



Examination of the effects of largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) on the ecosystem attributes of lake Kawahara-oike, Nagasaki, Japan

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ABSTRACT

The introduction of largemouth bass (*Micropterus salmoides*) and bluegill sunfish (*Lepomis macrochirus*) into the freshwater ecosystems of Japan has resulted in the suppression and/or replacement of native species, generating considerable concerns among resource managers. The impacts of largemouth bass and bluegill on native fauna have been examined in aquaria and isolated farm ponds, but there is limited work examining the likelihood to fundamentally modifying Japan's lakes. The objective of the present study is to examine the direct and synergistic ecological effects of largemouth bass and bluegill on the biotic communities of Lake Kawahara-oike, Nagasaki, Japan, using an ecosystem (Ecopath) modeling approach. Specifically, we examine whether the two fish species have played a critical role in shaping the trophodynamics of the lake. We attempt to shed light on the trophic interactions between largemouth bass and bluegill and subsequently evaluate to what extent these interactions facilitate their establishment at the expense of native species. We also examine how these changes propagate through the Lake Kawahara-oike food web. Our study suggests that the introduction of bluegill has induced a range of changes at multiple trophic levels. The present analysis also provides evidence that largemouth bass was unable to exert significant top-down control on the growth rates of the bluegill population. Largemouth bass and bluegill appear to prevail over the native fish species populations and can apparently coexist in large numbers in invaded lakes. Future management strategies controlling invasive species are urgently required, if the integrity of native Japanese fish communities is to be protected.

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1. Introduction

Exotic species are organisms introduced to foreign habitats, and become invasive if they are able to outcompete native species for resources. The number of species transported across biogeochemical borders is expansive, but only a small fraction becomes established, and even fewer become pests (Mooney and Cleland, 2001). Successful invasions can fundamentally alter competitive interactions and reduce native populations within a community, and lead to extinction. Early conceptual models describing species invasions were built upon the premise that species-rich communities were more resistant to invasion than species-poor communities, due to more efficient use of limiting resources as well as the presence of competitors/predators to ward off potential invaders (Elton, 1958). This framework is labeled the *Biotic Resistance* model, and postulates that successive invasion attempts yield robust communities with stronger competitors, more efficient predators, and well-defended prey, reducing establishment rates

of invaders (Ricciardi, 2001). More recently, Simberloff and Von Holle (1999) challenged this notion and proposed the *Invasional Meltdown* hypothesis, stating that frequent species introductions may undermine community integrity via: i) continuous population disruptions, resulting in vulnerability to invasion, ii) established invaders modifying habitat conditions, facilitating subsequent invasions and creating a positive feedback loop. Simberloff and Von Holle (1999) highlight several terrestrial cases in which invaders facilitated subsequent invasions via mutualism, commensalism, and habitat modification. While the ecological underpinnings of successful invasions remain controversial (i.e., *Biotic Resistance* vs. *Invasional Meltdown*), it is generally accepted that the consequences of mixing formerly segregated biota are irreversible (Mooney and Cleland, 2001).

The impact of fish invasions is considered among the most pervasive threats to the integrity of native ecosystems (Dextrase and Mandrak, 2006; Eby et al., 2006; Grosholz, 2005; Schindler, 2001). Whether intentionally or not, fish species have been introduced to new habitats via aquaculture, recreation, ecological manipulations, control of unwanted organisms, and commercial shipping (Ferguson, 1990; Lintermans, 2004; Mills et al., 1994; Naylor et al., 2001). Although fish introductions were originally made with limited consideration of the environmental

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ramifications (Jackson, 2002; Magnuson, 1976), they currently represent a major ecological concern due to the overwhelmingly negative pressure exerted on native species (Carey and Wahl, 2010; Rahel, 2000; Ricciardi, 2007; Vander Zanden et al., 1999, 2008). Invasive fish species not only compete with other native predators, but also alter the abundance or induce behavioral changes in native prey species, thereby shaping inter-specific competition patterns and ultimately disrupting food web dynamics (Eby et al., 2006; Knapp, 2005; Rahel, 2002; Scott and Helfman, 2001).

Largemouth bass (*Micropterus salmoides*) and bluegill sunfish (*Lepomis macrochirus*) are native North American fish. Their popularity as sport fish has made them two of the most widely introduced fish species in the world. Largemouth bass has spread to over 50 countries, and is considered as one of the worst invasive fish species in the world (Lowe et al., 2000; Welcomme, 1992). Largemouth bass is a piscivorous top-down regulator that significantly modulates predation and competition patterns of native communities, and can therefore cause substantial changes in existing food webs (Azuma, 2002; Christensen and Moore, 2007; Whittier and Kincaid, 1999). Its predatory prowess can alter fish assemblage structures by reducing the abundance and diversity of small-bodied native littoral fish populations (Jackson, 2002; MacRae and Jackson, 2001; Shelton et al., 2008; Trumppickas et al., 2011). The bluegill is another widely introduced species (over 20 countries), characterized by an opportunistic behavior that can lead to aggressive dominance (Marchetti et al., 2004). Bluegill prefers eating the eggs and spawn of other fish, potentially altering native species composition and prey density (Bain and Helfrich, 1983; Mittelbach, 1988). Bluegill also feeds upon macro-invertebrates and large zooplankton, potentially enhancing the levels of phytoplankton biomass through the direct suppression of herbivorous grazing (Hambright et al., 1986; Nowlin and Drenner, 2000; Turner and Mittelbach, 1992). In addition, the predation pressure exerted by bluegill on native macro-invertebrates (e.g., Aeshnidae, Odonata) indirectly facilitates the survival of bullfrog tadpoles in their introduced habitat range (Adams et al., 2003). Bluegill also induces inter-specific competition with other centrarchids, e.g., pumpkinseed (*Lepomis gibbosus*), by exploiting similar refuges and food resources (Baca and Drenner, 1995; Hambright et al., 1986; Hill and Lodge, 1995; Werner and Hall, 1988). Moyle et al. (1995) showed that the introduction of bluegill continually threatened a number of native fishes species in the United States, e.g., California roach (*Lavinia symmetricus*), Sacramento perch (*Archoplites interruptus*).

Largemouth bass and bluegill were introduced in Japanese freshwater ecosystems to create or enhance sport-fishing opportunities in 1925 and 1960, respectively (Azuma, 1992). Subsequently, both species have proliferated into many ponds, lakes, and rivers (Ecological Society of Japan, 2002), dominating or replacing native species, which in turn posed serious concerns among resource managers and the public about the prospects of Japanese freshwater ecosystems. Because the assessment of the full-scale ecological consequences of introduced species is challenging (Byers et al., 2002), the potential impacts of bass and bluegill on native Japanese fauna have been examined mainly in aquaria or isolated farm ponds, where the focus lies on their long-term dietary patterns (Azuma, 1992; Azuma and Motomura, 1998; Katano et al., 2002, 2003, 2005), impacts on native biotic abundance (Maezono and Miyashita, 2003; Tsunoda et al., 2010; Yonekura et al., 2004), and potential trophic cascade effects (Maezono and Miyashita, 2003; Maezono et al., 2005). Yonekura et al. (2004) found that the mean number of native species in undisturbed ponds in Shiga, Japan was three times higher than invaded ponds, and observed a negative relationship between invasive and native fish abundance. The authors concluded that invasions by bluegill and largemouth bass depleted native fish communities, but argued that the successful invasions may have been facilitated in ponds with weak native species. In Saitama prefecture, Japan, Maezono and Miyashita (2003) found lower numbers of fish, crustaceans, and nymphal odonates in successfully invaded farm ponds. In

the same ponds, however, tadpoles, chironomids, chaoborids, and oligochaeta were more abundant. The authors asserted that these observations reflect a trophic cascade driven by bass predation. Maezono and Miyashita (2003) further concluded that the conservation of native organisms requires attention not only through monitoring of the direct negative effects of invaders, but also through the indirect effects propagating to various trophic levels.

In this study, our primary research objective was to quantify the direct ecological effects of largemouth bass and bluegill on native fish assemblages in Lake Kawahara-oike with the Ecopath with Ecosim (EwE) model. Our primary research objective is to examine the direct ecological effects of bass and bluegill on native fish assemblages in the lake. Specifically, we ask several critical questions regarding the role that either largemouth bass or bluegill played in the diversity loss among the native fish populations, such as: What types of interactions (positive/negative) are taking place between the invasive bass and bluegill? Are these interactions establishing invasive populations at the expense of native species? How do these perturbations propagate through the Lake Kawahara-oike food web? We also conduct a network analysis (flow indices, cycles and pathways) aiming to elucidate the ecosystem attributes (e.g., primary production/biomass, biomass/total throughput, connectance, system omnivory index) of the lake in its current state. We conclude by underscoring the importance of developing management strategies that can effectively prevent the proliferation of largemouth bass and bluegill, and thus control their broader environmental impacts.

2. Materials and methods

2.1. Study area

Lake Kawahara-oike is a small vegetated eutrophic lake with a 13-ha surface area and a maximum depth of 9 m, located in Nagasaki Peninsula at N32°37' E129°50', in western Japan (Fig. 1). Lake Kawahara-oike was originally a brackish lagoon, with the salt water removed from its hypolimnion in 1974, but subsequently became a partly isolated system, when a sluice gate between the lake and the sea was installed in 1979 (Azuma, 2002). Submerged vegetation covers about 20% of the lake area and organic debris derived from this vegetation accumulates at the outer edge of the littoral zone. There are 14 fish species out of which three are non-indigenous to the lake (Table 1). Among the native species, there are two dominant landlocked gobies: the trident goby (*Tridentiger obscurus*) and the paradise goby (*Rhinogobius giurinus*). Deep-bodied crucian carp (*Carassius cuvieri*) was introduced from a nearby water body to promote sport fishing in 1957, and bluegill was unintentionally introduced by an unknown person in 1972. Largemouth bass was subsequently introduced to the lake to biologically control bluegill, and revive the declining population of crucian carp in 1977 (Azuma and Motomura, 1998). Nonetheless, the introduction of largemouth bass failed to control the bluegill population, and the two species appear to have reached a state of stable coexistence in the lake (Azuma and Motomura, 1998). Gut content analysis revealed native fish species (gobies) to be the primary diet of the two invasive species (Azuma, 1992; Azuma and Motomura, 1998). Populations of many native fish species are continually declining, which is a worrisome pattern that may undermine the long-term stability of Lake Kawahara-oike's food web.

2.2. Modeling approach and design

2.2.1. Ecopath with Ecosim software

Ecopath with Ecosim (EwE) is a free suite of ecosystem modeling tools, consisting of three main components: Ecopath, which provides a static, mass-balanced snapshot of the system (Christensen and Pauly, 1992; Polovina, 1984); Ecosim, representing a time dynamic module for policy analysis (Walters et al., 1997); and Ecospace, a

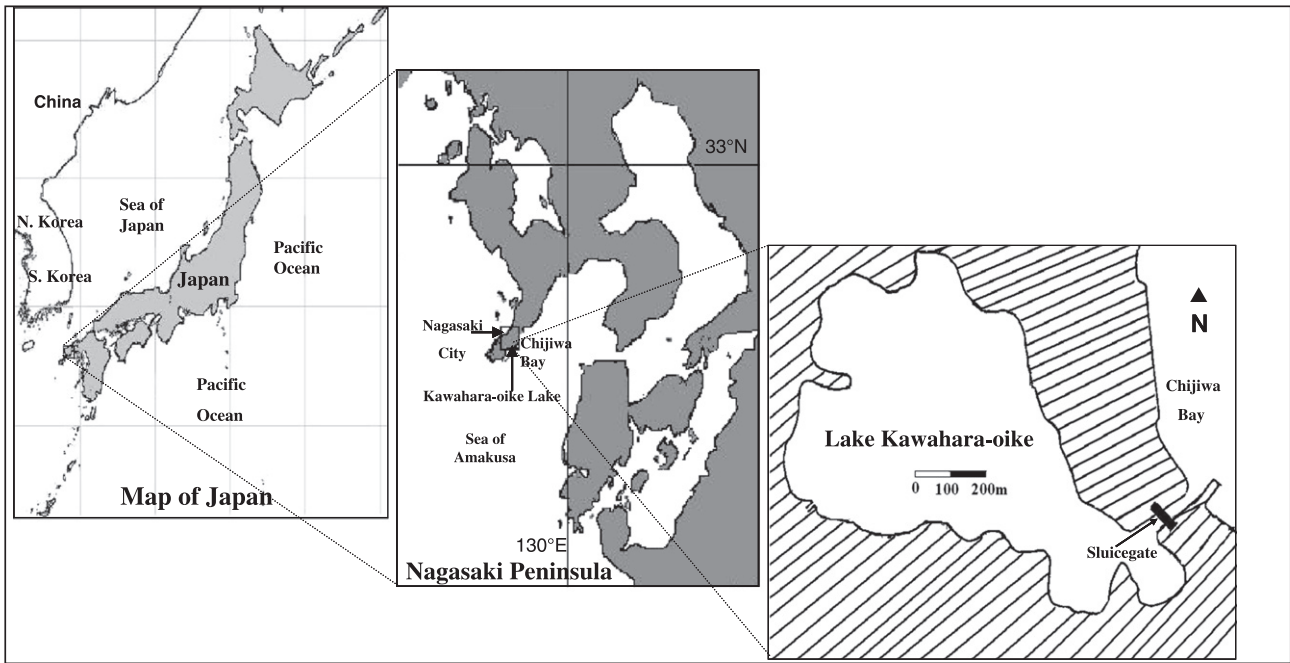


Fig. 1. Maps and location of Lake Kawahara-oike, Nagasaki, in western Japan.

spatial and temporal dynamic module aiming to delineate impacted sites (Pauly et al., 2000; Walters et al., 1999). *EwE* has been extensively used to examine ecosystem attributes, to evaluate ecosystem effects of fishing pressure, to analyze the impact of habitat restoration and the integrity of protected areas, to scrutinize the complex dynamics of invaded ecosystems, and to predict fate and transport of contaminants (*Ecotracer*) (Bondavalli et al., 2000; Feroz and Panikkar, 2009; Villanueva et al., 2008). The Ecopath model is founded upon a system of linear equations that express mass-balance over a given time period as follows:

$$B_i \cdot (P/B)_i \cdot EE_i = Y_i + \sum_{j=1}^n B_j \cdot (Q/B)_j \cdot DC_{ji} \quad (1)$$

where B_i is the biomass of the group i during the study period, $i = 1, \dots, n$ functional groups, $(P/B)_i$ is the production/biomass of group i

(equal to total mortality under the equilibrium assumption), EE_i is the ecotrophic efficiency (fraction of production consumed within the system or exported from it, including harvesting), Y_i is the fishing yield of the group i ($Y_i = F_i B_i$ where F_i is the fishing mortality rate), B_j is the biomass of the consumer j , $(Q/B)_j$ is the consumption/biomass of j , and DC_{ji} is the fraction of i in the diet of j . Eq. (1) expresses the steady-state model for each ecosystem component that guides the trophic flow analysis.

2.2.2. Model design

As previously mentioned, Lake Kawahara-oike is a partly isolated water body connected with the Chijiwa Bay through a narrow sluice gate; thus, the entries of particulate matter from the surrounding watershed represent the long-term import of material in the system. The model was parameterized to represent the average state of the ecosystem from 1999 to 2000. Although there are many interesting research questions related to ecosystem stability and resilience, Lake Kawahara-oike has not received adequate attention in the literature. Little is known about the food web structure or even the levels of the basic limnological variables (e.g., Secchi disc depth, nutrients, chlorophyll a). Our modeling analysis is the first attempt to compile all the existing empirical (often anecdotal) knowledge and get initial insights into the ecosystem functioning. The actual data used for the present analysis were the biomass estimates of the focal invasive species along with their diets, literature-based estimates of the production to biomass and consumption to biomass ratios, and educated guesses of the ecotrophic efficiency values. Because of the limited data availability, we opted for a model complexity that is commensurate to the empirical information from the system, and thus avoid building a complex construct that is profoundly overparameterized. This philosophy also underlies the design of our model, the conceptualization of the ecosystem structure, and the delineation of the fish functional groups considered.

Based on their ecological significance, the constituents of the Lake Kawahara food web were divided into 12 functional groups (see Table 2). The lower and mid-food web of the lake were represented by simple, aggregated entities, such as detritus, autotrophs, zooplankton, insects, and prawns. Both allochthonous particulate

Table 1
Fish species inhabiting Lake Kawahara-oike, Nagasaki, Japan.

No.	Common name	Scientific name	Comments
1	Largemouth bass	<i>Micropterus salmoides</i>	Alien in Japan and intentionally released into the lake in 1977
2	Bluegill	<i>Lepomis macrochirus</i>	Alien in Japan and intentionally released into the lake in 1972
3	Trident goby	<i>Tridentiger obscurus</i>	Native
4	Paradise goby	<i>Rhinogobius giurinus</i>	Native
5	Forktongue goby	<i>Gimnogobius arotaenia</i>	Native
6	Amur goby	<i>Rhinogobius brunneus</i>	Native
7	Common carp	<i>Cyprinus carpio</i>	Native
8	Silver crucian carp	<i>Carassius auratus langsdorfi</i>	Native
9	White crucian carp	<i>Carassius cuvieri</i>	Native in Japan but introduced into the lake from other water bodies of Japan before 1974.
10	Stone moroko	<i>Pseudorasbora parva</i>	Native
11	Dark chub	<i>Zacco temminckii</i>	Native
12	Japanese eel	<i>Anguilla japonica</i>	Native
13	Striped mullet	<i>Mugil cephalus cephalus</i>	Native
14	Medaka	<i>Oryzias latipes</i>	Native but nearly absent at present

matter and autochthonous detritus were represented by the “detritus” compartment in the model. The generic primary producers (i.e., phytoplankton, epiphytes, and macrophytes) were all labeled as “autotrophs”. All zooplankton species were aggregated into one single biotic compartment, labeled as “zooplankton”, assuming no fundamental differences in behavioral/dietary patterns. Benthic invertebrates and crustaceans fell under the label of “insects”, while “prawns” formed a separate group due to anecdotal evidence of significant presence in the system. The primary aim of the fish compartment was to provide a better delineation of native and non-native fish groups in the context of species invasion. Both largemouth bass and bluegill were treated as independent groups to identify their roles in the food web. Largemouth bass was subject to ontogenetic splitting, reflecting the changes in trophic positioning and bioenergetics with life stage. We assumed a complete ontogenetic shift in largemouth bass to take place when a threshold length of 300 mm is exceeded. Multi-stanza larger individuals are represented by “adults” and smaller ones by the “young of the year” (YOY) group. Major native species, such as the trident goby, paradise goby, and stone moroko (*Pseudorasbora parva*), were considered as distinct groups in the model. Low population fish species, e.g., common carp (*Cyprinus carpio*), silver crucian carp (*Carassius auratus langsdorfi*), white crucian carp (*C. cuvieri*), dark chub (*Zacco temminckii*), Japanese eel (*Anguilla japonica*), striped mullet (*Mugil cephalus*), and the nearly-extinct medaka (*Oryzias latipes*) were aggregated and labeled as “other fish”, although there may be dissimilarities with respect to their feeding behavior and feeding patterns. In the absence of empirical evidence, real verification of the model outputs cannot be performed, but the presented results can be used to form testable ecological hypotheses, to falsify some of the assumptions made, to dictate future data collection efforts, and to ultimately revisit/augment the model structure.

Table 2
Functional groups of the Lake Kawahara-oike ecosystem model, Nagasaki, Japan.

No.	Group name	Description
1	YOY largemouth bass	Largemouth bass (<i>Micropterus salmoides</i>) (<30 cm)
2	Adult largemouth bass	Largemouth bass (<i>Micropterus salmoides</i>) (>30 cm)
3	Bluegill	Includes only bluegill (<i>Lepomis macrochirus</i>) (all ages)
4	Paradise goby	Includes only paradise goby (<i>Rhinogobius giurinus</i>) (all ages)
5	Trident goby	Includes only trident goby (<i>Tridentiger obscurus</i>) (all ages)
6	Stone moroko	Includes only stone moroko (<i>Pseudorasbora parva</i>) (all ages)
7	Other fishes	Includes fork tongue goby (<i>Gimnogobius arotaenia</i>), amur goby (<i>Rhinogobius brunneus</i>), common carp (<i>Cyprinus carpio</i>), silver crucian carp (<i>Carassius auratus langsdorfi</i>), white crucian carp (<i>Carassius cuvieri</i>), dark chub (<i>Zacco temminckii</i>), Japanese eel (<i>Anguilla japonica</i>), striped mullet (<i>Mugil cephalus cephalus</i>), and medaka (<i>Oryzias latipes</i>)
8	Insects	Includes all types of aquatic insects [mainly <i>Sujiebi</i> (<i>Palaemon paucidens</i>), migratory terrestrial insects (mainly <i>Orthotrichia</i>)] and benthic invertebrates [mainly chironomidae larvae and trichoptera larvae]
9	Prawns	Includes all types of prawns [mainly atyid shrimps <i>Neocaridina denticulata</i> (DeHaan) and bryozoans, mainly <i>Lophopodella carteri</i> (Hyatt)]
10	Zooplankton	Includes all types of cladocera [mainly <i>Diaphanosoma brachyurum</i> (Lievin), <i>Daphnia longispina</i> (O. F. Müller), <i>Moina macrocopa</i> (Straus), and <i>Bosmina longirostris</i> (O. F. Müller)], copepoda [mainly <i>Neutrodiaptomus formosus</i> (Kikuchi)] and <i>Cyclops</i> spp.
11	Autotrophs	Includes all types of phytoplankton and submerged vegetations [mainly <i>Potamogeton Maackianus</i> (A. Bennet), <i>Vallisneria asiatica</i> (Miki), and <i>Egeria densa</i> (St. John)]
12	Detritus	Both exogenous and endogenous (biogenic) materials of the lake

2.3. Parameter estimation

2.3.1. Biomass estimation of the invasive alien fishes

Largemouth bass biomass estimates were derived from population estimates using the Schumacher and Eschmeyer method (Ricker, 1975).

$$N = \frac{\sum_{d=1}^n C_d M_d^2}{\sum_{d=1}^n R_d M_d} \quad (2)$$

where N is population estimate (numbers of fish); $C_d = U_d + R_d$ = total number of fish caught on day d ; U_d is the number of unmarked fish caught on day d ; R_d is the number of recaptures on day d (of the type of mark under consideration); M_d is the number of marked fish available for recapture at start of day d ; and n represents the total number of sampling days.

The biomass estimates of bluegill were derived from population estimates using Chapman’s modification of the Petersen estimator (Ricker, 1975).

$$N = (M + 1)(C + 1)/(R + 1) \quad (3)$$

where N is the population estimate (number of fish); M is the number of fish caught, marked and released in the first sample; C is the total number of fish caught in the second sample (unmarked + recaptures); R is the number of recaptures in the second sample (of fish marked and released in first sample). Population estimates of largemouth bass were based on the seine net and lure surveys conducted from 1988 to 1993, while the bluegill estimates were based on the seine net surveys carried out from 1988 to 1998.

2.3.2. Production and consumption rate estimation

The production rate (P/B) of invasive alien fish species was estimated using the following equation (Beverton and Holt, 1957):

$$P/B = \frac{K(L_\infty - \bar{L})}{\bar{L} - L_c} \quad (4)$$

where L_∞ and K are parameters of the von Bertalanffy’s growth: $L_t = L_\infty (1 - e^{-K(t-t_0)})$, L_c is the minimum body length in the catch, and \bar{L} is the average body length of catch. The parameters of von Bertalanffy’s growth function were estimated from the length measurements of the monthly samples collected with seine nets between 1988 and 1999. The peaks of the length frequency were assumed to be the average of a year-class population, and nonlinear optimization was used to fit the growth curve to the observed data. The hatching day was assumed to be April 1st.

Consumption rate (Q/B) of the fish species was estimated using the following empirical relationships (Palomares and Pauly, 1998):

$$\log(Q/B) = 7.964 - 0.204 \log W_\infty - 1.965T' + 0.083A + 0.532h + 0.398d \quad (5)$$

$$W_\infty = aL^b \quad (6)$$

where W_∞ is a parameter of the von Bertalanffy weight growth function; T is an expression for the mean annual temperature of the water body, expressed using $T' = 1000/\text{Kelvin}$ (Kelvin = °C + 273.15); A is the aspect ratio of the caudal fin which is closely related to the average level of activity and is calculated from $A = l^2/s$, where l is the height of the caudal fin and s is the surface area; h and d are dummy parameters, where $h = 1$ for herbivorous groups and $d = 1$ for detritus feeders (otherwise h and d were set equal to zero). For Lake Kawahara-oike, T was set as 19 °C (Matsuyama and Hirota, 1985), and $A = 2.0$ and

Table 4
 Ecopath outputs for the Lake Kawahara-oike ecosystem model. TL is the trophic level, B is biomass ($t\ km^{-2}$), P/B is the production rate (yr^{-1}), Q/B is the consumption rate (yr^{-1}), EE is the ecotrophic efficiency, P/Q is the production/consumption ratio, R/A is the ratio of respiration to assimilation, P/R is the ratio of production to respiration, FD is the flow to detritus ($t\ km^{-2}\ yr^{-1}$), NE is the net efficiency, and OI is the omnivory index.

Group name	TL	B	P/B	Q/B	EE	P/Q	R/A	P/R	FD	NE	OI
YOY largemouth bass	3.51	0.0031	2.55	21.77	0.05	0.12	0.85	0.17	0.03	0.15	0.48
Adult largemouth bass	3.90	0.019	1.68	8.25	0.01	0.20	0.75	0.34	0.06	0.25	0.28
Bluegill	2.62	0.437	1.74	10.51	0.13	0.17	0.79	0.26	1.58	0.21	0.52
Paradise goby	3.10	0.138	1.50	19.69	0.98	0.08	0.91	0.11	0.55	0.10	0.11
Trident goby	3.23	0.155	1.57	19.17	0.98	0.08	0.90	0.11	0.60	0.10	0.10
Stone moroko	3.20	0.010	1.55	13.97	0.90	0.11	0.86	0.16	0.03	0.14	0.00
Other fishes	2.89	0.239	1.70	10.53	0.95	0.16	0.80	0.25	0.54	0.20	0.28
Insects	2.22	0.126	68.00	200.00	0.95	0.34	0.58	0.74	5.46	0.43	0.19
Prawns	2.33	1.422	2.70	26.00	0.95	0.10	0.87	0.15	7.59	0.13	0.26
Zooplankton	2.02	0.234	65.00	277.00	0.95	0.23	0.71	0.42	13.71	0.29	0.02
Autotrophs	1.00	0.183	470.90	–	0.95	–	–	–	4.22	–	–
Detritus	1.00	2.000	–	–	0.88	–	–	–	0.00	–	0.23

Note: Numbers in bold font represent model outputs.

lake. Gross food efficiency values (production/consumption or P/Q) were physiologically realistic as suggested by Christensen et al. (2005), falling within the range of 0.1 – 0.3 for most consumers. Insects demonstrate the highest P/Q value (0.34) for all the biotic compartments considered. Based on our prior calculations, the two native goby groups yielded the lowest P/Q ratios (0.08), and a similarly low value (0.12) also characterized the YOY largemouth bass. Among the fish groups, the highest P/Q ratio was estimated for adult largemouth bass (0.20), and a fairly high P/Q ratio was also estimated for bluegill (0.17).

The omnivory index (OI) was calculated as the variance of the trophic level of a consumer's prey items (see Table 4). Large values indicate a consumer that feeds upon many trophic levels, while low values are indicative of food specialization. Stone moroko had an OI of 0.01, as this fish almost exclusively feeds on insects (see Table 3). Likewise, both paradise goby and trident goby had low OI values (0.12 and 0.10,

respectively), suggesting high specialization in their feeding habits. The highest OI values were obtained for the three groups of invasive alien species: bluegill, YOY largemouth bass and adult largemouth bass (0.54, 0.48, and 0.28, respectively), indicating multi-trophic level feeding strategies. The same inference can also be drawn for prawns and the “other fishes” group. Trophic linkages between adult largemouth bass and bluegill are shown in Fig. 3, providing evidence that the two groups are ecologically significant and important to the flow of energy through the lake ecosystem. Adult largemouth bass have no predators of their own in the system, and have relatively strong feeding interactions with the native gobies and bluegill (Fig. 3A). The largest food sources for bluegill are autotrophs, prawns, zooplankton, and detritus (Fig. 3B), while some predatory stress is exerted by largemouth bass. The latter trophic linkages suggest the likelihood of a “wasp-waist” pattern in the system (Madigan et al., 2012), although

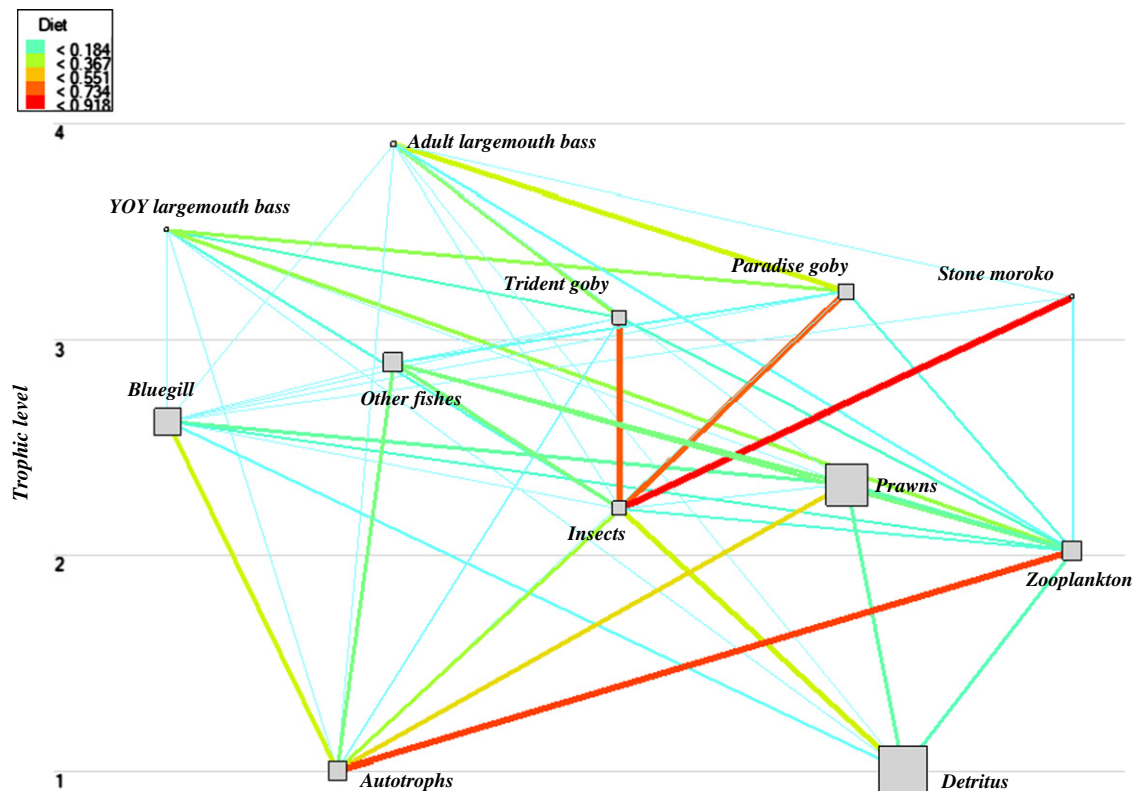


Fig. 2. The Ecopath outputs based on the Lake Kawahara-oike food web conceptualization. Thickness and color of the lines illustrate the magnitude of the flow rates. The vertical line demonstrates the functional trophic level (TL) of each biotic compartment. The estimated abundance values of the modeled groups are also displayed.

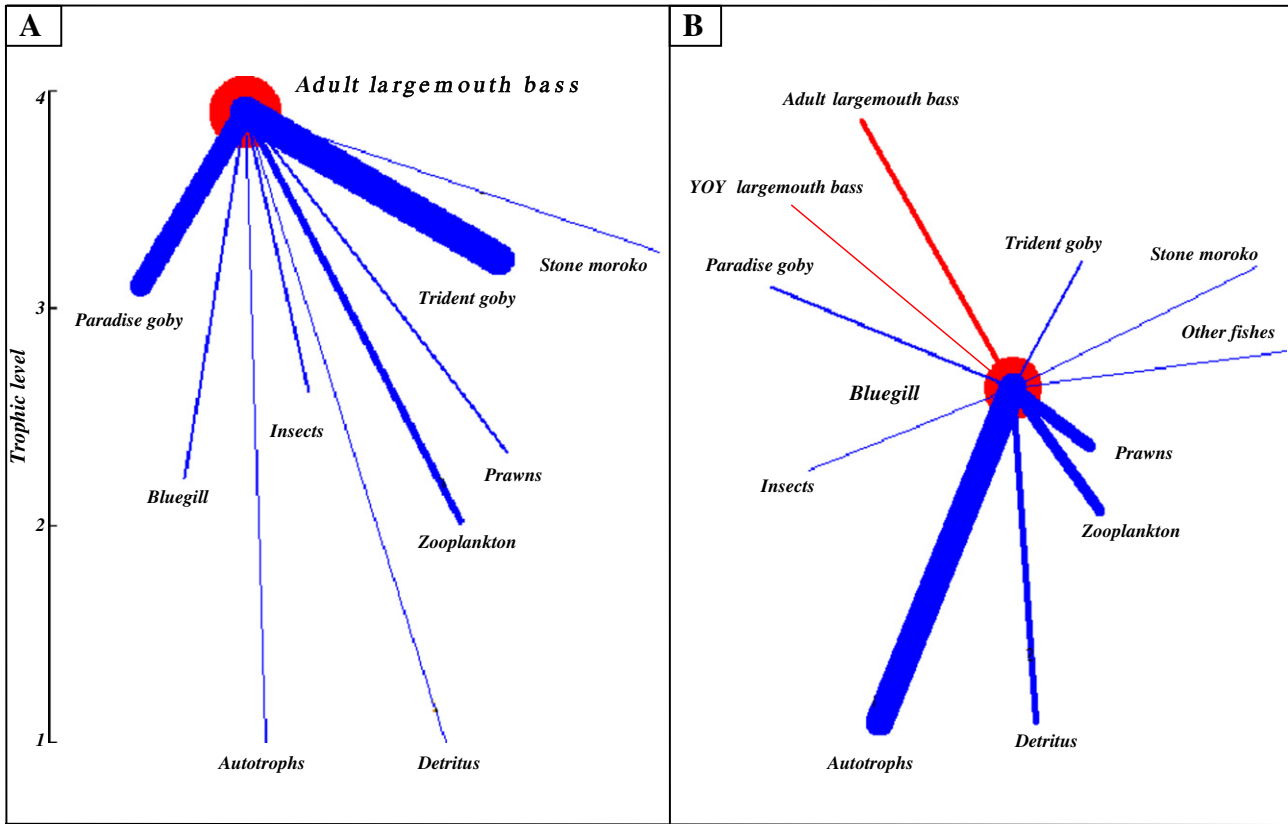


Fig. 3. Trophic interactions related to (A) largemouth bass and (B) bluegill. The relative width of each connection indicates its magnitude. Blue lines indicate prey species and red lines indicate predators. The trophic level of each group in the model is indicated by the Y-axis.

the limited empirical information along with the simple food web structure considered by our Ecopath exercise disallows consolidating this hypothesis.

Lake Kawahara-oike is a primary producer-based ecosystem, in which 71% of the total energy flow associated with the first trophic level stems from the autotrophs and only 28% originates from detritus (Table 5). Autotrophs are consumed by all groups (except from stone moroko), while detritus is mainly consumed by insects, prawns and zooplankton (see Table 3). Zooplankton dominates the flow of energy at the herbivore/detritivore level (II) (56%), followed by prawns (23%), and insects (17%). Insects, prawns, gobies, and other fish dominate the first-order carnivore level (III). The fourth trophic level primarily comprises energy flows associated with native gobies and bluegill, and to a lesser extent with largemouth bass. The geometric means of

Table 5
Trophic transfer matrix of Lake Kawahara-oike ecosystem model showing the distribution of flows ($t\ km^{-2}\ yr^{-1}$) by groups and trophic levels.

Group	Trophic level				
	I	II	III	IV	<V
YOY largemouth bass	–	0.01	0.04	0.033	
Adult largemouth bass	–	0.01	0.03	0.093	
Bluegill	–	2.50	1.45	0.523	
Paradise goby	–	0.20	1.97	0.391	
Trident goby	–	0.08	2.12	0.579	
Stone moroko	–	–	0.12	0.025	
Other fishes	–	0.61	1.50	0.287	
Insects	–	19.46	4.46	0.349	
Prawns	–	25.42	9.84	0.968	
Zooplankton	–	61.96	1.24	0.025	
Autotrophs	84.40	–	–	–	
Detritus	34.13	–	–	–	
Total	118.53	110.25	22.77	3.273	0.399

the transfer efficiencies of the flows originating from detritus and the primary producers through the trophic levels II–IV, calculated as the ratio between the sum of the exports from a given trophic level, plus the flow that is transferred from the trophic level to the next, and the throughput on that trophic level, were approximately 14.8% and 14.9%, respectively (Table 6).

Key ecosystem attributes and flows quantified by Ecopath are shown in Table 7. The sum of all consumption and all respiratory flows in the system were estimated to be 137 and 81 $t\ km^{-2}\ yr^{-1}$, respectively. We obtained a total system throughput (sum of consumption, export, flows to detritus, and respiration) of 256 $t\ km^{-2}\ yr^{-1}$, which represents the “size of the entire system in terms of flow” (Ulanowicz, 1986). Total biomass (excluding detritus) was calculated as 2.91 $t\ km^{-2}$, which is greater than the corresponding Ecopath estimate derived for the oligotrophic Lake Toya located in northern Japan (Hossain et al., 2010). The primary production/total biomass ratio was fairly high (29.04 yr^{-1}), indicating gradual biomass accumulation over time. Total biomass/total throughput is expected to increase as an ecosystem matures, and thus

Table 6
Transfer efficiency at various TLs showing the contribution of detritus and primary production to the Lake Kawahara-oike trophic network.

Sources	TL				
	II	III	IV	<V	
Producer	19.9	14.7	11.3		7.4–9.4
Detritus	22.6	13.6	10.5		5.4–8.9
All flows	20.7	14.4	11.0		7.2–9.3

Note: Proportion of total flow originating from detritus: 0.28.
Transfer efficiencies (calc. as geometric mean for TL II–IV):
Primary producers: 14.9%.
Detritus: 14.8%.
Total: 14.9%.

Table 7
Ecosystem indicators describing the Lake Kawahara-oike ecosystem structure.

Parameter	Values	Units
Sum of all consumption	136.69	t km ⁻² yr ⁻¹
Sum of all exports	4.06	t km ⁻² yr ⁻¹
Sum of all respiratory flows	80.84	t km ⁻² yr ⁻¹
Sum of all flows into detritus	34.13	t km ⁻² yr ⁻¹
Total system throughput	256.00	t km ⁻² yr ⁻¹
Sum of all production	112.00	t km ⁻² yr ⁻¹
Calculated total net primary production	84.40	t km ⁻² yr ⁻¹
Total primary production/total biomass	29.04	yr ⁻¹
Net system production	3.56	t km ⁻² yr ⁻¹
Total biomass (excluding detritus)	2.91	t km ⁻²
Total primary production/total respiration	1.04	
Total biomass/total throughput	0.011	yr ⁻¹
Connectance Index	0.471	
System Omnivory Index	0.201	

the low value (0.01) obtained from our analysis is indicative of a system undergoing its early developmental stages (Odum, 1969). In a similar manner, the fairly low connectance (0.47) and system omnivory index (0.20) values suggest a linear rather than “web-like” food chain structure. In stark contrast though, the estimated ratio of total primary production to total respiration is close to 1, reflecting a system in which the energy fixed tends to be balanced by the total energy cost of maintenance (community respiration).

The total ascendancy of the system (206 flow bits) primarily consists of the internal flows (118 flow bits or 10.9% of the total fluxes in the system), followed by a 6.9% of respiration and a 1.1% of export (Table 8). Notably, the internal redundancy (i.e., the overhead on the internal flow) and the system overhead are fairly high (81% of the development capacity) indicating that Lake Kawahara possesses substantial reserves to overcome unexpected external perturbations. The latter result is not surprising, given that the system has been subjected to disturbances due to the invasion of exotic species, and thus highly organized flow is unlikely to have developed. We also estimated that about 10% (Finn's cycling index) of the ecosystem's throughput is recycled (Table 9), and the average number of groups that an inflow or outflow passed through was 3.01 (Finn's mean path length). Both measures also indicate that Lake Kawahara-oike is probably an immature and relatively simple system (Christensen, 1995).

The mixed trophic impact (MTI) routine (Ulanowicz and Puccia, 1990) included in *EwE* illustrates the direct and indirect influences of one group to another (Fig. 4). Bluegill and (secondarily) adult largemouth bass have distinctly negative impact on almost all fish groups modeled. Our analysis also revealed that YOY largemouth bass has a negligible impact on the abundance and the composition of the fish community. The two gobies are preyed upon by invasive alien fish groups, and thus exhibit a positive influence on them, whereas their competition with the rest of the fish groups considered for the same food resources is manifested as a negative direct impact. Conversely, stone moroko have almost no effects on any group due to their small population biomass. Among the benthic groups considered, insects exert positive control on most fish functional groups. By contrast, prawns negatively impact most fish groups, with a notable exception in their weakly positive association with bluegill and the functional

Table 8
Totals of flux indices for the Lake Kawahara-oike ecosystem model.

Source	Ascendancy		Overhead		Capacity	
	Flowbits	%	Flowbits	%	Flowbits	%
Imports	1.5	0.1	3.0	0.3	4.5	0.4
Internal flow	118.2	10.9	636.9	58.9	755.0	69.9
Export	11.8	1.1	12.5	1.2	24.3	2.2
Respiration	74.2	6.9	222.8	20.6	297.0	27.5
Totals	205.7	19.0	875.2	81.0	1080.8	100.0

Table 9
Cycling and path lengths for the Lake Kawahara-oike ecosystem model.

Cycles and pathways	Values	Units
Throughput cycled (excluding detritus)	4.33	t km ⁻² yr ⁻¹
Predatory cycling index	2.36	% of throughput without detritus
Throughput cycled (including detritus)	24.03	t km ⁻² yr ⁻¹
Finn's cycling index	9.62	% of total throughput
Finn's mean path length	3.01	
Finn's straight-through path length	2.26	Without detritus
Finn's straight-through path length	2.72	With detritus

group “other fish”. The latter result likely reflects their role as a staple in the diets of the two groups (see Table 3). MTI analysis provides evidence that the compartments at the base of the food web, such as autotrophs and detritus, positively affect nearly all groups. The negative impact of the biomass increase of the autotrophs on their own group partly reflects the constraints imposed by the finite carrying capacity of the studied system and the potential ramifications on resource consumption. Another factor may be the increase of the zooplankton biomass which subsequently accentuates the herbivorous pressure on phytoplankton (e.g., boom and bust cycles). The decline of the autotrophic biomass production subsequently impacts the amount of biogenic detritus available in the system.

The measure of the model quality obtained through the pedigree index routine of *EwE* was 0.438, indicating that the model foundation is somewhat closer to literature-based than local information. To put this value into a broader context, we note that the Lake Kawahara-oike ecosystem model falls into the higher pedigree range (0.400–0.599) of Morissette's (2007) categorization, as developed by the evaluation of 50 balanced Ecopath models. Our sensitivity analysis showed that two of the major sources of uncertainty are i) the biomass estimates of the invasive alien species, and ii) the ecotrophic efficiency values assigned to stone moroko, other fish, insects, and zooplankton (see Fig. 5; detailed sensitivity analysis results are presented in Tables SI-1 to SI-10 in the Supporting information section).

4. Discussion

Both largemouth bass and bluegill have been introduced to many regions of the world due to their angling potential. Lake Kawahara-oike is one of the many freshwater systems in Japan, where the two species appear to have reached a state of stable co-existence (Azuma, 1992). While largemouth bass is piscivorous and bluegill omnivorous, with a bias towards carnivory and oophagy, both species have flexible feeding habits and readily adapt to new environments. Upon introduction, spawning and growth rates of largemouth bass and bluegill often surpass those of indigenous fish, resulting in increased abundance and gradual predominance in invaded systems (Jackson, 2002; Nishizawa et al., 2006; Welcomme, 1992). Despite their potential to alter habitat biodiversity and food web structure (Julien and Julian, 2011; Vander Zanden et al., 1999; Whittier and Kincaid, 1999), the literature lacks studies focusing on the ramifications of largemouth bass and bluegill stocked together outside their native ranges. In the present study, we used Ecopath modeling to elucidate the trophic interactions among biotic communities of the invaded Lake Kawahara-oike food web. Acknowledging the deficiency of the available information as well as the uncertainties associated with any modeling endeavor (Arhonditsis and Brett, 2004; Arhonditsis et al., 2006; Hossain et al., 2010), the present analysis primarily focused on the characterization of the basic ecosystem attributes, and the identification of the most important causal connections underlying the local trophodynamics. However, even for exploratory-type of applications like ours, we caution that the overparameterized character of any Ecopath exercise implies multiple ways to balance a model, and thus multiple ecosystem conceptualizations based on the same initial data (Essington, 2007).

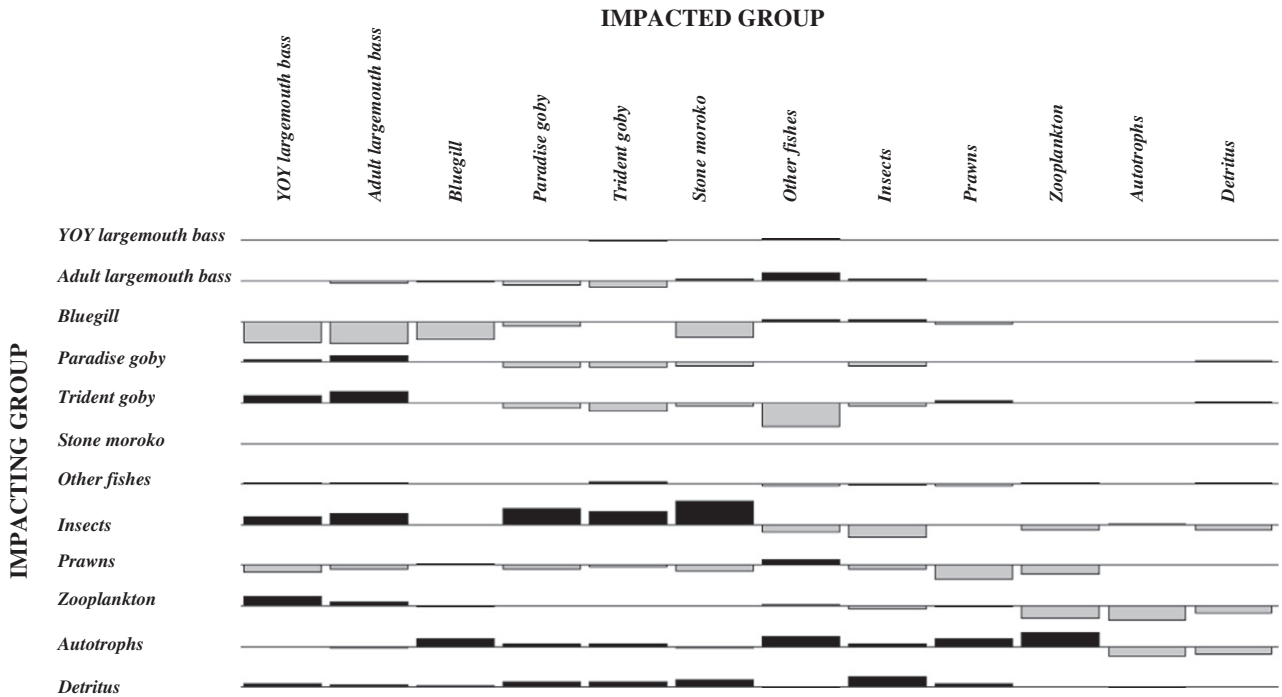


Fig. 4. The mixed trophic impact analysis of the Lake Kawahara-oike ecosystem model. Impacting and impacted groups are placed along the vertical and horizontal axis, respectively. Gray and black bars represent direct and indirect impact. The bars pointing upwards indicate positive impacts, while the bars pointing downwards show negative impacts. The bars should not be interpreted in an absolute sense: the impacts are relative, but comparable between groups.

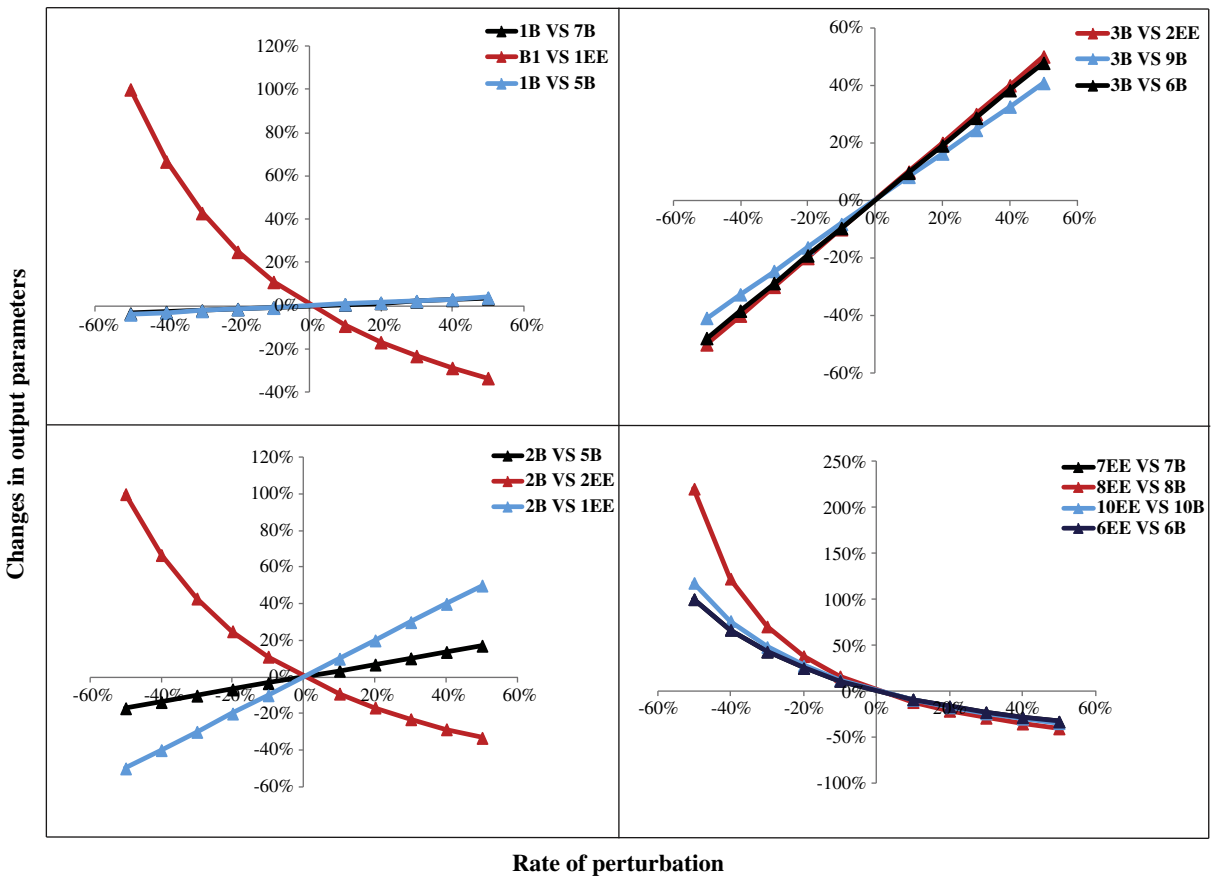


Fig. 5. Sensitivity analysis of the biomass values (B) assigned to (upper left panel) YOY largemouth bass (1), (lower left panel) adult largemouth bass (2), (upper right panel) bluegill (3), and (lower right panel) the ecotrophic efficiency (EE) values assigned to stone moroko (6), other fish (7), insects (8), and zooplankton (10). Numbers (5) and (9) correspond to the functional groups trident goby and prawns (see Table 2). X-axis shows the rate of perturbation and Y-axis shows the rate of change of the model outputs.

Many *EwE* applications have attempted to quantify the effects of different management actions and/or external perturbations (nutrient loading, fishing pressure, invasive species) through the relative values of metrics characterizing community energetics and structure, life histories, nutrient cycling, selection pressure, and homeostasis (Odum, 1969). The basic underlying principle is to characterize the stage of ecosystem development (mature or immature), which in turn may allow delineating the potential impact of external forcing factors and thus offer insights into the system stability (Fayram et al., 2006). Although the relationship between maturity and stability has been a controversial issue (Perez-Espana and Arreguin-Sanchez, 2001; Tilman, 1996; Ulanowicz, 1997), it is generally understood that mature ecosystems possess greater stability and therefore greater resilience, resistance, or persistence to overcome external perturbations (*sensu* Ulanowicz, 1997). In our study, several ecosystem bioenergetics such as primary production/biomass, biomass/total throughput, Finn's recycling index, Finn's mean length, connectance, and system omnivory index provided evidence that Lake Kawahara-oike experiences its early developmental stage with a linear food chain structure. Counter to this finding though, the estimated production to respiration ratio was close to unity (1.04), reflecting a system in a nearly mature stage based on Odum's (1969) specification. Putting this metric into perspective, the ratio between total primary production and total respiration falls within the second lowest range (0.8–1.6) of Christensen and Pauly's (1993) classification scheme (see their Table 2, pg. 341). Interestingly, our model parameterization assigned fairly low production to consumption values to prawns (0.10), implying that the consumption of the group is about 10 times higher than their production. Given that the same group was estimated to have excessively high areal biomass (1.422 t km^{-2}), we believe that the original assumptions made about its P/B and Q/B values predominantly drive our total primary production to respiration value. Notably, the P/B value of our autotrophic functional group (471 yr^{-1}) more closely resembles a phytoplankton rather than macrophyte characterization (Hossain et al., 2012; Milessi et al., 2010), and thus our analysis is unlikely to understate the primary production rates typically experienced in the current state of Lake Kawahara-oike.

Other indicators of mature ecosystems are the increased nutrient/energy recycling, and the high number of effective pathways a unit of (energy or nutrient) flow is passing through on its way from inflow to outflow (Vasconcellos et al., 1997). In the present study, our estimates fall within the Finn's cycling index vs. mean path length relationship reported by Christensen and Pauly (1993; see Fig. SI-1). In a similar manner, our results are marginally on par with the Finn's cycling index vs. primary productivity/respiration, although the mean trajectory postulated by the 41 ecosystem models compiled by Christensen and Pauly (1993) suggests a primary productivity to respiration ratio between 2 and 3 (Fig. SI-2). Our analysis also predicts a high system overhead (81%) suggesting that the lake possesses substantial reserves to overcome external disturbances. The latter result differs from the findings of Aoki (1995) and Fayram et al. (2006), and appears to contradict the general notion of a positive correlation between system maturity and stability. However, our study is not the first to report a relatively high system overhead ratio, counter to the evidence of an immature and relatively simple system (e.g., Hossain et al., 2010, 2012; Yunkai-Li et al., 2008). Moreover, our predictions for the system overhead–Finn's cycling index pair are fairly consistent with Christensen and Pauly's (1993) parabolic relationship (see their Fig. 6). In particular, Lake Kawahara-oike falls close to the upper end of the steepest segment, where the system overhead increases rapidly with the cycling until it levels off at an approximate cycling value of 12–15%. Our results are also in agreement with Vasconcellos et al.'s (1997) assertions that recycling is critical in modulating ecosystem stability, and thus systems with a high capacity to recycle particulate matter are more resilient to external perturbations. Similarly, Perez-Espana and Arreguin-Sanchez (2001) argued that there is an inverse relationship between ecosystem stability and maturity, where immature systems are relatively more

stable than complex systems. This argument is contrary to the historical hypothesis that the degree of stability increased with system maturity.

Both laboratory and small-scale field experiments found complex interactions between largemouth bass and bluegill when stoked together (Shoup et al., 2007). Bluegill typically feed upon zooplankton (e.g., daphnia, chydorids, and other cladocerans) and benthic macroinvertebrates (e.g., amphipods, chironomids, odonates, and gastropods) (Dewey et al., 1997). Using suitable refugia, bluegill has the capacity to minimize predation risks and optimize their foraging benefits. In the presence of largemouth bass, bluegill reduces large zooplankton and native fish species abundance, while boosting smaller zooplankton taxa, turbidity, nutrients, and phytoplankton (Lazzaro et al., 1992; Leibold, 1991; Yonekura et al., 2004). Our Ecopath analysis indeed provided a low *EE* value (0.17) for bluegill, indicative of limited predation pressure as well as fishing activity in the system. The dense macrophytes in the lake may adversely impact the foraging efficiency of largemouth bass on bluegill, as they are highly visual piscivorous predators (Kawamura and Kishimoto, 2002; Takamura, 2007). We hypothesize that the bluegill may have chosen to reside in the densely vegetated, large littoral zone to avoid the predatory largemouth bass. In addition, the empty niche space in the littoral zone may serve as a large grazing ground for juvenile bluegill, significantly enhancing their growth rates and thus increasing the likelihood of their survival in Lake Kawahara-oike.

A thriving bluegill population potentially reduces resource availability for native species (e.g., gobies and medaka), thereby suppressing their growth and productivity rates in the lake. The high omnivory index (0.54) for bluegill, yielded by our modeling analysis, reflects their large feeding spectrum and flexible foraging behavior. This finding is also on par with earlier work on bluegill diets, in which their feeding preferences and ontogenetic dietary shifts follow the sequence: planktivory–insectivory–shrimp eating–piscivory (Azuma, 1992; Dewey et al., 1997). Our MTI analysis highlights the negative impact of bluegill on most fish species (e.g., paradise goby, and stone moroko) in the system, which in turn renders support to the hypothesis that the bluegill success is achieved at the expense of native fish communities through competition for empty niche spaces and food resources (e.g., benthos, zooplankton) in the lake. If we also consider that largemouth bass becomes mainly piscivorous when they reach the adult stage, while the bluegills are more inclined to feed on autotrophs and prawns (see Table 3), the same interplay between bass' prey items and bluegill can conceivably explain their negative impact on the top predators in the system. Because of bluegill's adaptability and potential to exhibit both surface- and bottom-feeding, native species (e.g., stone moroko) are outcompeted for food and shelter, and thus the gradual reduction of niche space impairs their ability to mitigate successful invasions (Fridley et al., 2007; Ricciardi, 2001). An additional facet of bluegill's flexible foraging behavior is the capacity to be a controlling agent of the benthic and zooplankton community of the lake. In particular, the latter result underscores the likelihood of bluegill to modulate zooplankton dynamics in the system, and thus alleviate the grazing pressure on phytoplankton.

Counter to the notion that the introduction of largemouth bass can constrain the bluegill proliferation, our analysis suggests that bass has induced neither significant top-down effects, nor did it serve as a major determinant for bluegill community structure in Lake Kawahara-oike. Largemouth bass seems to have been preying on native species (i.e., trident goby and paradise goby), and the early ontogenetic shift from planktivory to piscivory has apparently increased their predation ability on gobies over bluegill (Azuma and Motomura, 1998; Katano et al., 2005; Takamura, 2007). Our MTI analysis reinforces the latter assertion, and the native gobies remain important contributors to the diets of largemouth bass in Lake Kawahara-oike. Largemouth bass (TL = 3.90) and bluegill (TL = 2.62) appear to have directly (or indirectly) mediated strong trophic cascade effects, although their impact varies significantly in that some species are still playing a critical role in the system (trident goby, paradise goby) while other

populations have declined (stone moroko, dark chub) or even went extinct (medaka). In addition to the predation pressure from invasive alien species, the entry of the Japanese eel and striped mullet through the sluice gate likely represents an additional stress factor to native fish species, as it further intensified the resource competition in the system (Azuma, 2002).

Primary production, nutrient levels, and turbidity in aquatic ecosystems can be altered by invasive species that use resources more efficiently or eliminate prominent life forms (Dukes and Mooney, 2004). McQueen et al. (1986) hypothesized, however, that top-down food web effects are felt strongest at the top of the food web and dissipate at lower trophic levels. Likewise, our analysis suggests that the extent to which bluegill and largemouth bass alter the lower food web and the primary productivity of the invaded Lake Kawahara-oike remains unclear and requires further investigation (see our MTI analysis in Fig. 4). While studying the top-down effects of largemouth bass in shallow pond ecosystems, Nowlin et al. (2006) did not find any evidence of cascading impacts down to the phytoplankton community, nor did they observe a significantly higher zooplankton density in the presence of the piscivorous largemouth bass. Contrary to Nowlin et al. (2006), several studies suggest that top-down pressure exerted by introduced piscivores may result in altered phytoplankton species composition, but leave total biomass unaffected (e.g., Benndorf et al., 2002; Drenner et al., 2002; Tremmel et al., 2001). The coexistence of invasive species can occlude direct impacts on primary production and abiotic conditions. For example, Maezono et al. (2005) report complex interactions among largemouth bass, bluegill, and invasive crayfish. Crayfish are shredders that can severely reduce macrophyte biomass, indirectly impacting phytoplankton, zooplankton, and juvenile fish (Nystrom et al., 2001; Gutiérrez-Yurrita et al., 1998). Removal of largemouth bass releases crayfish and suppresses macrophyte biomass, which in turn reduces refugia from fish predation (Crowder and Cooper, 1982), oviposition sites (Takasaki, 1994), and spatial niches that can potentially enable the stable coexistence of multiple species (Crowley and Johnson, 1982).

In conclusion, the basic lessons learned from the present Ecopath analysis reinforce empirical or anecdotal information from the system that:

- The introduction of bluegill and largemouth bass has likely altered the Lake Kawahara-oike food web, but not all native fish have responded in a similar way. The extent to which the native biotic community has been impacted depends on the nature of the pre-invasion trophodynamics. The lack of time series data for the lake though limits our ability to show direct evidence of said ecosystem changes. An interesting exercise originating from our study is the verification of the biomass of the two exotic species relative to the total fish biomass in the system.
- Our results have also demonstrated that largemouth bass and bluegill can coexist at the expense of native species abundance. The apparent paradox of the limited predation effects of largemouth bass on bluegills is likely due to the high macrophyte density as well as the availability of native prey fishes in Lake Kawahara-oike. The dense macrophytes may not only enhance bluegill's survival success by providing increased refugia and food sources (Azuma, 1992), but also adversely impact the foraging efficiency of largemouth bass due to its reliance upon visual cues (Takamura, 2007); the latter pattern could also be accentuated by the increasing eutrophication in the system.
- Our analysis also highlights the role of native gobies in Lake Kawahara-oike, demonstrating a wide range of effects on several functional groups at all trophic levels. In particular, being a substantial portion of the largemouth bass diet, both paradise and trident goby have a direct positive impact on the top predator of the system. Gut content analyses have revealed that gobies can account for more than 80% of the stomachs of invasive fish (Azuma, 1992; Azuma and Motomura, 1998). It can also be hypothesized that the trophic niche overlap and

resource competition between bluegill and native gobies may have rendered the latter group more susceptible to bass predation. Thus, the earlier introduction of bluegill is likely to have provided largemouth bass with an additional and profitable food source, thereby facilitating their establishment in Lake Kawahara-oike (Azuma and Motomura, 1998). Viewed from this perspective, the “largemouth bass–bluegill–gobies” facilitative interactions are on par with the predictions of the “Invasional Meltdown” model (Simberloff and Von Holle, 1999).

- On a similar note, we caution that the practical elimination of the native medaka likely due to the invasion of largemouth bass and bluegill may be a forewarning of additional extinction scenarios as invader populations grow in Lake Kawahara-oike (Azuma, 1992; Azuma and Motomura, 1998). This is consistent with recent findings in experimental ponds in north-eastern Japan, where the numbers of native fish dramatically decreased following the introduction of bass (Tsunoda et al., 2010). Further proliferation could potentially cause a collapse of a broader range of delicate native fish species favorite to Japanese people. Future management strategies controlling largemouth bass and bluegill populations are required, if the food webs of Japanese freshwater ecosystems are to remain intact and the integrity of native fish communities is to be protected (Nishizawa et al., 2006).
- Our modeling exercise offered a first approximation of the basic trophic relationships underlying the food web structure in Lake Kawahara-oike. However, we caution that the limited information from the system (e.g., biomass estimates) along with the substantial uncertainty associated with several critical inputs (e.g., ecotrophic efficiencies) poses constraints on its use and also invites a rigorous assessment of some of the assumptions made during its development. Acknowledging the knowledge gaps from the system as well as the uncertainties associated with any modeling endeavor, the present exercise should rather be viewed as the beginning of our efforts towards the development of a credible ecosystem model in the system.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.ecoinf.2013.07.005>.

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