (2003), Kornijow et al. (2010)
Cabomba caroliniana	Submerged	Native to the southern U.S.—invaded range is northeast and northwest U.S and Canada	NW	Increases habitat complexity	Hogsden et al. (2007), Király et al. (2008), Jacobs & Macisaac (2009)
Egeria densa	Submerged	Native to South America, invaded range includes Europe, Africa, the U.S., and Australasia	High GRR	Increases habitat complexity, alters fish community composition	Parsons et al. (2009)
Elodea canadensis	Submerged	Native to North America, invaded range includes northern and western Europe	NW	Increases habitat complexity, outcompetes native plants for resources, reduces feeding and growth of certain macroinvertebrates, does not alter feeding of a fish species	Erhard (2005), Kelly & Hawes (2005), Kornijow et al. (2005)
Elodea nuttallii	Submerged	Native to North America, invaded range includes northern and western Europe	NW	Increases habitat complexity, outcompetes native plants for resources, reduces feeding and growth of certain macroinvertebrates	Erhard (2005)
Hydrilla verticillata	Submerged	Native to Asia, specifically India and Korea, invaded range includes the Americas, Europe, Africa Australia, and New Zealand	High GRR, PP_{ET}	Increases habitat complexity, outcompetes native plants for resources, decreases fish foraging efficiency at high densities, facilitates non-native fishes	Thorp et al. (1997), Brown & Maceina (2002), Colon-Gaud et al. (2004), Nico & Muench (2004), Sammons & Maceina (2006), Troutman et al. (2007), Barrientos & Allen (2008), Hershner & Havens (2008), Hoyer et al. (2008), Theel et al. (2008) Thomaz et al. (2009), Bianchini et al. (2010), Mormul et al. (2010), Sousa et al. (2010)

Table 1 continued

Species	Structure	Range	Invasive trait(s)	Impact on native communities	References
Lagarosiphon major	Submerged	Native to southern Africa, invaded range includes Australia, New Zealand, and Europe	PP_{ET}	Increases habitat complexity, outcompetes native plants for resources, increases pH and decreases water CO_2 concentrations	Kelly & Hawes (2005), Bickel & Closs (2008, 2009)
Myriophyllum aquaticum	Submerged/ Floating	Native to South America, invaded range includes the U.S., Europe, Africa, New Zealand and Australia	High GRR, PP_{ET}	Outcompetes native plants for resources, decreases food source availability and quality for macroinvertebrates	Hussner (2008), Stiers et al. (2011)
Myriophyllum spicatum	Submerged	Native to Europe, Asia and northern Africa, invaded range includes the U.S. and Canada	NW	Increases habitat complexity, outcompetes native plants for resources, decreases food source availability and quality for macroinvertebrates, facilitates non-native fishes, alters fish diets and trophic dynamics	Dibble & Harrel (1997), Weaver et al. (1997), Cheruvelil et al. (2001, 2002), Valley & Bremigan (2002b), Balci & Kennedy (2003), Bremigan et al. (2005), Linden & Lehtiniemi (2005), Slade et al. (2005), Ward & Newman (2006), Phillips (2008), Kovalenko et al.(2009), Parsons et al. (2009), Wilson & Ricciardi (2009), Collingsworth & Kohler (2010), Kovalenko et al. (2010), Lapointe et al. (2010), Kovalenko & Dibble (2011)
Potamogeton crispus	Submersed	Native to Eurasia, invaded range includes Canada and the U.S.	High GRR	Increases habitat complexity, outcompetes native plants for resources	Croft & Chow-Fraser (2007), Kovalenko et al. (2009)
Hymenachne amplexicaulis	Emergent	Native to the central and tropical America, invaded range includes Florida, Australia, Indonesia and Papua New Guinea	High GRR, PP_{ET}	Reduces water flows, resulting in lower fish recruitment, decreases habitat complexity, facilitates non-native fishes	Kibbler & Bahnisch (1999), Houston & Duivenvoorden (2002)
Phragmites australis	Emergent	Found worldwide in temperate areas, is considered alien and/or invasive in the U.S. New Zealand and Burkina Faso	PP_{RA}	Outcompetes native vegetation, no adverse effects on fish populations, increases gastropod abundance	Aday (2007), Kulesza et al. (2009), Holomuzki & Klarer (2010)

Species and their structure, native and invaded ranges, invasive traits, and effects on native communities are listed along with references

The invasive traits are novel weapons (NW), high growth/reproduction rate (High GRR), phenotypic plasticity allowing for a greater range of environmental (PP_{ET}), and phenotypic plasticity allowing for a greater range of resource allocation (PP_{RA}) (sensu Ren & Zhang, 2009)

Species invaded and native ranges were derived from the Global Invasive Species Database (http://www.issg.org/database)

(Cheruvelil et al., 2002; Hessen et al., 2004; Stiers et al., 2011) or were not different (Phillips, 2008; Theel et al., 2008) compared with native vegetation. For example, macroinvertebrate densities were negatively related to percent cover of three invasive macrophytes (*Hydrocotyle ranunculoides* L. f., *Ludwigia grandiflora* (Michx.) Greuter & Burdet, and *Myriophyllum aquaticum* (Vell.) Verdc.), probably due to anoxic conditions caused by dense mats that limited diffusion of oxygen and excess detritus (Stiers et al., 2011).

Macroinvertebrate assemblages

Changes in macrophyte composition and structural complexity can also alter macroinvertebrate assemblages (i.e., species diversity and composition). Species diversity of macroinvertebrates increased when habitat heterogeneity increased due to macrophyte invasion (e.g., *Phragmites australis* (Cav.) Trin. ex Steud., Holomuzki & Klarer, 2010; *Eichhornia crassipes* (Mart.) Solms, Masifwa et al., 2001; Brendonck et al., 2003; Kouame et al., 2010). For instance, in Lake Erie wetlands, presence of *P. australis* indirectly increased macroinvertebrate diversity by shading out *Lemna* spp. and reducing the prevalence of a dominant detrivore (Kulesza et al., 2009; Holomuzki & Klarer, 2010). Researchers found structural complexity of native and invasive species accounted for differences in macroinvertebrate species composition (e.g., *H. amplexicaulis*, Houston & Duivenvoorden, 2002; *H. verticillata*, Colon-Gaud et al., 2004; Mormul et al., 2010). In the Atchafalaya Basin, densities of Gastropods were four times greater and Hydrachnida were two times greater in native *Ceratophyllum demersum* L. than *H. verticillata* likely due to higher dissection of *C. demersum* leaves and related increase of surface area available to periphyton (Colon-Gaud et al., 2004).

Fish abundance

Effects of invasive macrophytes on fish abundance depend in part on quantity and quality of habitat prior to invasion. Systems with historically low densities of submerged vegetation tended had greater fish abundances after macrophyte invasion because habitat and food availability increased for fish (e.g., Kelly & Hawes, 2005; Barrientos & Allen, 2008; Bickel & Closs, 2008). In relatively vegetated areas, fish abundance decreased in invaded vegetation following a drop in water depth due to increased habitat complexity and decreased dissolved oxygen concentrations (Troutman et al., 2007). In contrast, other studies have shown that fish abundance did not differ between areas with or without invasive macrophytes (e.g., *M. spicatum*, Slade et al., 2005; *H. verticillata*, Hoyer et al., 2008; *Phragmites austalis*, Aday, 2007; Kulesza et al., 2009).

Fish foraging, growth, and diet

At a fine scale (<1 m^2), foraging efficiency of fish decreases with the presence of an invasive macrophyte when habitat complexity surpasses a threshold limit (Valley & Bremigan, 2002a; Theel & Dibble, 2008). For example, largemouth bass had longer prey search times and fewer attacks in dense monocultures of artificial *M. spicatum* than less dense communities because prey fish were able to hide in dense canopies (Valley & Bremigan, 2002a). At the whole lake scale, increased habitat complexity can affect fish growth rates when shallow lakes become choked with invasive vegetation (Brown & Maceina, 2002; Cheruvelil et al., 2005; Sammons & Maceina, 2006). In Lake Seminole, Georgia, cover of *H. verticillata* was reduced from 76 to 22% and growth of largemouth bass increased; however, bass diets did not change to a great extent suggesting that growth responded primarily to increased predation efficiency (Brown & Maceina, 2002; Sammons & Maceina, 2006).

In some cases, fish diets changed when invasive macrophytes were present, either due to an increase in macroinvertebrate density (Njiru et al., 2004; Bickel & Closs, 2008) or differences in plant architecture (Dibble & Harrel, 1997). For instance, Njiru et al. (2004) speculate that the shift in Nile tilapia (*Oreochromis niloticus* L.) diet from a predominance of algae to insects is due to invasion of *E. crassipes* into the largely unvegetated Lake Victoria in Kenya. However, Dibble & Harrel (1997) found that prey of largemouth bass was predominately macroinvertebrates in enclosures of native *Potamogeton nodosus* Poir., but switched to preying on predominately fish in *M. spicatum* enclosures.

Fish habitat and assemblage

Non-native fish species can benefit from shelter and nesting habitat resulting from a macrophyte invasion (Houston & Duivenvoorden, 2002; Nico & Muench, 2004; Lapointe et al., 2010). For example, *H. verticillata* beds in a shallow Florida lake facilitated an invasive catfish, *Hoplosternum littorale* Hancock, by providing nest material and refuge from predators (Nico & Muench, 2004). Native fishes also benefit from habitat provided by invasive macrophytes, depending on environmental conditions (Collingsworth & Kohler, 2010). Following a water level drawdown, juvenile sunfish (*Lepomis* spp.) shifted habitat preference from native *Potamogeton nodosus* to *M. spicatum*, which colonized in deeper water (Collingsworth & Kohler, 2010).

There is some evidence that invasive macrophytes influence species composition and structure (age and size classes) of fish assemblages. For example, Houston & Duivenvoorden (2002) found that 79% of the fish in areas invaded by *H. amplexicaulis* were non-native compared with 3% non-native fish species in areas of native macrophytes. Weaver et al. (1997) found that age 0 bluegill were associated with areas of patchy *M. spicatum,* whereas yearling and adult bluegill were associated with areas of native macrophytes in Lake Mendota in the USA. Similarly, in Lake Chivero, Zimbabwe, smaller fish were found in the littoral zone dominated by *E. crassipes* in comparison to the pelagic zone (Brendonck et al., 2003). However, the above-mentioned studies did not show any evidence for an effect of invasive macrophytes on species diversity; and Slade et al. (2005) and Hoyer et al. (2008) found no differences in fish assemblages between invaded and native macrophyte communities.

Effects of invasive macrophytes on physico-chemical properties of the aquatic environment

Macrophytes alter physico-chemical properties of aquatic environments both structurally and functionally. Macroinvertebrates and fish are sensitive to changes in the water environment including dissolved oxygen levels, light penetration, water clarity, and allelopathic chemicals. The extent to which these parameters change influences the aquatic community.

Dissolved oxygen concentration

Invasive macrophytes limit concentrations of dissolved oxygen in water when they form dense floating mats that decrease atmospheric exchange with water (Masifwa et al., 2001; Strayer et al., 2003; Troutman et al., 2007; Villamagna & Murphy, 2010; Kornijow et al., 2010). Most aquatic species including macroinvertebrates and fish are sensitive to low dissolved oxygen concentrations; therefore, species assemblages would be expected to be different under floating mats of invasive macrophytes. Indeed, macroinvertebrate communities in ponds invaded by mat-forming macrophytes (*H. ranunculoides*, *L. grandiflora,* and *M. aquaticum*) were less diverse and were comprised primarily of species that tolerate low oxygen levels (e.g., Chironomidae and Naidadae) than non-invaded ponds with submerged vegetation (Stiers et al., 2011). Toft et al. (2003) found lower densities of epibenthic and benthic macroinvertebrates in floating mats of *E. crassipes* than native *H. umbellata* L. likely due to relatively lower oxygen levels beneath *E. crassipes*. However, researchers found greater densities of macroinvertebrates in roots of *T. natans* floating mats compared with native submergent species *Vallisneria americana* Michx., indicating that organisms can use oxygen exuded from *T. natans* roots and find refuge from underlying hypoxia (Strayer et al., 2003; Kornijow et al., 2010).

Light penetration

Floating mat species intercept light entering aquatic environments. Under reduced light conditions, submersed macrophyte and algae production is limited, thus changing aquatic community composition and food web structure with the introduction of a floating macrophyte (Troutman et al., 2007; Villamagna & Murphy, 2010). In a lake in Italy, researchers estimated that floating mats of *T. natans* reduced light transmission to 7% and supported two to eight times less algal biomass and two to ten times fewer macroinvertebrates (#g DW^{-1}) than submerged species (Cattaneo et al., 1998).

Water clarity

Presence of rooted macrophytes, especially submerged macrophytes, is associated with greater water clarity through minimizing sediment resuspension and phytoplankton populations (see reviews by Barko & James, 1998; Madsen et al., 2001). Many fish species respond to an increase in turbidity by foraging less efficiently and selecting different prey (e.g., Hargeby et al., 2005; Shoup & Wahl, 2009). Researchers have not directly tested how invasive macrophytes affect water clarity; however, specific mechanisms could enable them to be more effective at reducing turbidity than native species (e.g., tolerance of extreme environmental conditions, Irfanullah & Moss 2004; high surface area to increase sedimentation, Rybicki & Landwehr 2007; allelopathy limiting phytoplankton growth, Hilt & Gross, 2008). For instance, Irfanullah & Moss (2004) reestablished non-native *Elodea nuttallii* (Planch.) H. St. John in a turbid, shallow lake in England to return the lake to a clear water state. The authors concluded that reestablishment was successful due to the species' high tolerance of nitrogen concentrations and ability to grow under low light conditions.

Allelopathic chemicals

Certain invasive macrophytes exude allelopathic chemicals that affect epiphytic, herbivore, and fish growth and survival. *Elodea canadensis* Michx. and *E. nuttallii* were both shown to have allelopathic effects on cyanobacteria and lepidopteron larvae resulting in a competitive advantage over native species, which are depredated by herbivores (Erhard, 2005). *M. spicatum* can be lethal or sublethal to fish larvae (i.e., *Neomysis integer* Leach and *Praunus flexuosus* Müller, and *Gasterosteus aculeatus* L.) and has the potential to change fish distributions and occurrence of affected species in invaded habitats (Linden & Lehtiniemi, 2005). Kovalenko & Dibble (unpublished data) hypothesize that *M. spicatum* also changes the epiphytic community by exuding allelopathic compounds, resulting in macroinvertebrates avoiding *M. spicatum* as feeding habitat, and therefore, insectivorous fish as well.

Effects of invasive macrophytes on trophic dynamics

Trophic dynamics may also be affected by invasive macrophytes; however, these effects are likely species specific (Kornijow et al., 2005; Kovalenko & Dibble, 2011). Kovalenko & Dibble (2011) found that invertivorous and piscivorous fish in lakes dominated by *M. spicatum* had twice the isotopic niche (or trophic diversity) of fish in lakes dominated by native vegetation, indicating that primary consumers were feeding on a greater variety of carbon sources in invaded communities. As food resources decrease, there tends to be an increase in variety of resources that are incorporated into diets, which would show up as a greater range of ^{13}C depletion all the way up the food chain. This could point to negative effects of *M. spicatum* on typical food resources for primary consumers, especially epiphyton (Kovalenko & Dibble, unpublished data). However, researchers found that *E. canadensis* did not affect *Rutilus rutilus* feeding preference for zooplankton even in dense vegetation, thus trophic dynamics were not significantly altered by the invasive plant (Kornijow et al., 2005).

Invasive plant traits and effects on the aquatic community

In 86% of studies we reviewed (43 out of 50 articles), researchers rejected the null hypothesis that aspects of aquatic communities did not differ based on presence or absence of invasive macrophytes. For instance, invasive macrophytes increased habitat complexity, hypoxia, allelopathic chemicals, facilitation of other exotic species, and inferior food quality leading to a decrease in abundance of native fish and macroinvertebrate species. However, mechanisms underlying invasive macrophyte impacts on fish and macroinvertebrate communities (i.e., biomass production, photosynthesis, decomposition, and substrate stabilization) were not fundamentally different than those of native macrophytes. In fact, in certain instances, there were increases or no changes in abundance, richness, etc., of native aquatic fish and macroinvertebrate species resulting from presence of an invasive macrophyte; even a species was shown to have the opposite effect in a different study system (e.g., *H. verticillata*, Sammons & Maceina, 2006; Barrientos & Allen, 2008; Hoyer et al., 2008; Theel et al., 2008). These results indicate that fish and macroinvertebrate communities respond to invasive species depending on both characteristics of the invader as well as the environment they are invading.

To explain what was fundamentally different in responses of fish and macroinvertebrate communities to invasive species as opposed to native species, we looked at specific characteristics that define invasions and invasive macrophytes. Shea & Chesson (2002) recommend using niche theory to understand biological invasions and identified three main factors that determine success of an invader: resources, natural enemies, and the physical environment. Putting invasive macrophytes into the "niche opportunity" framework developed by Shea & Chesson (2002), we see that resources (e.g., nutrients and light), competitors, and herbivores limit invasive macrophytes potential for expansion (Fig. 2). For example, Chase & Knight (2006) found that *M. spicatum* was only able to outcompete native vegetation under high nutrient conditions and absence of snails. However, generalist herbivores that consume competitors and carnivores that consume herbivores have indirect positive effects on invasive macrophyte success. For example, *M. spicatum* biomass was less in fish exclosures because sunfish reduced the abundance of herbivores, and therefore reduced herbivore consumption of *M. spicatum* (Ward & Newman, 2006). Thus, the extent of an invasion is a function of environmental/ecological factors and species' ability to overcome limitations to growth.

Researchers have proposed a number of mechanisms invasive plants use to overcome these limitations (see review by Levine et al., 2003). For instance, some species have greater growth rates as a result of being released from natural enemies (i.e., enemy release hypothesis, Keane & Crawley, 2002). Another strategy is to use allelopathy to limit competitors [i.e., novel weapons (NWs) hypothesis, Callaway & Ridenour, 2004]. Other species have high resource-use efficiency and phenotypic plasticity to adapt to a range of environmental conditions (see review by Ren & Zhang 2009). It is important to note that traits associated with invasive species are only meaningful relative to traits expressed in the native community (Levine et al., 2003). Invasive macrophytes reviewed here utilized a variety of these mechanisms, and it is the expression of certain traits associated with successful invaders that resulted in greater impacts on the environment and biotic community.

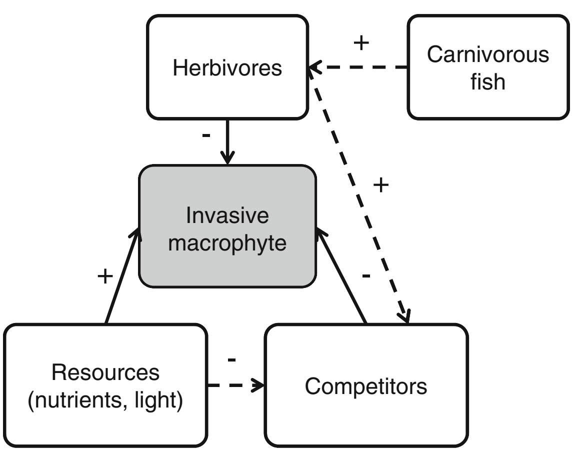

Fig. 2 Direct (*solid line*) and indirect effects (*dashed*) of the physical environment and biota on invasive macrophytes (modified from Shea & Chesson, 2002). Whether the interactions affect the invasive macrophyte positively or negatively are denoted with + and − signs, respectively

In a recent review, Ren & Zhang (2009) categorized invasion mechanisms and traits of 133 species including 5 of 15 species detailed in this review. Each species was categorized based on literature that either explicitly stated invasive traits of a certain species or in which traits were readily apparent. Pertaining to invasive macrophytes included in our review, four species were categorized as having a NW (i.e., *C. caroliniana, E. crassipes, E. canadensis*, and *E. nuttallii*). One species was categorized as having phenotypic plasticity to adapt to a range of environmental conditions (PP_{ET}) (i.e., *E. crassipes*). One species was categorized as having phenotypic plasticity allowing for a greater range of resource allocation (PP_{RA}) (i.e., *P. australis*). And one species was categorized as having a high growth or reproduction rate (High GRR) (i.e., *E. crassipes*). We further categorized an additional ten species included in this review based on the literature. *M. spicatum* and *L. grandiflora* have been documented as allelopathic (NW). *T. natans, Egeria densa, Potamogeton crispus, H. ranunculoides, H. amplexicaulis, H. verticillata, L. grandiflora,* and *M. aquaticum* have been shown to have a high growth or reproduction rate relative to native species (High GRR). Finally, *H. ranunculoides, H. verticillata, H. amplexicaulis, L. major, L. grandiflora,* and *M. aquaticum* have been shown to have phenotypic plasticity allowing them to have a greater range of environmental tolerance (PP_{ET}).

Many of these invasive traits (e.g., high growth rate, phenotypic plasticity, and NWs) can be directly related to how invasive species affected aquatic community dynamics (see Table 1 for a species-specific description of invasive macrophytes and their effects on fish, macroinvertebrates, and native vegetation). Researchers indicated changes in habitat structure and environmental conditions in part explained invasive species effects on fish foraging, growth, and abundance as well as macroinvertebrate richness and abundance. How invasive macrophyte species change habitat structure and environmental conditions can be attributed to a high growth rate (increase in density/habitat complexity and formation of thick mats that create hypoxic zones) and greater colonization of areas due to an increased ability to tolerate extreme environmental conditions (increase in total vegetated area). However, effects on fish and macroinvertebrate communities depended on characteristics of the invaded environment. For instance, researchers found that aquatic communities invaded by *H. verticillata* did not differ from communities without the invasive macrophyte if they were either located in an area with a small littoral zone or a nutrient-limited area (Barrientos & Allen, 2008; Hoyer et al., 2008).

Other studies indicated that NWs (i.e., allelopathic chemicals) determined impacts on fish and macroinvertebrate communities, particularly on reducing abundance and survival of macroinvertebrates that feed on these allelopathic species (e.g., *Elodea* spp., Erhard et al., 2007). In terms of fish, invasive macrophytes exhibiting a NW trait can have lethal and sublethal effects on certain fish through direct effects of toxicity and a potential reduction in food items due to effects on macroinvertebrates (Linden & Lehtiniemi, 2005; Erhard, 2005).

Conclusion

In this review, we sought to define specific ways in which invasive macrophytes affect fish and macroinvertebrate communities to answer the question: "If invasive macrophytes are affecting fish and macroinvertebrate communities differently than native macrophytes, *how* are they doing it?" We reviewed literature spanning continents, aquatic ecosystem types, and a wide variety of invasive plant species, and we defined specific mechanisms by which invasive species affect fish and macroinvertebrate communities (Fig. 1). Considering the accepted model of how plant structure influences fish and macroinvertebrate communities, we would expect that an increase of plant density would have positive effects on macroinvertebrate abundance and negative effects on fish foraging, growth, and populations. We found that positive effects of invasive macrophytes on fish and macroinvertebrate communities were associated with characteristics held in common with native macrophytes such as photosynthesis, increasing habitat complexity, and stabilizing substrate. Thus, removal of all or most plants in aquatic systems tends to have a negative effect on fish and macroinvertebrate communities (e.g., Mangas-Ramírez & Elías-Gutiérrez, 2004; Parsons et al., 2009), whereas selective removal of invasive species and/or immediate restoration of native vegetation tends to maintain the system's diversity and density (e.g., Rybicki & Landwehr, 2007; Kovalenko et al., 2010). Negative effects, on the other hand, were associated with traits that invasive species use to invade. We found that three traits are largely responsible for negative effects on fish and macroinvertebrate communities: increased growth rate, allelopathic chemical production, and phenotypic plasticity that allow for greater adaptation to environmental conditions and resource utilization than native species.

It is apparent from our review that invasive traits are related to specific effects on fish and macroinvertebrate communities. While researchers have proposed using invasive traits to predict future invaders (Ren & Zhang, 2009), to our knowledge, there is currently no framework to predict effects on communities using these traits. Work on this topic would integrate data on environmental conditions with plant-specific information to model changes in structural and environmental aspects of aquatic systems as well as aquatic community response (Strayer, 2010). Furthermore, ecological engineering, keystone, and foundational effects of invasive macrophytes should be assessed in addition to functional traits, because impacts on ecosystems and communities likely result from a combination of these characteristics (Ehrenfeld, 2010).

Future research needs

After reviewing the literature, we identified areas we feel would further improve our knowledge of how invasive macrophytes influence fish and macroinvertebrate communities. Currently researchers have focused on responses of sport fishes to invasive species; therefore, a diversification of research effort to assess impacts on phytophylic fishes (especially rare and threatened species) is necessary to assess what different responses fish species have to invasions. For instance, Valley et al. (2010) observed that fishes with declining populations (i.e., killifish, darters, and rare minnows) were positively associated with plant biovolume of a native macroalgae (*Chara* sp.). In the event of an invasion, *Chara* would likely be replaced by invasive macrophytes, but fish response to this change would be difficult to predict. Furthermore, most studies focused on only one component of aquatic communities; however, interactions among community components are likely and research into impacts of invasive macrophytes on trophic relationships among plankton, macroinvertebrates, and fishes in early life and adult stages would give insight into these dynamics.

Due to incongruences of fish and macroinvertebrate responses at different spatial scales, an assessment of appropriate scales and methods to approach specific questions (multi-scale manipulative experimentation in ponds, mesocosms, field or laboratory) is necessary to clarify whole-system responses to macrophyte invasions. At a fine scale, investigation into whether habitats for parasites and pathogens are plant specific are necessary to determine mechanisms of invasion meltdown whereby introduction of one species leads to facilitation of another, and so on (Simberloff & Von Holle, 1999). At coarser scales, for example, research on how littoral–pelagic interactions are affected when an invasive species colonizes the littoral zone will increase understanding of different factors that determine responses at the system level.

Research is also necessary to develop management applications using information about how invasive macrophytes influence aquatic communities. For instance, applications using invasive traits to predict effects of an invasive species on a system would be a key tool for managers interested in prioritizing management efforts. Also, managers impact aquatic communities through aquatic plant management (e.g., herbicide, mechanical shedding, shading, etc.). While we did not address management effects in our review, an evaluation of these effects and costs should also be conducted in addition to invasive macrophyte effects when developing a comprehensive management plan.

Acknowledgments The authors thank Jonathan Fleming and two anonymous reviewers for their comments on earlier drafts of this manuscript. Financial support for this study was kindly provided by the U.S. Geological Survey, Department of Wildlife, Fisheries & Aquaculture, and the Geosystems Research Institute at Mississippi State University.

References

Aday, D., 2007. The presence of an invasive macrophyte (*Phragmites australis*) does not influence juvenile fish habitat use in a freshwater estuary. Journal of Freshwater Ecology 22: 535–537.

Balci, P. & J. H. Kennedy, 2003. Comparison of chironomids and other macroinvertebrates associated with *Myriophyllum spicatum* and *Heteranthera dubia*. Journal of Freshwater Ecology 18: 235–247.

Barko, J.W. & W.F. James, 1998. Effects of submerged aquatic macrophytes on nutrient dynamics, sedimentation, and resuspension. In Jeppesen, E., Sondergaard, M. & K. Christoffersen (eds), Structuring role of Submerged Macrophytes in Lakes. Ecological Studies: Analysis and Synthesis: 197–214

Barrientos, C. A. & M. S. Allen, 2008. Fish abundance and community composition in native and non-native plants following hydrilla colonisation at Lake Izabal, Guatemala. Fisheries Management and Ecology 15: 99–106.

Bianchini, I., M. B. Cunha-Santino, J. A. M. Milan, C. J. Rodrigues & J. H. P. Dias, 2010. Growth of *Hydrilla verticillata* (L.f.) Royle under controlled conditions. Hydrobiologia 644: 301–312.

Bickel, T. O. & G. P. Closs, 2008. Fish distribution and diet in relation to the invasive macrophyte *Lagarosiphon major* in the littoral zone of Lake Dunstan, New Zealand. Ecology of Freshwater Fish 17: 10–19.

Bickel, T. O. & G. P. Closs, 2009. Impact of partial removal of the invasive macrophyte *Lagarosiphon major* (Hydrocharitaceae) on invertebrates and fish. River Research and Applications 25: 734–744.

Bremigan, M. T., S. M. Hanson, P. A. Soranno, K. S. Cheruvelil & R. D. Valley, 2005. Aquatic vegetation, largemouth bass and water quality responses to low-dose fluridone two years post treatment. Journal of Aquatic Plant Management 43: 65–75.

Brendonck, L., J. Maes, W. Rommens, N. Dekeza, T. Nhiwatiwa, M. Barson, V. Callebaut, C. Phiri, K. Moreau, B. Gratwicke, M. Stevens, N. Alyn, E. Holsters, F. Ollevier & B. Marshall, 2003. The impact of water hyacinth (*Eichhornia crassipes*) in a eutrophic subtropical impoundment (Lake Chivero, Zimbabwe). II. Species diversity. Archiv Fur Hydrobiologie 158: 389–405.

Brown, S. J. & M. J. Maceina, 2002. The influence of disparate levels of submersed aquatic vegetation on largemouth bass population characteristics in a Georgia reservoir. Journal of Aquatic Plant Management 40: 28–35.

Callaway, R. M. & W. M. Ridenour, 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2: 436–443.

Caraco, N. F. & J. J. Cole, 2002. Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. Ecological Applications 12: 1496–1509.

Carpenter, S. R. & D. M. Lodge, 1986. Effects of submersed macrophytes on ecosystem processes. Aquatic Botany 26: 341–370.

Cattaneo, A., G. Galanti, S. Gentinetta & S. Romo, 1998. Epiphytic algae and macroinvertebrates on submerged and floating-leaved macrophytes in an Italian lake. Freshwater Biology 39: 725–740.

Chase, J. M. & T. M. Knight, 2006. Effects of eutrophication and snails on Eurasian watermilfoil (*Myriophyllum spicatum*) invasion. Biological Invasions 8: 1643–1649.

Cheruvelil, K. S., P. A. Soranno & J. D. Madsen, 2001. Epiphytic macroinvertebrates along a gradient of Eurasian watermilfoil cover. Journal of Aquatic Plant Management 39: 67–72.

Cheruvelil, K. S., P. A. Soranno, J. D. Madsen & M. J. Roberson, 2002. Plant architecture and epiphytic macroinvertebrate communities: the role of an exotic dissected macrophyte. Journal of the North American Benthological Society 21: 261–277.

Cheruvelil, K. S., N. A. Nate, P. A. Soranno & M. T. Bremigan, 2005. Lack of a unimodal relationship between fish growth and macrophyte cover in 45 north temperate lakes. Archives of Hydrobiology 164: 193–215.

Collingsworth, P. D. & C. C. Kohler, 2010. Abundance and habitat use of juvenile sunfish among different macrophyte stands. Lake and Reservoir Management 26: 35–42.

Colon-Gaud, J. C., W. E. Kelso & D. A. Rutherford, 2004. Spatial distribution of macroinvertebrates inhabiting hydrilla and coontail beds in the Atchafalaya Basin, Louisiana. Journal of Aquatic Plant Management 42: 85–91.

Croft, M. V. & P. Chow-Fraser, 2007. Use and development of the wetland macrophyte index to detect water quality impairment in fish habitat of Great Lakes coastal marshes. Journal of Great Lakes Research 33: 172–197.

Cyr, H. & J. A. Downing, 1988. Empirical relationships of phytomacrofaunal abundance to plant biomass and macrophyte bed characteristics. Canadian Journal of Fisheries and Aquatic Sciences 45: 976–984.

Dandelot, S., C. Robles, N. Pech, A. Cazaubon & R. Verlaque, 2008. Allelopathic potential of two invasive alien *Ludwigia* spp. Aquatic Botany 88: 311–316.

Dextrase, A. & N. Mandrak, 2006. Impacts of alien invasive species on freshwater fauna at risk in Canada. Biological Invasions 8: 13–24.

Dibble, E.D., K.J. Killgore & S.L. Harrel, 1996. Assessment of fish–plant interactions. In L.E. Miranda & D.R. Devries (ed.), Multidimensional Approaches to Reservoir Fisheries Management. American Fisheries Society, Bethesda: 357–372.

Dibble, E. D. & S. L. Harrel, 1997. Largemouth bass diets in two aquatic plant communities. Journal of Aquatic Plant Management 35: 74–78.

Dibble, E. D. & K. Kovalenko, 2009. Ecological impact of grass carp: a review of the available data. Journal of Aquatic Plant Management 47: 1–15.

Ehrenfeld, J. G., 2010. Ecosystem consequences of biological invasions. Annual Review of Ecology, Evolution, and Systematics 41: 59–80.

Erhard, D., 2005. Chemoecological investigations of the invasive waterweeds *Elodea* spp. Dissertation, Universität Konstanz, Constance, Germany. 140.

Erhard, D., G. Pohnert & E. M. Gross, 2007. Chemical defense in *Elodea nuttallii* reduces feeding and growth of aquatic herbivorous Lepidoptera. Journal of Chemical Ecology 33: 1646–1661.

Ferrer, O. J. & E. D. Dibble, 2005. Effect of aquatic plants and associate microhabitats on early life stages of fish. Ciencia 13: 416–428.

Greenfield, B., G. Siemering, J. Andrews, M. Rajan, S. Andrews & D. Spencer, 2007. Mechanical shredding of water hyacinth (*Eichhornia crassipes*): effects on water quality in the Sacramento-San Joaquin River Delta, California. Estuaries and Coasts 30: 627–640.

Hargeby, A., H. Blom, I. Gunnar & G. Andersson, 2005. Increased growth and recruitment of piscivorous perch, *Perca fluviatilis*, during a transient phase of expanding submerged vegetation in a shallow lake. Freshwater Biology 50: 2053–2062.

Hershner, C. & K. J. Havens, 2008. Managing invasive aquatic plants in a changing system: strategic consideration of ecosystem services. Conservation Biology 22: 544–550.

Hessen, D. O., J. Skurdal & J. E. Braathen, 2004. Plant exclusion of a herbivore; crayfish population decline caused by an invading waterweed. Biological Invasions 6: 133–140.

Hilt, S. & E. M. Gross, 2008. Can allelopathically active submerged macrophytes stabilise clear-water states in shallow lakes? Basic and Applied Ecology 9: 422–432.

Hogsden, K. L., E. P. S. Sager & T. C. Hutchinson, 2007. The impacts of the non-native macrophyte *Cabomba caroliniana* on littoral biota of Kasshabog Lake, Ontario. Journal of Great Lakes Research 33: 497–504.

Holomuzki, J. & D. Klarer, 2010. Invasive reed effects on benthic community structure in Lake Erie coastal marshes. Wetlands Ecology and Management 18: 219–231.

Houston, W. A. & L. J. Duivenvoorden, 2002. Replacement of littoral native vegetation with the ponded pasture grass *Hymenachne amplexicaulis*: effects on plant, macroinvertebrate and fish biodiversity of backwaters in the Fitzroy River, Central Queensland, Australia. Marine and Freshwater Research 53: 1235–1244.

Hoyer, M., M. Jackson, M. Allen & D. Canfield, 2008. Lack of exotic hydrilla infestation effects on plant, fish and aquatic bird community measures. Lake and Reservoir Management 24: 331–338.

Hussner, A., 2008. Ökologische und ökophysiologische Charakteristika aquatischer Neophyten in Nordrhein-Westfalen, PhD Thesis, Universität Düsseldorf, Germany.

Irfanullah, H. M. & B. Moss, 2004. Factors influencing the return of submerged plants to a clear-water, shallow temperate lake. Aquatic Botany 80: 177–191.

Jacobs, M. J. & H. J. Macisaac, 2009. Modelling spread of the invasive macrophyte *Cabomba caroliniana*. Freshwater Biology 54: 296–305.

Johnson, D. L., R. A. Beaumier & W. E. Lynch, 1988. Selection of habitat structure interstice size by bluegills and largemouth bass in ponds. Transactions of the American Fisheries Society 117: 171–179.

Keane, R. M. & M. J. Crawley, 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17: 164–170.

Kelly, D. J. & I. Hawes, 2005. Effects of invasive macrophytes on littoral-zone productivity and foodweb dynamics in a New Zealand high-country lake. Journal of the North American Benthological Society 24: 300–320.

Kibbler, H. & L. M. Bahnisch, 1999. Physiological adaptations of *Hymenachne amplexicaulis* to flooding. Australian Journal of Experimental Agriculture 39: 429–435.

Király, G., D. Steták & D. Bányász, 2008. Spread of invasive macrophytes in Hungary. Biological invasions-from ecology to conservation. NEOBIOTA 7: 123–130.

Kornijow, R., K. Vakkilainen, J. Horppila, E. Luokkanen & T. Kairesalo, 2005. Impacts of a submerged plant (*Elodea canadensis*) on interactions between roach (*Rutilus rutilus*) and its invertebrate prey communities in a lake littoral zone. Freshwater Biology 50: 262–276.

Kornijow, R., D. L. Strayer & N. F. Caraco, 2010. Macroinvertebrate communities of hypoxic habitats created by an invasive plant (*Trapa natans*) in the freshwater tidal Hudson River. Fundamental and Applied Limnology 176: 199–207.

Kouame, M. K., M. Y. Dietoa, S. K. Da Costa, E. O. Edia, A. Ouattara & G. Gourene, 2010. Aquatic macroinvertebrate assemblages associated with root masses of water hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laubach, 1883 (Commelinales: Pontederiaceae) in Taabo Lake, Ivory Coast. Journal of Natural History 44: 257–278.

Kovalenko, K. E., E. D. Dibble & R. Fugi, 2009. Fish feeding in changing habitats: effects of invasive macrophyte control and habitat complexity. Ecology of Freshwater Fish 18: 305–313.

Kovalenko, K. E. & E. D. Dibble, 2011. Effects of invasive macrophyte on trophic diversity and position of secondary consumers. Hydrobiologia 663: 167–173.

Kovalenko, K. E., E. D. Dibble & J. G. Slade, 2010. Community effects of invasive macrophyte control: role of invasive plant abundance and habitat complexity. Journal of Applied Ecology 47: 318–328.

Kulesza, A. E., J. R. Holomuzki & D. M. Klarer, 2009. Benthic community structure in stands of *Typha angustifolia* and herbicide–treated and untreated *Phragmites australis*. Wetlands 28: 40–56.

Lapointe, N. W. R., J. T. Thorson & P. L. Angermeier, 2010. Seasonal meso- and microhabitat selection by the northern snakehead (*Channa argus*) in the Potomac river system. Ecology of Freshwater Fish 19: 566–577.

Lassuy, D. R., 1995. Introduced species as a factor in extinction and endangerment of native fish species. In Schramm, H. L. & R. G. Piper (eds.), Uses and Effects of Cultured Fishes in Aquatic Ecosystems. American Fisheries Society, Bethesda: 391–396.

Levine, J. M., M. Vilà, C. M. D. Antonio, J. S. Dukes, K. Grigulis & S. Lavorel, 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London Series B: Biological Sciences 270: 775–781.

Linden, E. & M. Lehtiniemi, 2005. The lethal and sublethal effects of the aquatic macrophyte *Myriophyllum spicatum* on Baltic littoral planktivores. Limnology and Oceanography 50: 405–411.

Madsen, J. D., P. A. Chambers, W. F. James, E. W. Koch & D. F. Westlake, 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia 444: 71–84.

Mangas-Ramírez, E. & M. Elías-Gutiérrez, 2004. Effect of mechanical removal of water hyacinth (*Eichhornia crassipes*) on the water quality and biological communities in a Mexican reservoir. Aquatic Ecosystem Health & Management 7: 161–168.

Masifwa, W. F., T. Twongo & P. Denny, 2001. The impact of water hyacinth, *Eichhornia crassipes* (Mart) Solms on the abundance and diversity of aquatic macroinvertebrates along the shores of northern Lake Victoria, Uganda. Hydrobiologia 452: 79–88.

Mormul, R., S. Thomaz, J. Higuti & K. Martens, 2010. Ostracod (Crustacea) colonization of a native and a non-native macrophyte species of Hydrocharitaceae in the Upper Paraná floodplain (Brazil): an experimental evaluation. Hydrobiologia 644: 185–193.

Nico, L. G. & A. M. Muench, 2004. Nests and nest habitats of the invasive catfish *Hoplosternum littorale* in lake Tohopekaliga, Florida: a novel association with non-native *Hydrilla verticillata*. Southeastern Naturalist 3: 451–466.

Njiru, M., J. B. Okeyo-Owuor, M. Muchiri & I. G. Cowx, 2004. Shifts in the food of Nile tilapia, *Oreochromis niloticus* (L.) in Lake Victoria, Kenya. African Journal of Ecology 42: 163–170.

Parsons, J. K., A. Couto, K. S. Hamel & G. E. Marx, 2009. Effect of fluridone on macrophytes and fish in a coastal Washington lake. Journal of Aquatic Plant Management 47: 31–40.

Petr, T., 2000. Interactions Between Fish and Aquatic Macrophytes in Inland Waters: A Review. Food and Agriculture Organization of the United Nations, Rome.

Phillips, E. C., 2008. Invertebrate colonization of native and invasive aquatic macrophytes in Presque Isle Bay, Lake Erie. Journal of Freshwater Ecology 23: 451–457.

Ren, M. X. & Q. G. Zhang, 2009. The relative generality of plant invasion mechanisms and predicting future invasive plants. Weed Research 49: 449–460.

Rybicki, N. B. & J. M. Landwehr, 2007. Long-term changes in abundance and diversity of macrophyte and waterfowl populations in an estuary with exotic macrophytes and improving water quality. Limnology and Oceanography 52: 1195–1207.

Sammons, S. M. & M. J. Maceina, 2006. Changes in diet and food consumption of largemouth bass following large-scale hydrilla reduction in Lake Seminole, Georgia. Hydrobiologia 560: 109–120.

Savino, J. F. & R. A. Stein, 1989. Behavior of fish predators and their prey—habitat choice between open water and dense vegetation. Environmental Biology of Fishes 24: 287–293.

Shea, K. & P. Chesson, 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution 17: 170–176.

Shoup, D. E. & D. H. Wahl, 2009. The effects of turbidity on prey selection by piscivorous largemouth bass. Transactions of the American Fisheries Society 138: 1018–1027.

Simberloff, D. & B. Von Holle, 1999. Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1: 21–32.

Slade, J. G., E. D. Dibble & P. C. Smiley, 2005. Relationships between littoral zone macrophytes and the fish community in four urban Minnesota lakes. Journal of Freshwater Ecology 20: 635–640.

Sousa, W. T. Z., S. M. Thomaz & K. J. Murphy, 2010. Response of native *Egeria najas* Planch. and invasive *Hydrilla verticillata* (L.f.) Royle to altered hydroecological regime in a subtropical river. Aquatic Botany 92: 40–48.

Stiers, I., N. Crohain, G. Josens & Triest, L., 2011. Impact of three aquatic invasive species on native plants and macroinvertebrates in temperate ponds. Biological Invasions: 1–12. doi:10.1007/s10530-011-9942-9.

Strakosh, T. R., K. B. Gido & C. S. Guy, 2009. Effects of American water willow establishment on density, growth, diet, and condition of age-0 largemouth bass in Kansas reservoirs. Transactions of the American Fisheries Society 138: 269–279.

Strayer, D. L., 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55: 152–174.

Strayer, D. L., C. Lutz, H. M. Malcom, K. Munger & W. H. Shaw, 2003. Invertebrate communities associated with a native (*Vallisneria americana*) and an alien (*Trapa natans*) macrophyte in a large river. Freshwater Biology 48: 1938–1949.

Theel, H. J. & E. D. Dibble, 2008. An experimental simulation of an exotic aquatic macrophyte invasion and its influence on foraging behavior of bluegill. Journal of Freshwater Ecology 23: 79–89.

Theel, H. J., E. D. Dibble & J. D. Madsen, 2008. Differential influence of a monotypic and diverse native aquatic plant bed on a macroinvertebrate assemblage; an experimental implication of exotic plant induced habitat. Hydrobiologia 600: 77–87.

Thomaz, S. M., P. Carvalho, R. P. Mormul, F. A. Ferreira, M. J. Silveira & T. S. Michelan, 2009. Temporal trends and effects of diversity on occurrence of exotic macrophytes in a large reservoir. Acta Oecologica 35: 614–620.

Thorp, A. G., R. C. Jones & D. P. Kelso, 1997. A comparison of water-column macroinvertebrate communities in beds of differing submersed aquatic vegetation in the tidal freshwater Potomac River. Estuaries 20: 86–95.

Toft, J., C. Simenstad, J. Cordell & L. Grimaldo, 2003. The effects of introduced water hyacinth on habitat structure, invertebrate assemblages, and fish diets. Estuaries and Coasts 26: 746–758.

Troutman, J. P., D. A. Rutherford & W. E. Kelso, 2007. Patterns of habitat use among vegetation-dwelling littoral fishes in the Atchafalaya River Basin, Louisiana. Transactions of the American Fisheries Society 136: 1063–1075.

Valéry, L., H. Fritz, J.-C. Lefeuvre & D. Simberloff, 2008. In search of a real definition of the biological invasion phenomenon itself. Biological Invasions 10: 1345–1351.

Valley, R. D. & M. T. Bremigan, 2002a. Effects of macrophyte bed architecture on largemouth bass foraging: Implications of exotic macrophyte invasions. Transactions of the American Fisheries Society 131: 234–244.

Valley, R. D. & M. T. Bremigan, 2002b. Effects of selective removal of Eurasian watermilfoil on age-0 largemouth bass piscivory and growth in southern Michigan lakes. Journal of Aquatic Plant Management 40: 79–87.

Valley, R. D., M. D. Habrat, E. D. Dibble & M. T. Drake, 2010. Movement patterns and habitat use of three declining littoral fish species in a north-temperate mesotrophic lake. Hydrobiologia 644: 385–399.

Villamagna, A. M. & B. R. Murphy, 2010. Ecological and socioeconomic impacts of invasive water hyacinth (*Eichhornia crassipes*): a review. Freshwater Biology 55: 282–298.

Ward, D. M. & R. M. Newman, 2006. Fish predation on Eurasian watermilfoil (*Myriophyllum spicatum*) herbivores and indirect effects on macrophytes. Canadian Journal of Fisheries and Aquatic Sciences 63: 1049–1057.

Weaver, M. J., J. J. Magnuson & M. K. Clayton, 1997. Distribution of littoral fishes in structurally complex macrophytes. Canadian Journal of Fisheries and Aquatic Sciences 54: 2277–2289.

Wilson, S. J. & A. Ricciardi, 2009. Epiphytic macroinvertebrate communities on Eurasian watermilfoil (*Myriophyllum spicatum*) and native milfoils *Myriophyllum sibericum* and *Myriophyllum alterniflorum* in eastern North America. Canadian Journal of Fisheries and Aquatic Sciences 66: 18–30.