Ecology of Freshwater Fish 2007: 16: 362–372
Printed in Singapore · All rights reserved

ECOLOGY OF
FRESHWATER FISH

Larger body size with higher predation rate

Nakazawa T, Ishida N, Kato M, Yamamura N. Larger body size with higher predation rate.
Ecology of Freshwater Fish 2007: 16: 362–372. © 2007 The Authors.
Journal compilation © 2007 Blackwell Munksgaard

Abstract – Many studies have reported that prey fish increase in body size with an increase in piscivore abundance, and this change may be explained mainly by two processes: release from intraspecific competition because of a reduction in the prey fish population and size-dependent selection by the piscivore. However, the evolutionary mechanism is not yet fully understood. Here, we first show the body-size dynamics of the semelparous gobiid fish *Gymnogobius isaza*, which is one of the prey fishes of the introduced largemouth bass, *Micropterus salmoides*. The data show the possibility that the goby body size might have changed in parallel to the number of largemouth bass from 1975 to 2002, which may be one of the best examples of the positive relationship between body size and predation rate. Furthermore, we explored a mathematical model to consider a body-size change of semelparous fish from an evolutionary viewpoint. The model provided the following qualitative predictions: (1) the optimal assimilation rate increases with predation pressure; (2) a rapid large-scale increase in predation pressure may exterminate the prey fish because of delayed evolution of the assimilation rate; and (3) the optimal assimilation rate increases when the prey fish is more likely to die through predation than through natural mortality or when it is difficult to grow larger because of low resource availability or insufficient foraging efficiency. Moreover, we propose a theoretical framework to evaluate the relative effects of ecological and evolutionary processes over the long term.

T. Nakazawa[1], N. Ishida[2], M. Kato[3], N. Yamamura[1]
[1]Center for Ecological Research, Kyoto University, Otsu, Shiga, Japan, [2]Laboratory of Public Environment, Sakyo-ku, Kyoto, Japan, [3]Graduate School of Human and Environmental Studies, Kyoto University, Sakyo-ku, Kyoto, Japan

Key words: freshwater ecosystem; invasion; long-term data; pairwise invasibility plot; prey–predator interaction

T. Nakazawa, Center for Ecological Research, Kyoto University, 509-3, 2-chome, Hirano, Otsu, Shiga 520-2113, Japan;
e-mail: nkzw@ecology.kyoto-u.ac.jp

Accepted for publication December 23, 2006

Introduction

Body size is one of the most important characteristics of organisms. Body size is directly related to various life-history processes, such as predation, defence, competition, reproduction and dispersal (Peters 1983; Cohen et al. 1993). Intraspecific variation in fish body size is very large; thus, the long-term dynamics of changes in fish body size have been investigated as a significant index of aquatic ecosystem function (Heessen & Daan 1996; Millner & Whiting 1996).

The most basic pattern of fish body-size dynamics is a negative correlation between body size and abundance (Tonn & Paszkowski 1986, 1992; Damsgård & Langeland 1994; Brönmark et al. 1995; Millner & Whiting 1996). The release from intraspecific competition because of a reduction in the population size leads to an increase in resource availability per individual, which results in a larger body size.

Interspecific interactions also produce other patterns. For example, under intense intraspecific competition, if the top-down effect of predation by piscivores is also intense, an increase in piscivore abundance may facilitate the growth rate of the prey fish by relaxing intraspecific competition among the prey fish. In such cases, prey fish body size may be expected to be positively correlated with the piscivore abundance (Tonn & Paszkowski 1986, 1992; Damsgård & Langeland 1994; Brönmark et al. 1995; Olsen et al. 2001). In contrast, fish body size may decrease with increases in piscivore abundance in other situations. Piscivores force prey fish to alter behaviours, such as schooling, refuge use and feeding time (Persson & Eklöv 1995; Jacobsen & Perrow 1998). In such cases, piscivores may cause a decrease in the body size or growth rate of prey fish by preventing optimal foraging (Gilliam & Fraser 1987).

doi: 10.1111/j.1600-0633.2007.00234.x

Furthermore, growing evidence suggests that fish growth rates evolve rapidly (Reznick et al. 1997). Most fish species experience size-dependent predation or pressure from fishery. Olsen et al. (2004) reported fishery-induced evolution toward an earlier age or smaller size at maturation. Conover & Munch (2002) illustrated experimentally that artificial size-dependent selection changes the body size of fish within a few generations. Thus, evolutionary change in fish body size may be no longer negligible when considering fish body-size dynamics.

In the case of evolution toward a smaller body size, fishery pressure is frequently found to be the main cause, because fishery managers tend to target larger fish (Law 2000; Heino & Godø 2002). Large body size achieves many advantages, e.g., superiority in foraging and reproduction. Therefore, the trade-off between the merits of large body size and the low growth rate favoured by fishery pressure is significant (Gårdmark et al. 2003).

In the case of evolution toward a larger body size, the main cause appears to be natural piscivores. Piscivores can more efficiently consume smaller than larger prey fish (Christensen 1996; Cowan et al. 1996; Olsen 1996; Lundvall et al. 1999; Kristiansen et al. 2000) because of the gape limitation of piscivores and good avoidance ability of large prey fish.

However, evolution toward a larger body size is still the subject of extensive debate; in particular, the cost of a high growth rate remains elusive (see review by Blanckenhorn 2000). Furthermore, interactions between ecological and evolutionary processes are very intricate (Thompson 1998; Law 2000), which also makes the problem more troublesome. Therefore, when prey fish body size is observed to increase with increases in predation pressure, it is difficult to determine whether the main causal factor is reduced intraspecific competition or size evolution. As Blanckenhorn (2000) argued, empirical data and theoretical work are required to resolve this problem.

In this study, we first report the long-term body-size dynamics of the annual goby *Gymnogobius isaza* in Lake Biwa, Japan (Fig. 1). The population of the largemouth bass, *Micropterus salmoides*, in this lake has continued to grow since its introduction in 1974 (Nakanishi & Sikino 1996; Fig. 2a), and native fish communities have subsequently suffered dramatic declines and changes (Yuma et al. 1998; Nakai 1999). One of the most affected species is the endemic goby (Fig. 2b). The goby population decreased remarkably in the 1990s, during which the largemouth bass population increased explosively (see below).

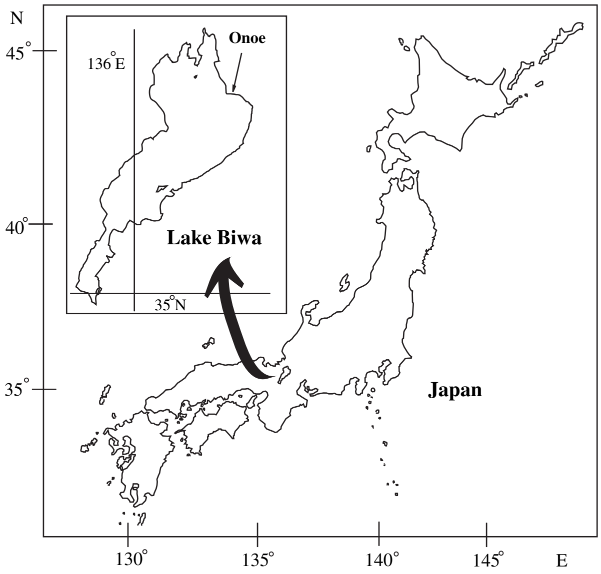

Fig. 1. Location of Lake Biwa and sampling site.

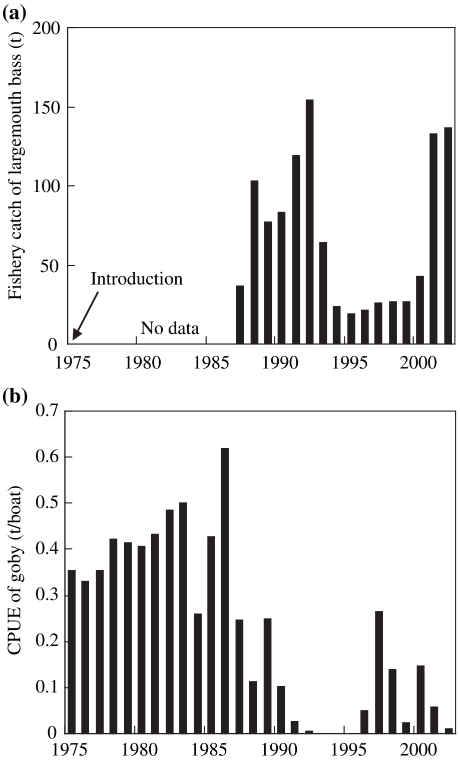

Fig. 2. Annual fluctuations in (a) fishery catches of largemouth bass and (b) CPUE of goby fish in Lake Biwa during the sampling period. (a) The largemouth bass was introduced into the lake in 1974 and there are not available data until 1986. (b) CPUE was obtained by dividing total fishery catch by the number of trawl boat.

Furthermore, we developed a mathematical model to consider a long-term change in body size of semelparous fish from an evolutionary viewpoint. Here, we assumed that the change in body size would be accomplished by natural selection for higher growth rates. An increase in the consumption rate of prey fish would also increase prey body size, but this is not the mechanism considered here, because the growth rate would decrease in the presence of piscivores (see above). High growth rates without a sufficient food supply should increase some costs of development. In the evolutionary process, however, the main question is the cost of a high growth rate. Although there is still debate over the problem, the most accepted cost is an increase in natural mortality caused by excessively rapid growth (reviewed by Arendt 1997; Blanckenhorn 2000; cf. Carlson et al. 2004). The characteristic changes, accompanied by rapid evolution, may represent the evolutionary costs that increase mortality. For the evolutionary process in the model, we considered that an increase in predation pressure would select for a higher growth rate, accompanied by the evolutionary cost of an increase in natural mortality. This model will aid in understanding the mechanisms underlying the positive relationship between prey body size and predator abundance.

Empirical data

Gymnogobius isaza is an annual fish that breeds in spring and dies thereafter (Nagoshi 1981). The juvenile grow during the summer, and the growth ceases in winter (Nagoshi 1966).

Figure 2 shows the total catch for the largemouth bass and the catch per unit effort (CPUE) for this goby from 1975 to 2002 (Shiga Statistics and Information Office 1975–2002). We showed the total catch as the abundance index for the largemouth bass because it is difficult to estimate the fishery effort. The goby CPUE was obtained by dividing the total fishery catch by the number of trawl boats. The goby experienced a dramatic population decline during the 1990s (Fig. 2b); the catch was near zero in 1994 and 1995, after which it appeared to recover slightly. Azuma & Motomura (1998) reported that largemouth bass introduced into Japanese lakes frequently feed on gobiid fishes, and gobies have been observed in the stomach contents of largemouth bass caught in Lake Biwa (T. Nakazawa, personal observation). Currently, the goby is listed as a nearly threatened species (Japanese Ministry of the Environment 2003).

From 1975 to 2002, *G. isaza* was netted commercially by trawling offshore near Onoe (30°26′N, 136°11′E) at the northernmost part of Lake Biwa (Fig. 1) in winter (mainly in December). We annually collected several hundreds of specimens during one trawl catch, and preserved them in 10% formalin solution. We measured standard body length and wet weight of 100 randomly selected individuals per collection year.

An outstanding trend in the temporal dynamics of the size of this species from 1975 to the early 1990s was the progressive increase in both standard body length and wet weight (Fig. 3). During this period, the mean standard body length and mean wet weight increased about 1.5 and four times, respectively. The increase in body size ceased in the mid-1990s, when the goby population collapsed. Subsequently, the body size began to decrease in the late 1990s, when the goby population recovered.

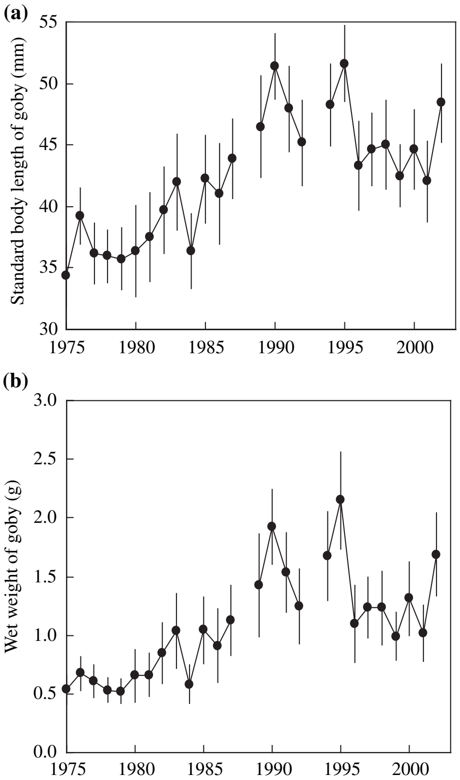

Fig. 3. Annual fluctuations in (a) mean standard body length and (b) mean wet weight of the goby fish. Vertical bars represent standard deviation.

What was the cause of the increase in body size? The minimum standard body length (45 mm) in 1995, when mean body size was maximised, was larger than the maximum (41 mm) in 1975, when mean body size was minimised. Therefore, the change in body size cannot be explained by the simple reason that the introduced piscivore shifted the average prey body size by removing the smaller prey, i.e., ‘apparent growth’.

The goby body size was negatively correlated with the CPUE (standard body length: $r = 0.690$, $n = 26$, $P < 0.001$; wet weight: $r = 0.680$, $n = 26$, $P < 0.001$). This suggests that the goby experienced intense density-dependent effects from 1975 to 2002. This result is consistent with that of Nagoshi (1981), who reported the body-size dynamics of the goby in the 1950s to 1970s.

The CPUE of the goby was not significantly correlated with the fishery catch of largemouth bass ($r = 0.266$, $n = 16$, $P = 0.319$). However, there are no available data for the largemouth bass abundance between its introduction in 1974 and 1986; the relationship may be significant if the largemouth bass abundance was low during this period. Considering that the increase in goby body size was extremely large and that the goby is an annual fish, and thus has a potentially high evolutionary rate, we cannot exclude the possibility of rapid evolution. Thus, we developed a mathematical model to consider such a body-size increase from an evolutionary viewpoint.

Mathematical model

First, we developed a consumer–resource model that included the size dynamics of the consumer for the process without evolution to analyse cohort size, growth of individual consumers and resource dynamics within the consumer life span. Here, the consumer is the prey fish. In the model, we did not consider the piscivore density explicitly, because the largemouth bass is a generalist and thus is not greatly affected by the condition of one prey species. The model is:

$$\frac{\mathrm{d}R(t)}{\mathrm{d}t} = r\left\{1 - \frac{R(t)}{K}\right\}R(t) - aR(t)C(t)W(t)^x \quad (1a)$$

$$\frac{\mathrm{d}W(t)}{\mathrm{d}t} = baR(t)W(t)^x - cW(t)^y \quad (1b)$$

$$\frac{\mathrm{d}C(t)}{\mathrm{d}t} = -zC(t) \quad (1c)$$

where $R(t)$, $W(t)$ and $C(t)$ represent the amount of resources, the body size and the surviving population of the prey fish, respectively, at time t within the life span of the prey fish. Body size was measured as the mass of individual prey fish. The resource grows logistically and is consumed by the prey fish following a linear functional response for simplicity (Eq. 1a). The resource consumption rate of the prey fish is proportional to the amount of resources, the prey fish cohort size and the xth power of the body size of the prey fish, where a represents the coefficient of consumption. For individual growth (Eq. 1b), we applied the growth expression of von Bertalanffy (1938), which is often used in fishery studies (e.g., Charnov et al. 1993). The first and second terms of the right-hand side represent assimilation and metabolism, respectively. Because $aR[t]W[t]^x$ is the resource consumption rate per individual prey fish, b is the gross assimilation rate. Metabolism is proportional to the yth power of body size. We first assumed a constant mortality rate z in Eq. (1c). In this case, survivorship follows a type-II curve, which is frequently observed in fish populations (Deevey 1947).

We also modelled size-dependent predation avoidance as the evolutionary force that increases the prey fish body size such that larger individuals have lower predation mortality. As an evolutionary trade-off, we considered that the cost of rapid growth is an increase in natural mortality other than predation (Arendt 1997; Blanckenhorn 2000), assuming that a larger body size is attained by a higher assimilation rate b. We then divided mortality m into two terms: predation and natural mortality other than predation,

$$z = pf[W(t)] + m[b] \quad (2)$$

where predation mortality is the product of predation pressure p and a function $f[W]$ that expresses size-dependent predation avoidance; and natural mortality $m[b]$ is a function of the assimilation rate b. The trade-off is that larger individuals with higher assimilation rate can avoid piscivory more efficiently, but natural mortality increases, i.e., $f'[W] < 0$ and $m'[b] > 0$.

The size-dependent predation rate in fish is usually expressed in terms of the relative body length of prey fish to the body length of piscivores (Paradis et al. 1996; see also Turesson et al. 2006). For example,

$$\log P = \alpha + \beta_1 \log Q + \beta_2 (\log Q)^2 + \cdots \quad (3)$$

where P is the predation rate and Q is the relative body length. Using only the first and second terms and assuming a constant predator body size for simplicity, the size-dependent predation rate is expressed as

$$f[W(t)] = gW(t)^h \quad (4)$$

where $g > 0$ and $h < 0$ because $f'[W] < 0$. We assume that the natural mortality term is a function similar to that in Eq. (4):

$$m[b] = kb^l \quad (5)$$

where $k > 0$ and $l > 0$ because $m'[b] > 0$.

In this study, b is the most important parameter, considering that the ecological process without evolution (when the assimilation rate is constant) and the evolutionary process (when the assimilation rate evolves) have different effects on changes in prey body size. We define the former effect as the 'ecological effect', which is caused by release from intraspecific competition. In the evolutionary process, prey body size changes with both release from intraspecific competition and the evolutionary response of the assimilation rate. We defined the difference between the two effects as the 'evolutionary effect', which is generated only by the evolution of the assimilation rate.

We analysed the evolutionary process by establishing two types of prey fish strains with differential assimilation rates ($i = 1$ and 2). The dynamics of these two types of prey fish are represented as

$$\frac{\mathrm{d}R(t)}{\mathrm{d}t} = r\left\{1 - \frac{R(t)}{K}\right\}R(t) - aR(t)\sum_{i=1,2} C_i(t)W_i(t)^x \quad (6a)$$

$$\frac{\mathrm{d}W_i(t)}{\mathrm{d}t} = b_i a R(t) W_i(t)^x - c W_i(t)^y \tag{6b}$$

$$\frac{\mathrm{d}C_i(t)}{\mathrm{d}t} = -\{pf[W_i(t)] + m[b_i]\} C_i(t) \tag{6c}$$

where i refers to the two competing phenotypes. Later, we will treat one as resident and the other as a mutant.

T denotes generation time. Here, we assume semelparity for the goby; thus, T is also the time of reproduction, after which all adults die. Alternation of generations is expressed as

$$R_{j+1}(0) = R_j(T) \tag{7a}$$

$$W_{i,j+1}(0) = w \tag{7b}$$

$$C_{i,j+1}(0) = \frac{v\ \mathrm{C}_{i,j}(T) W_{i,j}(T)}{w} \tag{7c}$$

where j is the generation number or year number if prey fish reproduce annually. Equation (7a) represents the continuous connection of resource dynamics over prey generations. Reproductive investment by a parent $vW_{i,j}(T)/w$ is proportional to its body size and is allocated evenly to individuals of the next generation with an initial body size of w for egg size. Therefore, parameter v in Eq. (7c) is the product of reproductive investment and the hatching probability. We assumed asexual reproduction for simplicity; thus, hybridisation between the two types was not considered. This is an expedient assumption for the analysis of evolutionary dynamics.

We simulated Eqs (6a–c) and (7a–c) to examine whether the mutant ($i = 2$) spreads or disappears after invading the resident population ($i = 1$). For each simulation, we set the predation pressure to a value between 1 and 100 and the resident and mutant assimilation rates (b_1, b_2) to a pair of values between 0.0 and 1.0, with a minimum difference of 0.01. The initial cohort size of the resident $C_1(0)$ was the equilibrium value of the system without the mutant. Under this equilibrium state, we obtained cyclic within-generation prey fish population dynamics, which is the stable equilibrium state for between-generation dynamics. We set the initial frequency of mutant individuals at 0.001. The subsequent mutant frequency in this model is expressed as

$$\frac{vC_2(T)W_2(T)/w}{[vC_1(T)W_1(T)/w] + [vC_2(T)W_2(T)/w]} = \frac{C_2(T)W_2(T)}{C_1(T)W_1(T) + C_2(T)W_2(T)} \tag{8}$$

In several trials using the parameter set (b_1, b_2), we observed that once the mutant invades, its frequency decreases to 0.0 or increases to 1.0 progressively, without oscillation; i.e., the mutant and the resident can never coexist. Based on this result, we determined that the mutant replaces the resident when the mutant frequency increases after one generation.

Table 1. Definitions and default values of the parameters used in the model.

Parameters	Definitions	Default values
a	Per biomass consumption rate	0.001
b	Assimilation rate	variable
c	Per biomass metabolism rate	0.01
x	Allometric exponent in size-dependent consumption	2/3
y	Allometric exponent in size-dependent metabolism	1
g	Allometric scaler in size-dependent predation avoidance	0.005
h	Allometric exponent in size-dependent predation avoidance	−1
k	Allometric scaler in natural mortality	0.2
l	Allometric exponent in natural mortality	2
v	Product of reproductive investment and hatching rate	0.1
w	Egg size	1
T	Reproduction cycle	100
r	Growth rate of resource	0.2
K	Carrying capacity of resource	1000

The definitions and default values of the parameters used in the model are listed in Table 1. In our model, the resident and mutant differed only in parameter b. The default parameters were $r = 0.2$, $K = 1000$, $a = 0.001$, $c = 0.01$, $x = 2/3$, $y = 1$, $g = 0.005$, $h = -1$, $k = 0.2$, $l = 2$, $v = 0.1$, $w = 1$ and $T = 100$. Values of $x = 2/3$ and $y = 1$ were used in accordance with the original equation (von Bertalanffy 1938). Most of these values are actually unknown; therefore, we chose values by trial and error so that the prey fish would have moderate mortality rates ($f[W]$ and $m[b]$) and numerical simulations would run well within a reasonable range of predation pressure, p ($0 < p < 100$). We examined the parameter sensitivities by changing some parameter values after analysis using the default parameters.

Finally, we provide a theoretical framework to evaluate the relative effects of ecological and evolutionary processes over the long term. However, we did not assume evolutionary speed, which is determined by intraspecific variation, selection differential and heritability. Therefore, the model can be used for between-population comparisons or time-series analyses accompanying rapid evolution. In either case, it must be assumed that population dynamics are at equilibrium, and in the evolutionary process, the prey fish population has already adapted to the predation pressure. In the purely ecological process, the assimilation rate does not change, but body size increases with predation pressure because the resource consumption rate per individual, $aR[t]W[t]^x$, increases due to the reduced population size. In the evolutionary process, both the resource availability per individual and the assimilation rate b increase with predation pressure. We calculate the equilibrium body size, population size and population biomass (i.e., body size × population size) at various predation pressures in the absence or presence of assimilation rate evolution using the default parameter set.

Results

To evaluate the evolutionary dynamics, we drew pairwise invasibility plots (PIPs; Geritz et al. 1998), where the horizontal and vertical axes represent values of the assimilation rate b for the resident and mutant, respectively. PIPs illustrate whether the mutant can invade the resident population (Fig. 4).

We always obtained similar patterns of PIPs for different values of predation pressure p. The assimilation rates (b^*) at the nodes of the patterns were convergent stable because any mutant strategy between a resident strategy and b^* could invade (Eshel 1983), and they were evolutionarily stable because no mutant strategy could invade (Maynard-Smith & Price 1973). The optimal assimilation rate b^* varied with predation pressure and the values of other parameters.

The resident was unviable at extreme values of b, which were indicated as grey areas in the PIPs. We called the system ‘unviable’ when the population went to extinction at initial equilibrium. Populations with an extreme assimilation rate were unviable for the following reasons. When the assimilation rate was extremely low ($<b_{\min}$), size-dependent predation mortality was very high and reproductive investment was reduced because of the small body size at reproduction. By contrast, when the assimilation rate was extremely high ($>b_{\max}$), natural mortality increased markedly because the assimilation rate was too high.

Figure 5 illustrates the relationship between the optimal assimilation rate b^* and the predation pressure p, where b^* increases gradually with p. The borders between the white and grey areas are $b_{\max}$ and $b_{\min}$. With greater predation pressure, the range of viable values becomes narrower, i.e., b^*, $b_{\max}$ and $b_{\min}$ are closer. The intersection of these three lines is the maximum predation pressure above which the population is not viable at any assimilation rate.

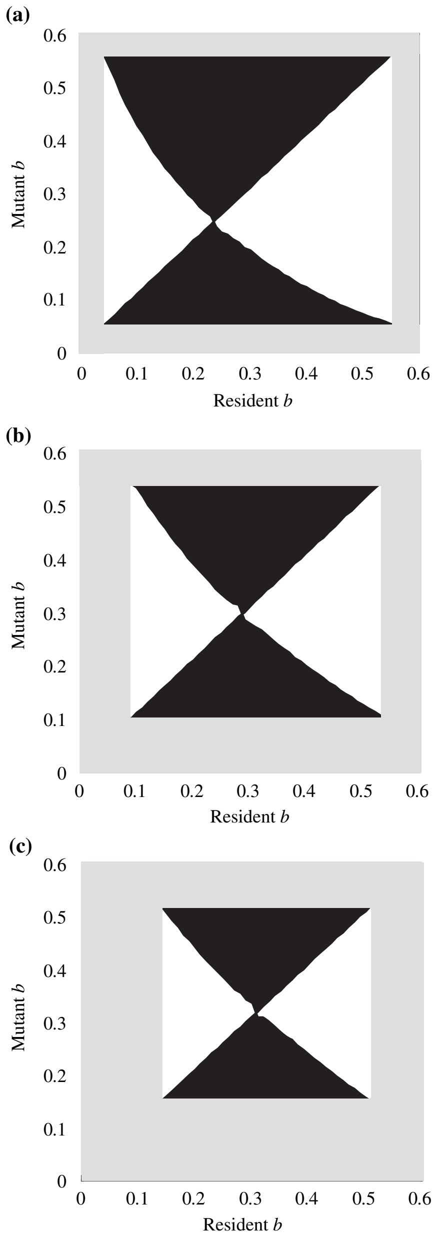

Fig. 4. Pairwise invasibility plots (PIPs) for different predation pressures p: (a) $p = 1$, (b) $p = 20$, (c) $p = 40$. The horizontal and vertical axes represent the assimilation rates of the resident ($i = 1$) and mutant ($i = 2$), respectively. White areas indicate that the mutant can become established, whereas black areas indicate that the resident expels the mutant. In grey areas, the resident is unviable.

Next, we examined the parameter dependence of the relationship between optimal assimilation rate and predation pressure by substituting various parameter sets. For changes in any parameter, a positive relationship between predation pressure and b^* always appeared (Fig. 6). The closed circles were obtained using the default parameter set; the open circles show results in which only one parameter was changed (see Table 1 for parameter definitions). When the absolute value of h is small, the function $f[W]$ is steep for a large W, and an increasing assimilation rate becomes advantageous. In contrast, when the absolute value of h is large, an increasing assimilation rate is not advantageous for a small W because predation avoidance does not improve and natural mortality increases. When k increases or l decreases, i.e., when $m[b]$ increases, the cost of a rapid assimilation rate increases, so the curve is lower (Fig. 5). When K or r increases, even small values of b assure high growth

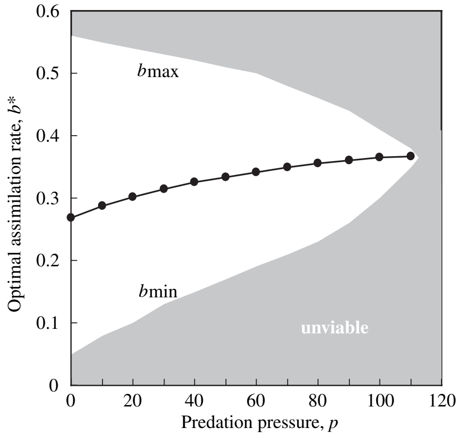

Fig. 5. Optimal (b^*), maximum viable ($b_{\max}$), and minimum viable ($b_{\min}$) assimilation rates at various predation pressures. The upper and lower grey areas are unviable areas that correspond to the margin in Fig. 4.

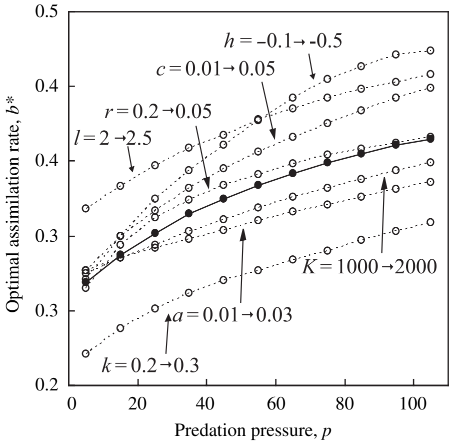

Fig. 6. Parameter dependence on the relationship between optimal assimilation rate and predation pressure. The solid line with closed circles indicate the default parameter set; dotted lines with open circles indicate parameter sets in which one parameter value was changed.

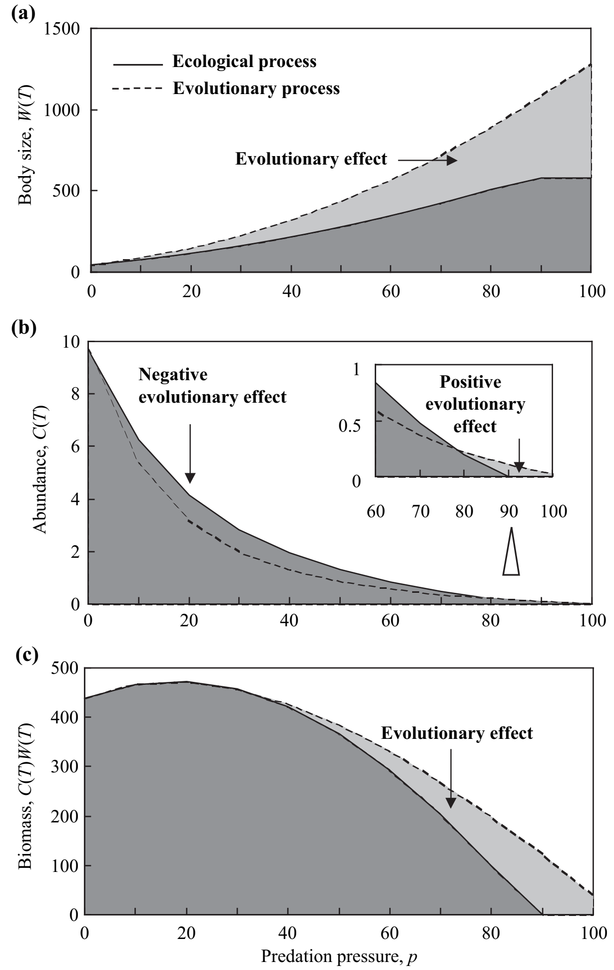

Fig. 7. Equilibrium value of (a) body size, (b) population size and (c) population biomass for various levels of predation pressure p in ecological and evolutionary processes. Solid and dotted line represent the simulations in ecological and evolutionary processes. Evolutionary effects (light-grey areas) are defined as the difference between the two processes.

rates because resources are abundant, so the curve is lower (Fig. 5). For the same reason, when a increases or c decreases, the curve is lower (Fig. 5). We also examined the parameter sensitivity of the relationship between optimal assimilation rate b^* and predation pressure p using several other parameter value sets, and always obtained similar increasing patterns (not shown).

We calculated the equilibrium body size and population size and population biomass (body size × population size) with and without assimilation rate evolution for various levels of predation pressure (Fig. 7). In these calculations, the system reached equilibrium within a few dozen generations. In the simulations both with and without evolution, the initial assimilation rate was set at the optimal value when $p = 1$. First, we calculated the equilibrium values of body size, population size and population biomass at $t = T$, with various predation pressures and under a constant assimilation rate (Fig. 7, solid line). The difference from the simulation at $p = 1$ is interpreted as ecological effect. We then calculated the equilibrium values with the optimal assimilation rate at each predation pressure (Fig. 7 dotted line). The evolutionary effect was calculated as the difference between the simulations with and without evolution (Fig. 7, light grey areas).

Both the ecological and evolutionary effects on body size increased with predation pressure, but the relative effect of the evolutionary process on the increase in body size was greater under higher predation pressure because the ecological effect had a maximum value (Fig. 7a). Saturation of the body size with an increase in predation pressure in ecological process is attributable to that the resource density reaches the carrying capacity as a result of extremely low levels of prey fish population size, which nullify the density dependence in the body-size growth rate in Eq. (1b). The evolutionary effect on population size was negative for almost all values of p because prey fish with an evolved large body size suffered high natural mortality (Fig. 7b). For the highest values of p, however, the evolutionary effect was positive and the population was viable until $p \fallingdotseq 100$ in the evolutionary process, whereas it reached zero at $p \fallingdotseq 90$ in the pure ecological process (small panel in Fig. 7b). The evolutionary effect on population biomass was always positive, but near zero for lower values of p because the positive effect of body size and negative effect of population size cancelled each other out (Fig. 7c). The population biomass peaked at a certain predation pressure and then declined because moderate predation pressure relaxes intraspecific competition and promotes the growth of individual prey fish.

We conducted the same simulations for the different parameter sets. For parameter changes that caused increases in the slope of the optimal assimilation rate curves, the evolutionary effects increased relative to the ecological effects, but we obtained results qualitatively similar to those for the default parameter values (not shown). Therefore, we concluded that the tendencies for the ecological and evolutionary effects (Fig. 7) are robust.

Discussion

We first reported the long-term body-size dynamics of the goby (Fig. 3). A negative relationship between body size and abundance is common in fish (e.g., Tonn & Paszkowski 1986, 1992; Damsgård & Langeland 1994; Brönmark et al. 1995; Millner & Whiting 1996). Therefore, many researchers have found positive relationships between prey fish body size and predation pressure (e.g., Tonn & Paszkowski 1986, 1992; Damsgård & Langeland 1994; Brönmark et al. 1995; Olsen et al. 2001). However, we think our data are outstanding for the following reasons. First, sampling was conducted over 28 consecutive years. Intraspecific competition within the goby population was also reported for the 1950s to 1970s (Nagoshi 1981). Compiling the data of Nagoshi (1981), it is suggested that goby body size has been consistently affected by intraspecific competition for over 50 years. Secondly, we observed that goby body size increased considerably (about 1.5 times in length and four times in weight). Finally, there is a possibility of size evolution (see also below). It would be of significant interest to confirm size evolution in a natural ecosystem. In future, we will explore the possibility of size evolution in the goby. The body-size dynamics of the goby will be one of the clearest and longest measured examples of this subject.

We also developed a mathematical model to consider the increase in body size with increases in predation pressure from an evolutionary viewpoint. The model provided several qualitative predictions. First, we obtained a positive correlation between the optimal assimilation rate and predation pressure (Fig. 7). The optimal assimilation rate increased when prey fish were more likely to die through predation than through natural mortality (higher p, g, h and l, and lower k), when resource availability was low (lower r and K) or when resource consumption was less efficient (lower a and higher c). We did not change g because it is equivalent to a change in predation pressure p [see Eqs (2) and (4)]. Because v and w cancelled each other out in Eq. (7), changes in these parameters would not affect the optimal assimilation rate. We set $y = 1$ following the original von Bertalanffy growth equation (von Bertalanffy 1938), but $y = 3/4$ is more common (McMahon 1973; Dodds et al. 2001; but also see Peters 1983). If $y = 3/4$, the optimal assimilation rate would decrease because it becomes easier to grow larger. Although it is impossible to confirm the robustness of the positive relationship between optimal assimilation rate and predation rate by examining exhaustive parameter space, these interpretations seem to be quite reasonable.

The mode of correlation will naturally depend on the detailed model assumptions. We think that saturation of the optimal assimilation rate curve with increasing predation pressure is attributable to the functional forms of size-dependent predation avoidance $f[W]$ and natural mortality $m[b]$. If we assume different shapes for the functions, we would obtain different results (e.g., exponential curve). Although some studies have examined size-dependent predation (Paradis et al. 1996; Turesson et al. 2006), none have investigated the actual form of the function $m[b]$ for natural mortality caused by rapid growth. It is important to obtain such data to predict body-size evolution more precisely.

We obtained another interesting evolutionary insight. The range of assimilation rates assuring a viable population over the long term decreased with increasing predation pressure (Fig. 5). We can predict the viability of the prey fish following an increase in piscivore abundance using Fig. 5. For example, suppose that predation pressure is constant ($p = 1$) over some long term, and the assimilation rate reaches and remains at the optimal level corresponding to the value of p. When p increases, the assimilation rate should evolve toward the optimal value corresponding to the new value of p. If p continues to increase slowly enough to an extremely high value ($p > 100$), the assimilation rate can change along the curve defined by the optimal values. If *p* increases fairly rapidly, however, the population may not be viable because (p, b^*) shifts horizontally and enters the region where the system is 'unviable'. This suggests that the prey fish population could become extinct if a piscivore increases rapidly, whereas it would be viable if the predation pressure increased slowly or the prey fish evolved rapidly such that an 'evolutionary rescue' would be possible. The positive evolutionary effect on the population size (small panel in Fig. 7b) is explained by this evolutionary rescue effect. The introduction of piscivores into freshwater ecosystems and their subsequent ecological effects have sparked serious concern worldwide (Rahel 2002); in many cases, they are the top predators (Eby et al. 2006). Our result suggests that we should focus on both the absolute value and the rate of change of the abundance of introduced piscivores to conserve native prey fish populations.

We proposed a theoretical framework to evaluate the relative effects of ecological and evolutionary processes over the long term by calculating the body size and abundance at equilibrium (Fig. 7). This is a previously introduced method of extracting the evolutionary effect by fixing the parameter values (Yamauchi & Yamamura 2004). We found that the prey fish body size grew to a certain limit value under high predation pressure in ecological process, whereas there was no limit in evolutionary process. This may be helpful in judging size evolution; when population size is extremely small, body size would fluctuate with predation pressure if evolution is present, but be saturated if absent because the resource is superfluous. From this viewpoint, the goby body size appears to be fluctuating in early 1990s (Fig. 3) despite that the CPUE was almost zero (Fig. 2b), which may suggest the possibility of size evolution. Although this is a speculation, further research would be motivated. Obtaining life-history parameters, we could determine whether the causal factor is reduced intraspecific competition or size evolution. To evaluate the relative effects of evolutionary process over a short period of time, the evolutionary speed must be considered explicitly. A model including intraspecific variation, selection differential and heritability, such as size-structured model, is necessary for this type of analysis.

The model contains several assumptions that may require modification for application to other cases. First, we assumed the prey fish, the goby, was semelparous. This can be changed easily to iteroparity. In fact, we obtained similar patterns for the relationship between optimal assimilation rate and predation pressure by assuming an iteroparous prey fish (not shown). However, this altered model will only work if the assimilation rate remains constant throughout the life span and there are no trade-offs between other characteristics, which may not be satisfied in iteroparous cases. Therefore, many previous studies have considered an evolutionary response in growth rate or age at maturity caused by size- or stage-dependent predation pressure. For example, Day et al. (2002) suggested that high size-dependent predation pressure would select for faster growth when productivity is high, assuming a trade-off between resource availability and fecundity. Gårdmark et al. (2003) suggested that the age at maturity would evolve depending on the size-dependent predation pressure relative to the pressure of fisheries targeting large fish. However, most studies assumed reduced fecundity or growth rate in later life stages, rather than increased natural mortality, as the evolutionary cost of rapid growth or precocity. These assumptions would be inappropriate in semelparous species because they have only one reproductive opportunity.

Next, we only considered the evolutionary response of the prey fish population, because the largemouth bass is a generalist that is affected very little by the condition of one prey species. The generation cycle (and thus, evolutionary timescale) of the predator is much longer than that of the prey fish. Therefore, this assumption is not strict. In some cases, however, piscivores may adapt their foraging behaviour evolutionarily or phenotypically according to characteristics or behaviour of the prey fish community (Stephens & Krebs 1986). Therefore, we should also consider the evolutionary and ecological response of the predator in such cases. Furthermore, we did not address interspecific competition with other prey fish because intraspecific competition within the goby population was very intense (Nagoshi 1981). For the purpose of generalisation, however, it may be better to develop a food web model that considers the body-size dynamics and adaptive foraging.

We assumed a linear functional response, as in many other theoretical studies. It is difficult to analyse the invasion process using models that contain nonlinear interactions. Size-structure, spatial structure and environmental fluctuations were also neglected for the purpose of facilitating the analysis. These problems should be addressed in future work.

We used PIPs to analyse the evolutionary process (Geritz et al. 1998), but other methods may also be useful in considering evolutionary dynamics; for example, the qualitative genetics model is one of the most popular methods (Bulmer 1985). However, it is very difficult to derive a fitness equation when working with high-dimensional models, e.g., containing body-size dynamics. Likewise, it is also difficult to work with canonical equations (Dieckmann & Law 1996) in models that contain body-size dynamics. PIPs would produce results similar to those obtained by calculating invasion fitness directly using the equilibrium value of the resident population (c.f. Geritz et al. 2002 for numerical analysis).

There is still debate over what constitutes an evolutionary cost of high individual growth rate. An increase in natural mortality rate as the cost of high individual growth rates is one of various possible costs. As Blanckenhorn (2000) suggested, there are many unknowns, and we do not yet fully understand the goby case. However, we think it may be possible to understand what happened to the goby using our model by obtaining life-history parameter values and using more realistic model assumptions.

Finally, we insist upon the necessity of long-term monitoring. Catch data and fish specimens collected over long periods in freshwater fisheries provide opportunities to detect not only the ecological, but also the potential evolutionary effects of environmental changes on fish species. The data will provide significant insights into ecological and evolutionary aspects of fish body size.

Acknowledgements

We thank two anonymous referees and the editor for their valuable comments. This research was partly supported by a Grant for Biodiversity Research of the 21st Century Center of Excellence Program (A14). TN was also supported by a Japan Society for the Promotion of Science Research Fellowships for Young Scientists.

Reference

Arendt, J.D. 1997. Adaptive intrinsic growth rates: an integration across taxa. The Quarterly Review of Biology 72: 149–177. DOI: 10.1086/419764.

Azuma, M. & Motomura, Y. 1998. Feeding habits of largemouth bass in non-native environment: the case of small lake with bluegill in Japan. Environmental Biology of Fishes 52: 379–389. DOI: 10.1023/A:1007359826470.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws, ii). Human Biology 10: 181–213.

Blanckenhorn, W.U. 2000. The evolution of body size: what keeps organisms small? The Quarterly Review of Biology 75: 385–407. DOI: 10.1086/393620.

Brönmark, C., Paszkowski, C.A., Tonn, W.M. & Hargeby, A. 1995. Predation as a determinant of size structure in populations of crucian carp (*Carassius carassius*) and tench (*Tinca tinca*). Ecology of Freshwater Fish 4: 85–92. DOI: 10.1111/j.1600-0633.1995.tb00121.x.

Bulmer, M.G. 1985. The mathematical theory of quantitative genetics, 2nd edn. Oxford: Oxford University Press.

Carlson, S.M., Hendry, A.P. & Letcher, B.H. 2004. Natural selection acting on body size, growth rate and compensatory growth: an empirical test in a wild trout population. Evolutionary Ecology Research 6: 955–973.

Charnov, E.L., Berrigan, D. & Shine, R. 1993. The M/k ratio is the same for fish and reptiles. The American Naturalist 142: 707–711.

Christensen, B. 1996. Predator foraging capabilities and prey behaviours: pre- versus postcapture constraints on size dependent predator–prey interactions. Oikos 76: 368–380.

Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldaña, J. 1993. Body sizes of animal predators and animal prey in food webs. Journal of Animal Ecology 62: 67–78.

Conover, D.O. & Munch, S.B. 2002. Sustaining fisheries yields over evolutionary time scales. Science 297: 94–96. DOI: 10.1126/science.1074085.

Cowan, J.H. Jr, Houde, E.D. & Rose, K.A. 1996. Size-dependent vulnerability of marine fish larvae to predation: an individual-based numerical experiment. ICES Journal of Marine Science 53: 23–37. DOI: 10.1006/jmsc.1996.0003.

Damsgård, B. & Langeland, A. 1994. Effects of stocking of piscivorous brown trout, *Salmo trutta* L. on stunted arctic charr, *Salvelinus alpinus* (L.). Ecology of Freshwater Fish 3: 59–66. DOI: 10.1111/j.1600-0633.1994.tb00107.x.

Day, T., Abrams, P.A. & Chase, J.M. 2002. The role of size-specific predation in the evolution and diversification of prey life histories. Evolution 56: 877–887. DOI: 10.1554/0014-3820(2002)056[0877:TROSSP]2.0.CO;2.

Deevey, E.S. Jr 1947. Life tables for natural populations of animals. The Quarterly Review of Biology 22: 283–314.

Dieckmann, U. & Law, R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. Journal of Mathematical Biology 34: 579–612. DOI: 10.1007/s002850050022.

Dodds, P.S., Rothman, D.H. & Weitz, J.S. 2001. Re-examination of the "3/4-law" of metabolism. Journal of Theoretical Biology 209: 9–27. DOI: 10.1006/jtbi.2000.2238.

Eby, L.A., Roach, W.J., Crowder, L.B. & Stanford, J.A. 2006. Effects of stocking-up freshwater food webs. Trends in Ecology & Evolution 21: 576–584. DOI: 10.1016/j.tree.2006.06.016.

Eshel, I. 1983. Evolutionary and continuous stability. Journal of Theoretical Biology 103: 99–111. DOI: 10.1016/0022-5193(83)90201-1.

Gårdmark, A., Dieckmann, U. & Lundberg, P. 2003. Life-history evolution in harvested populations: the role of natural predation. Evolutionary Ecology Research 5: 239–257.

Geritz, S.A.H., Kisdi, É., Meszėna, G. & Metz, J.A.J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary Ecology 12: 35–57. DOI: 10.1023/A:1006554906681.

Geritz, S.A.H., Gyllenberg, M., Jacobs, F.J.A. & Parvinen, K. 2002. Invasion dynamics and attractor inheritance. Journal of Mathematical Biology 44: 548–560. DOI: 10.1007/s002850100136.

Gilliam, J.F. & Fraser, D.E. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68: 1856–1862.

Heessen, H.J.L. & Daan, N. 1996. Long-term trends in ten non-target North Sea fish species. ICES Journal of Marine Science 53: 1063–1078. DOI: 10.1006/jmsc.1996.0133.

Heino, M. & Godø, O.R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science 70: 639–656.

Jacobsen, L. & Perrow, M.R. 1998. Predation risk from piscivorous fish influencing the diel use of macrophytes by planktivorous fish in experimental ponds. Ecology of Freshwater Fish 7: 78–86. DOI: 10.1111/j.1600-0633.1998.tb00174.x.

Japan Ministry of the Environment 2003. Threatened wildlife of Japan, red data book, 2nd edn. Tokyo: Japan Wildlife Research Center.

Kristiansen, T.S., Otterå, H. & Svåsand, T. 2000. Size-dependent mortality of juvenile reared Atlantic cod released in a small fjord. Journal of Fish Biology 56: 792–801.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science 57: 659–669. DOI: 10.1006/jmsc.2000.0731.

Lundvall, D., Svanbäck, R., Persson, L. & Byström, P. 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. Canadian Journal of Fisheries and Aquatic Sciences 56: 1285–1292.

Maynard-Smith, J. & Price, G.R. 1973. The logic of animal conflicts. Nature 246: 15–18.

McMahon, T. 1973. Size and shape in biology. Science 179: 1201–4.

Millner, R.S. & Whiting, C.L. 1996. Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. ICES Journal of Marine Science 53: 1185–1195. DOI: 10.1006/jmsc.1996.0143.

Nagoshi, M. 1966. Ecological studies on the population of isaza, *Chaenogobius isaza* TANAKA, in Lake Biwa, with special reference to the effects of population density upon its growth. Researches on Population Ecology 8: 20–36.

Nagoshi, M. 1981. Annual fluctuations in the growth of isaza. Japanese Journal of Freshwater Fish 7: 129–133 (in Japanese).

Nakai, K. 1999. Recent, faunal changes in Lake Biwa, with particular reference to the bass fishing boom in Japan. In: Kawanabe, H., Coulter, G.W. & Roosevelt, A.C., eds. Ancient lakes: their cultural and biological diversity. Ghent: Kenobi Productions, pp. 227–241.

Nakanishi, M. & Sikino, T. 1996. Recent drastic changes in Lake Biwa biocommunities, with attention to exploitation of the littoral zone. GeoJournal 40: 63–67. DOI: 10.1007/BF00222532.

Olsen, M.H. 1996. Predator–prey interactions in size-structured fish communities: implications of prey growth. Oecologia 108: 757–763. DOI: 10.1007/BF00329052.

Olsen, M.H., Green, D.M. & Rudstam, L.G. 2001. Changes in yellow perch (*Perca flavescens*) growth associated with the establishment of a walleye (*Stizostedion vitreum*) population in Canadarago Lake, New York (USA). Ecology of Freshwater Fish 10: 11–20. DOI: 10.1034/j.1600-0633.2001.100102.x.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. & Dieckmann, U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428: 932–935. DOI: 10.1038/nature02430.

Paradis, A.R., Pepin, P. & Brown, J.A. 1996. Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. Canadian Journal of Fisheries and Aquatic Sciences 53: 1226–1235.

Persson, L. & Eklöv, P. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. Ecology 76: 70–81.

Peters, R.H. 1983. The ecological implications of body size. Cambridge, Cambridge University Press.

Rahel, F.J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology and Systematics 33: 291–315.

Reznick, D.N., Shaw, F.H., Rodd, F.H. & Shaw, R.G. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275: 1934–1937. DOI: 10.1126/science.275.5308.1934.

Shiga Statistics and Information Office. 1975–2002. Annual report of the agriculture, forestry and fisheries statistics of Shiga. Shiga, Japan: Shiga Prefecture.

Stephens, D.W. & Krebs, J.R. 1986. Foraging theory. Princeton, NJ: Princeton University Press.

Thompson, J.N. 1998. Rapid evolution as an ecological process. Trends in Ecology and Evolution 13: 329–332. DOI: 10.1016/S0169-5347(98)01378-0.

Tonn, W.M. & Paszkowski, C.A. 1986. Size-limited predation, winterkill, and the organization of Umbra-Perca fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences 43: 194–202.

Tonn, W.M. & Paszkowski, C.A. 1992. Piscivory and recruitment: mechanism structuring prey populations in small lakes. Ecology 73: 951–958.

Turesson, H., Brönmark, C. & Wolf, A. 2006. Satiation effects in piscivore prey size selection. Ecology of Freshwater Fish 15: 78–85. DOI: 10.1111/j.1600-0633.2005.00124.x.

Yamauchi, A. & Yamamura, N. 2004. Herbivory promotes plant production and reproduction in nutrient-poor conditions: effects of plant adaptive phenology. The American Naturalist 163: 138–153. DOI: 10.1086/380569.

Yuma, M., Hosoya, K. & Nagata, Y. 1998. Distribution of the freshwater fishes of Japan: an historical overview. Environmental Biology of Fishes 52: 97–124. DOI: 10.1023/A:1007451417556.