

Trends and stability of inland fishery resources in Japanese lakes: introduction of exotic piscivores as a driver

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Abstract. Although many studies have focused on marine resources, few studies have considered the resources of inland fisheries. Inland fishery resources are typically either monitored on the basis of catch data alone or are not assessed quantitatively at all, despite their social, economic, and ecological importance. Because freshwater ecosystems have been severely degraded by human activities, evaluating the trends and current status of fishery resources and assessing their drivers are urgent tasks. We compiled long-term data on the annual catch, fishing effort, and fishing power of 23 Japanese lakes, using two sets of government statistics that date back to the 1950s, which were previously neglected because of the large number of missing values. Using Bayesian state-space models, we examined the trajectories of the catch per unit effort (CPUE) of entire communities, considering changes in fishing effort and fishing power, and quantified both changes in the CPUE over the 10-, 20-, and 30-year periods preceding 2008 and the temporal detrended stability of the CPUE over the three periods. We also investigated the relationships among the CPUE changes and stability, anthropogenic drivers, and lake morphometric characteristics. The CPUE declined in 17, 19, and 15 of the 23 lakes over the past 10-, 20-, and 30-year periods, respectively. Our macroecological analyses demonstrate that the functional group richness of exotic piscivores was the most important predictor of changes in the CPUE among the drivers we considered. The stability of the CPUE was positively related to lake area; larger lakes have more stable CPUE. The functional group richness of exotic piscivores also negatively affected the stability of the CPUE. The effect of overfishing was considered to be small because both fishing effort and power declined in almost all of the lakes. Thus, our findings suggest that increasing exotic piscivore species may diminish the resources and their stability, particularly in Japanese lakes where native piscivores are rare. This might lead to a substantial decline in ecosystem services. Our study highlights the importance of assessing inland fishery resources in a comprehensive manner and the need for restoration strategies to mitigate the effects of exotic piscivores.

Key words: capture fisheries; commercially important species; ecosystem goods; fishing efficiency; human stressors; invasions; lake size; macroecology; piscivorous fish; sustainability; top-down drivers.

INTRODUCTION

Capture fisheries provide ecosystem services that are essential for human well-being (Costanza et al. 1997, Holmlund and Hammer 1999). However, capture fishery resources have rapidly declined on a global scale as a result of human activities, often with serious ecological and socioeconomic consequences (Myers and Worm 2003, Lotze and Milewski 2004, Lotze et al. 2011). Thus, it is critical to conduct comprehensive resource assessments to monitor the temporal changes and trends in fishery resources and to understand their possible drivers (Matsuda et al. 2009, Thurstan et al. 2010, Lotze et al. 2011). Moreover, it is becoming increasingly important to evaluate the stability and resilience of fishery

resources (Worm and Duffy 2003, McClanahan et al. 2008). However, fishery assessments have typically focused exclusively on marine resources; inland fishery resources have attracted little attention (Allan et al. 2005). Only a limited number of inland resource assessments rely exclusively on catch data, and thus, reliable estimates of the trends, status, and drivers of inland fishery resources have never been obtained (Beard et al. 2011).

Lake ecosystems throughout the globe are becoming heavily degraded by human activities, with negative effects on native fish and fisheries (Millennium Ecosystem Assessment 2005, Dudgeon et al. 2006). One of the most pervasive and damaging anthropogenic drivers is the introduction of exotic piscivorous fish (hereafter referred to as piscivores), which have direct or cascading effects on native fish and fisheries and dramatically alter the structure, stability, and function of the ecosystems (Mills et al. 1994, Moyle and Light 1996, Vander Zanden et al. 1999, Eby et al. 2006, Gozlan et al. 2010).

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For example, introductions of the exotic Nile perch (*Lates niloticus*) to Africa's Lake Victoria increased the economic and social benefits, while accelerating the decline of the diverse endemic haplochromine cichlid species and altering the food web structure (Goldschmidt et al. 1993). Furthermore, lakes now often support multiple exotic species, and increases in the number of exotic piscivores may further reduce inland fishery resources (Findlay et al. 2000, Miyake and Miyashita 2011). However, the effects of multiple exotic piscivores on the provision of ecosystem goods and services have seldom been documented empirically (Pejchar and Mooney 2009, Strayer 2012).

Inland fisheries are crucial to the livelihoods and social well-being of many communities in Asian countries (Allan et al. 2005, Welcomme et al. 2010). In 2009, Asia contributed 67.4% of the global inland fish production, and the total catches in China, South Asia, Southeast Asia, and West Asia have been increasing sharply since the 1950s (The Food and Agriculture Organization; FAO). However, the status of Japanese inland fisheries differs from the status of inland fisheries in other Asian countries: both total catch and fishing effort have declined in Japan. The total catch exceeded 120 000 metric tons (1 metric ton = 1 Mg) in the mid-1970s but has declined since then, dropping to less than 40 000 metric tons in the late 2000s (Katano and Matsuzaki 2012). Awareness of the ecological and economic impacts of exotic piscivores on commercially important species has increased in Japan, where there are few native piscivores (Azuma and Motomura 1998, Yuma et al. 1998, Nakai 1999, Kitano 2004, Matsuzaki et al. 2011, Katano and Matsuzaki 2012). However, assessing the effects of exotic piscivores on the resources based on catch data or short-term data may be misleading, and the relative importance of anthropogenic drivers, including eutrophication and lakeshore development, must be assessed to prioritize management and restoration actions.

Although data on inland fishery resources are extremely limited in Japan, compiling independent data on fishery statistics and exploring the macroecological patterns would enable us to assess their trends and current status. In Japanese lakes, two successive and unique schemes for tracking the lakes' fisheries were organized in the early 1950s by the Ministry of Agriculture, Forestry and Fisheries (MAFF): the Annual Statistics of Fishery and Aquaculture Production (ASFAP) and the Census of Fisheries (CF). The ASFAP and CF databases contain catch data and data on fishing effort and power, respectively. Although the CF database has been neglected in the past due to the large number of missing values (Katano and Matsuzaki 2012), recent progress in Bayesian hierarchical models can help estimate population dynamics from data with observation errors, missing values, or uneven census intervals (Clark and Bjornstad 2004, Nadon et al. 2012). Therefore, in the absence of other available information,

unique fishery statistics present a rare opportunity to reconstruct the trajectories of entire communities (Matsuda et al. 2009).

The aims of this study were to examine the long-term trends, changes, and the temporal stability of inland fishery resources in Japanese lakes and to identify the potential underlying drivers of the changes in and the stability of CPUE (catch per unit effort). We compiled total annual catch data for 23 lakes from the ASFAP database and the total fished days per year (as an indicator of fishing effort) and the number of powered and nonpowered fishing boats per year (as an indicator of fishing power) from the CF database. Using a Bayesian state-space modeling approach, we estimated the long-term trends in the species-aggregated CPUE of entire communities (Myers and Worm 2003, Thurstan et al. 2010, Buchheister et al. 2013) for each lake as the only possible measure of relative abundance. Although the aggregated CPUE metrics can be biased and hyper-responsive indices of community abundance if species catchabilities are not constant (Maunder et al. 2006), we used these metrics because they provide relatively simple characterizations of the state of the resources for government agencies and decision-makers, preserve the directionality of community changes, and accurately represent the trends of the dominant species (Lorenzen et al. 2006, Hoeninghaus et al. 2009, Rist et al. 2010, Buchheister et al. 2013). In ecosystem-based fisheries management, species-aggregated indicators can also provide a more comprehensive ecosystem assessment than any single measure (Rist et al. 2010). Furthermore, we quantified CPUE changes and stability over the 10, 20, and 30 years preceding 2008 using the estimated CPUE trends, and we examined the relationships between the changes and stability of CPUE and anthropogenic drivers, including exotic piscivores, lakeshore development, and eutrophication. In this analysis, we also included the effects of morphometric characteristics of the lake because lake morphology can be related to the food web structure and thus community dynamics (Post 2002, Mehner et al. 2005).

METHODS

Data collection

To estimate the aggregated CPUE of entire communities, we collected three types of fisheries data: total annual catch data, total number of days fished per year, and the number of powered and nonpowered fishing boats per year. We targeted 23 natural lakes for which all three types of data are available (Fig. 1).

The long-term annual total catch data gathered annually from each lake between 1954 and 2008 were obtained from the ASFAP database (Appendix A), which contains catch data, in tons per year, for commercially important fish and invertebrate species or groups caught using various types of fishing gears, including trawl nets, gill nets, longlines, stationary nets, and rakes. These data were collected once per year by

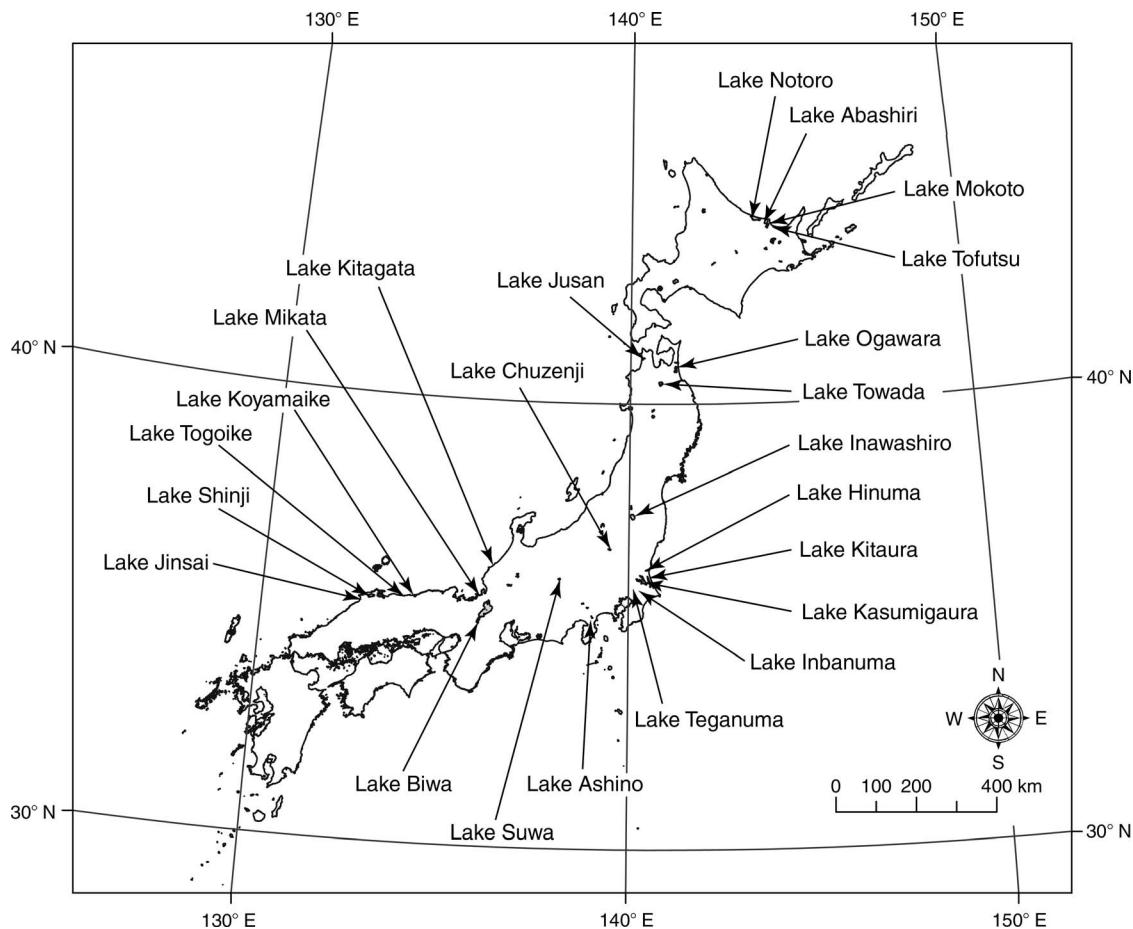


FIG. 1. Map of the 23 studied lakes, which represent important inland fisheries in Japan.

mail surveys of the Inland Water Fisheries Cooperative Associations for each lake (i.e., a self-reporting survey). We used only the total catch data because there are no fishing effort data available at the species or group level. The raw data originally included 21 species or groups: salmon (mainly *Oncorhynchus keta*), pink salmon (*Oncorhynchus gorbuscha*), kokanee (*Oncorhynchus nerka*), masu salmon (*Oncorhynchus masou*), seema (*Oncorhynchus masou masou*), rainbow trout (*Oncorhynchus mykiss*), char (*Salvelinus*, spp.), pond smelt (*Hypomesus nipponensis*), sweet fish (*Plecoglossus altivelis*), icefish (*Salangichthys microdon*), common carp (*Cyprinus carpio*), crucian carp (*Carassius*, spp.), Japanese dace (*Tribolodon hakonensis*), pale chub (*Zacco platypus*), loach (*Misgurnus anguillicaudatus*), eel (*Anguilla japonica*), flathead mullet (*Mugil cephalus*), gobies (mainly *Tridentiger brevispinis*), shrimp (mainly *Macrobrachium nipponense*), freshwater clam (Cyrenidae), and others.

Long-term data on the total fishing effort and power, collected every five years from 1954 to 2008, were obtained from the CF database. The CF database includes data on the total number of days that licensed fishermen worked on lakes throughout a year (Appendix B). These data were collected every five years by mail

surveys from the Inland Water Fisheries Cooperative Associations for each lake (i.e., self-reporting), but there are no effort data available at the species or group level. Data on the number of nonpowered and powered fishing boats operating on each lake (1954–2008) were also obtained from the CF database (Appendices C and D). Any fishing boat with an engine installed in the hull and a propulsion unit attached outside the hull is considered to be a powered boat.

The annual averages of total catch data, days fished, and the number of powered and nonpowered fishing boats were available for 46 years (range 25–55), 8 years (range 5–11), and 9 years (range 7–11), respectively (Appendices A–D).

Estimating long-term trends in the CPUE

Because there were many missing values (years with no census) in the fishery data, we applied a Bayesian state-space formulation that incorporated the catch data, the fishing effort data, and the number of powered fishing boats to estimate long-term trends in the CPUE (tons/day/fisherman) of the entire community of each lake. The state-space modeling approach is well suited for the analysis of sparse long-term data, which often

has missing values (Humbert et al. 2009, Swain et al. 2009, Fay and Punt 2013).

Observation models.—We assumed that the log-transformed data for catch (CATCH) and fishing effort (EFFORT) in year t on lake i would follow normal distributions. We assumed a common variance σ_1^2 for catches among lakes because the catch data were recorded in a standardized manner in every lake. However, we assumed a different variance, $\sigma_{2,i}^2$, for fishing effort to account for different degrees of data uncertainty among lakes. In our notation, we use uppercase variable names for observed data and lowercase variable names for parameters that are estimated in the statistical model specified as follows:

$$\log(\text{CATCH}_{i,t}) \sim N(\log(\text{catch}_{i,t}), \sigma_1^2) \quad (1)$$

$$\log(\text{EFFORT}_{i,t}) \sim N(\log(\text{effort}_{i,t}), \sigma_{2,i}^2). \quad (2)$$

Process models.—We then defined the expected value of CATCH (i.e., catch) as:

$$\text{catch}_{i,t} = c_{1,i} \times \text{cpue}_{i,t} \times \text{effort}_{i,t} \times \text{power}_{i,t} \quad (3)$$

where $c_{1,i}$ is a constant for lake i , $\text{effort}_{i,t}$ is the fishing effort in year t at lake i and $\text{power}_{i,t}$ is the fishing efficiency in year t on lake i . In this definition, we assumed that $\text{cpue}_{i,t}$ represents the relative fish density at time t in lake i , given that the value for the first year is 1. This assumption is appropriate and parsimonious because we only focus on temporal changes and trends within a lake. We estimated the CPUE for each year and lake, calculated as $c_{1,i} \times \text{cpue}_{i,t}$, based on Eq. 3. The terms on the right side of the equation are defined as follows:

$$\text{cpue}_{i,t} = r_{i,t} \times \text{cpue}_{i,t-1} \quad (4)$$

$$\log(r_{i,t}) \sim N(\log(r_{i,t-1}), \sigma_{3,i}^2) \quad (5)$$

where $r_{i,t}$ is the rate of change of $\text{cpue}_{i,t}$ per year. We assumed that the degree of the rate of change exhibited temporal autocorrelation with the rate in the previous year. The term $\sigma_{3,i}^2$ reflects the strength of the autocorrelation between the years. Effort is then defined as:

$$\log(\text{effort}_{i,t}) = c_{2,i} + \tau_{1,i,t} \quad (6)$$

where $c_{2,i}$ are constants and $\tau_{1,i,t}$ is a conditional autoregression term (CAR; Latimer et al. 2006) that reflects the autocorrelation with years $t - 1$ and $t + 1$, and the strength of the autocorrelation is controlled by the variance among years (i.e., $\sigma_{4,i}^2$). Power is define as:

$$\text{power}_{i,t} = a(1 - \text{med.rpb}_{i,t}) + \text{med.rpb}_{i,t} \quad (7)$$

where a is the relative efficiency of a nonpowered boat, given that the efficiency of a powered boat is assumed to be 1. We assumed that all lakes had a common efficiency, a . The value of a can range from 0 to 1.

The term $\text{med.rpb}_{i,t}$ is the posterior median of the ratio of powered boats to total boats, $\text{rpb}_{i,t}$, which is estimated in Eqs. 8–12.

Models for estimating the ratio of powered boats.—We assumed that the log-transformed data for the number of powered boats (PB) and the number of nonpowered boats (NPB) in year t on lake i would follow normal distributions with a variance of σ_{is}^2 :

$$\log(\text{PB}_{i,t}) \sim N(\log(\text{pb}_{i,t}), \sigma_{5,i}^2) \quad (8)$$

$$\log(\text{NPB}_{i,t}) \sim N(\log(\text{npb}_{i,t}), \sigma_{6,i}^2) \quad (9)$$

$$\log(\text{pb}_{i,t}) = c_{3,i} + \tau_{2,i,t} \quad (10)$$

$$\log(\text{npb}_{i,t}) = c_{4,i} + \tau_{3,i,t} \quad (11)$$

$$\text{rpb}_{i,t} = \text{pb}_{i,t} / (\text{pb}_{i,t} + \text{npb}_{i,t}) \quad (12)$$

where $c_{3,i}$ and $c_{4,i}$ are constants and $\tau_{2,i,t}$ and $\tau_{3,i,t}$ are conditional autoregression terms (Latimer et al. 2006) that reflect the autocorrelation with years $t - 1$ and $t + 1$, and the strength of the autocorrelation is controlled by variance among the years (i.e., $\sigma_{7,i}^2$ and $\sigma_{8,i}^2$ for $\tau_{2,i,t}$ and $\tau_{3,i,t}$, respectively). Separating the estimation from the main models could underestimate the uncertainty in the estimation of CPUE. However, this underestimation is unlikely because the trend of the ratio of powered boats was a simple increase over time for all of the lakes (Appendix E), and additionally, both the numbers of powered boats and nonpowered boats were estimated precisely by the model specified here (>99% data fit for all of the lakes; see Appendices C and D).

Priors, parameter estimation, and model checking.—The models were fitted to the 23 lake data sets simultaneously using the Bayesian simulation-based method (Markov chain Monte Carlo, MCMC) in WinBUGS 1.4 in combination with R release 3.0.2 (package R2WinBUGS). We assigned vague priors for the parameters to be estimated. We used normal priors with a mean of 0 and a variance of 1.0×10^{-4} for $c_{1,i}$ and used improper uniform distributions for other c_s values, as suggested by Spiegelhalter et al. (2003). For the conditional autoregression terms (i.e., τ_s), we used the normal setting of the *car.normal* function in WinBUGS (Spiegelhalter et al. 2003). We used gamma distributions with shape parameters of 1.0×10^{-2} and 1.0×10^{-2} for the precision of the conditional autoregression terms in the main model (i.e., $1/\sigma_{4,i}^2$), 5.0×10^{-1} and 5.0×10^{-3} for those in the models of the ratio of powered boats ($1/\sigma_{7,i}^2$ and $1/\sigma_{8,i}^2$), and 1.0×10^{-3} and 1.0×10^{-3} for the other precision terms (i.e., $1/\sigma_{2,i}^2$ s). For the relative efficiency of a nonpowered boat, a , we assumed a uniform prior ranging from 0 to 1. For the estimation of the main model, we performed three chains of 600 000 MCMC iterations with 100 000 steps as the burn-in, which was discarded as samples before convergence. We

sampled from the posterior distributions at each 100 MCMC iterations (i.e., 100 thin numbers), which amounted to 5000 posterior samples for each parameter for each chain. Convergence was assessed using the estimates from the three chains by checking whether the R-hat indicator (Gelman and Rubin 1992) of each parameter had reached a value of approximately 1. In addition, we calculated the Geweke diagnostic (Geweke 1992) and Heidelberger-Welch diagnostic (Heidelberger and Welch 1983) to check the convergence of each parameter. These diagnostics were calculated using the R package CODA with default settings.

In addition, to assess the fit of the models to the data, we estimated the predictive distributions (Ntzoufras, 2009) of the four observed variables (catch, fishing effort, number of powered boats, and number of nonpowered boats) at each time and lake by sampling from the posterior distributions specified in Eqs. 1, 2, 8, and 9. We obtained 1000 samples of the predictive distributions of the four variables at each time and lake and then regressed their medians onto the corresponding observed data for each lake. To evaluate the goodness of fit of the predictive distributions to the data, we calculated determination coefficients (R^2) based on linear regression analysis with the median of the predictive distribution as the explanatory variable and the observed data as the response variable.

Quantifying CPUE changes and stabilities

Using the estimated CPUEs, we quantified the changes in and the stability of CPUE over 10 years (1998–2008), 20 years (1988–2008), and 30 years (1978–2008) for each lake. This approach is very useful for calculating population changes (e.g., Amano et al. 2010).

To quantify the changes in CPUE from the base to latest year (i.e., 2008), we set 1998, 1988, and 1978 as the base years (i.e., the CPUE in the base year equals 1) and calculated the CPUE changes over the past 10, 20, and 30 years, respectively.

To measure the temporal stability of the CPUE over 10, 20, and 30 years, we calculated two stability indices using the estimated CPUEs for each lake. First, we calculated the inverse of the coefficient of variation (CV^{-1}), that is, the mean CPUE divided by the detrended standard deviation of the CPUE (Tilman et al. 2006). Detrending was performed by calculating the standard deviation for the residuals from a linear regression of CPUE vs. year, which provided a better error distribution and fit the data better (Tilman et al. 2006). Increased CV^{-1} values indicate greater temporal stability. Second, as another proxy of stability, we calculated the variability in the rate of CPUE change, that is, the standard deviation of the annual rate of CPUE change (SD_{cr}) over the 10-, 20- and 30-year periods. If the trends in CPUEs were nonlinear, this index would be more robust with regard to the effects of the trend component in CPUEs than CV^{-1} . Lower SD_{cr}

values indicate greater temporal stability. To consider the uncertainty in the parameter estimation, we randomly sampled a set of 100 CPUE values from the MCMC samples and calculated the metrics for each of the data sets (i.e., 100 replications for each metric at each lake).

Analyzing the factors associated with CPUE changes and stabilities

We analyzed the relationships between CPUE changes or stabilities and seven predictor variables related to lake morphometry and anthropogenic drivers. The lake morphometric variables considered were the maximum depth (m), lake area (km^2), a variable for brackish or freshwater, and the catchment : lake area ratio. The data for these variables were obtained from Tanaka (1992). We examined the total phosphorus concentrations (TP; mg/L) and total nitrogen concentrations (TN; mg/L) as proxies for eutrophication. We obtained data on the annual mean TP and TN in 2000 from the results of the Water Quality Survey of Public Water Areas (Ministry of the Environment 2002). We selected TP alone because there is a high correlation between TP and TN ($r = 0.9$). We also obtained the percent coverage of concrete bank protection (%) as a proxy for shoreline development from the results of the Fourth National Survey on the Natural Environment, conducted in 1991 by the Ministry of the Environment (Tanaka 1992).

We determined the presence and absence of seven exotic piscivores by gathering information from regional museum specimen collections and records from peer-reviewed and unpublished literature sources. The seven exotic species are as follows: largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), channel catfish (*Ictalurus punctatus*), rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), and snakehead (*Channa argus*). Largemouth bass, bluegill, brown trout, brook trout, and snakehead were illegally introduced into Japanese lakes mainly for sport fishing or, in a few cases, invaded when contaminated stock were added to enhance native populations of commercially important fish species (Kitano 2004, Katano and Matsuzaki 2012). Channel catfish were originally introduced to Japan for aquaculture and successfully established in certain lakes after escaping from aquaculture facilities or after being illegally released (Matsuzaki et al. 2011). In the 23 lakes in this study, these six exotic piscivores are not commercially targeted by local fishermen. In contrast, rainbow trout is an important fish for cultivation and fishing and has been introduced intentionally into certain lakes (Katano and Matsuzaki 2012). In two of the 23 lakes (Lake Ashino and Lake Chuzenji), they have been stocked and caught as commercially important species since the 1960s.

Largemouth bass, rainbow trout, and brown trout are listed among the 100 of the world's worst invasive alien species because of their severe impacts on native

communities (Lowe et al. 2000). Many earlier studies have reported that these seven species of fish have had serious impacts on native communities and commercial fisheries in Japanese freshwater ecosystems (Nakai 1999, Kitano 2004, Matsuzaki et al. 2011, Katano and Matsuzaki 2012). In particular, largemouth bass, bluegill, and channel catfish were designated invasive alien species (IAS) by the Ministry of the Environment of Japan in 2006.

Because all exotic piscivores species are not ecologically identical, their impacts depend greatly on the functional traits of species. The most important issue is how new functional groups (rather than species) invade an ecosystem. Thus, we used functional group richness (FGR; the number of functional groups) rather than species richness to characterize the effect of exotic piscivores on the fishery resources. We could not use functional diversity (FD) because this index cannot distinguish between species richness of 0 or 1. We identified functional groups based on traits (i.e., trait-based functional group classification; Petchey and Gaston 2006). We classified the seven exotic fish species into functional groups using a functional dendrogram based on 16 functional traits that reflect resource use and life-history strategies (Matsuzaki et al. 2013). We identified five clusters as functional groups (Appendix F). The cut-off for the number of clusters was determined based on biological interpretations.

To investigate the factors that determine the changes and stability of the CPUE, we fitted generalized linear mixed-effect models (GLMMs) to the data using the *lmer* function implemented in the *lme4* library of the R package. The GLMMs were fitted using a Gaussian distribution with an identity link function. The models included the seven predictor variables as fixed factors and lake identity as a random factor to consider uncertainty within each lake, i.e., variance among 100 replications.

We then used an information theoretic approach (Burnham and Anderson 2002). We created a GLMM using all possible combinations of the explanatory variables and identified the best model on the basis of the Akaike Information Criterion (AIC) with a correction for small sample sizes (AIC_c) and Akaike weight (w_i). When there are several similarly weighted top models, model averaging can be used to incorporate the model uncertainty into the estimated parameters with respect to inferences from a single-best model from the model set (Burnham and Anderson 2002). In this study, the best model was not strongly supported. Therefore, we performed model averaging with the *model.avg* function within the *MuMIn* package (Barton 2009). Model averaging provides unconditional model variances and more reliable parameter estimates for each predictor. To determine the reliability of the predictor estimates from averaging, we calculated model-averaged parameter estimates and standard errors for each predictor variable using the relative AIC_c weights of

the models in which the variables appeared. Once the model-averaged parameters were obtained, the significance of each explanatory variable was tested using Wald tests based on Z values. We also calculated the relative importance of each explanatory variable as the sum of w_i over all of the models ($\sum w_i$) in which the parameter of interest appears. To examine the importance of the random effect (i.e., the variability in the posterior for each lake), we compared the variance of the random effect with that of the residual using the best model with the lowest AIC_c (Appendix G).

All of the response variables and several explanatory variables were log-transformed to improve normality and linearity. The collinearity between explanatory variables was tested using Pearson correlation coefficients (r). All r values were below 0.55, indicating that multicollinearity did not bias the interpretations (if $r > 0.7$, then the regression may be biased). The statistical analyses were conducted using the statistical package R 3.0.3 (R Development Core Team 2014).

RESULTS

Long-term trends in CPUE

Using Bayesian state-space models, we successfully estimated long-term trends in the CPUE of entire communities in each lake (Fig. 2). All of the parameters and state variables in the models were well converged in terms of the \hat{R} indicator (presented in further detail in the Supplement). Additionally, the predictive distribution estimated from the models precisely matched the observed data (catch, fishing effort, number of powered boats, and number of nonpowered boats; Appendices A–D). The estimates of CPUE between the early 1950s and the early 1970s had wider credible intervals due to the relatively small amount of raw data available. The fishing effort declined significantly in 19 lakes over the 30-year period analyzed (simple regression, $P < 0.05$), whereas fishing efforts increased significantly for Lake Jusan and Lake Jinsai ($P < 0.05$), and there were no significant trends in the fishing effort of Lakes Ogawara and Togoike (Appendix B). In all lakes, the proportion of powered boats increased throughout the late 1970s but subsequently remained constant (Appendix E).

The CPUEs declined in 17, 19, and 15 of the 23 lakes over the 10-, 20-, or 30-year-analysis periods, respectively. The CPUEs of 13 lakes exhibited a consistent decline in all three periods. The mean 10-, 20-, and 30-year rates of the CPUE declines for these 13 lakes were 48.7%, 42.2%, and 45.1%, respectively.

Drivers of change and temporal stability of the CPUE

The model-averaging analysis revealed that the FGR of exotic piscivores was the strongest predictors of the CPUE changes in all three periods and had a negative effect on CPUE (Table 1, Fig. 3). Other anthropogenic drivers had low relative importance values for all three periods. Lake area had a moderate relative importance value only in the past 20 years and had positive impacts

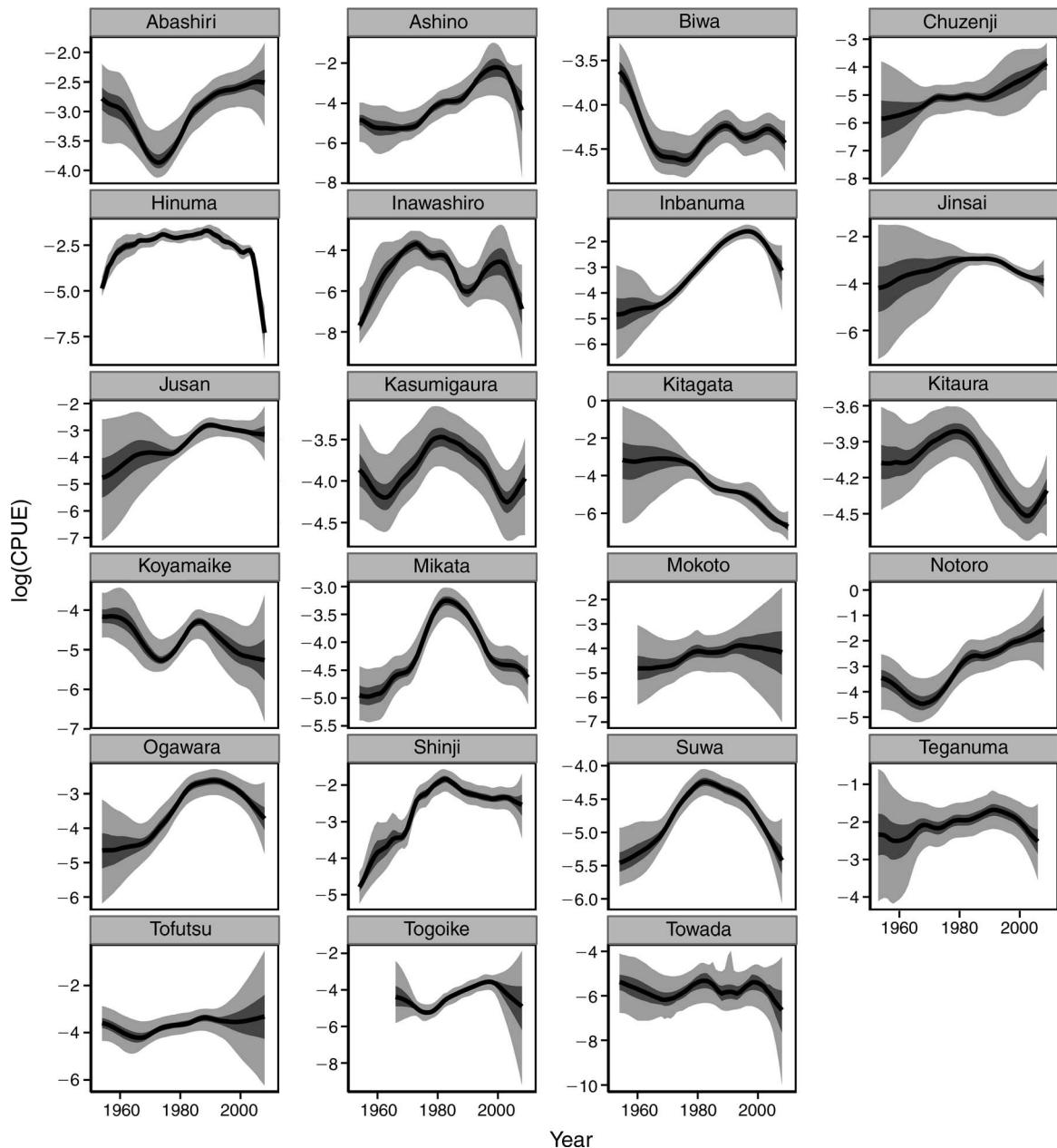


FIG. 2. Estimated long-term trends in the log-transformed CPUEs of entire communities in the 23 lakes. Solid lines indicate posterior median values, and dark and light gray shaded areas indicate 50% and 95% credible intervals, respectively.

on the CPUE changes (Table 1). For the CPUE changes in the three time periods, the variance of the random variable in the best model was the same or slightly greater than those of the residual (Appendix G), implying that there is somewhat high variability within the lakes, but these variabilities did not affect the results.

The factors influencing the stability of the CPUE were different between the two detrended temporal stability indices (Table 1). The model-averaging analysis revealed that lake area contributed substantially to explaining the

variation in CV^{-1} in all three periods. Larger lakes have more stable CPUE (Fig. 4a–c). For the 10-year period, the relative importance value of the FGR of exotic piscivores was high (0.81) and the FGR of exotic piscivores negatively affected CV^{-1} (Fig. 4d). However, CV^{-1} was not influenced by other anthropogenic drivers. For SD_{cr} , the FGR of exotic piscivores was the most important predictor in the 10- and 20-year periods, but the relationships between the FGR of exotic piscivores and the SD_{cr} were marginally significant negative (Table 1, Figs. 4e, f). For the 30-year period, no factors

TABLE 1. Model-averaged parameter estimates and relative variable importance, RVI (0, not predictive; 1, highly predictive) from the generalized linear mixed models (GLMMs), which investigated the relationships between CPUE changes or stability indices and seven predictor variables over 10 (1998–2008), 20 (1988–2008), and 30 (1978–2008) years.

| Response variable and predictors | 10 yr (1998–2008) | | | | 20 yr (1988–2008) | | | | 30 yr (1978–2008) | | | |
|---|-------------------|------|--------------|------|-------------------|------|--------------|------|-------------------|------|--------------|------|
| | Est. (SE) | Z | P | RVI | Est. (SE) | Z | P | RVI | Est. (SE) | Z | P | RVI |
| A) CPUE changes | | | | | | | | | | | | |
| Intercept | -0.16 (0.88) | 0.18 | 0.859 | | 0.56 (1.20) | 0.47 | 0.639 | | 0.47 (1.19) | 0.40 | 0.691 | |
| Lake area | 0.24 (0.15) | 1.58 | 0.114 | 0.56 | 0.26 (0.15) | 1.71 | <i>0.088</i> | 0.60 | 0.30 (0.18) | 1.62 | 0.105 | 0.57 |
| Maximum depth | -0.01 (0.00) | 1.22 | 0.221 | 0.47 | -0.01 (0.01) | 1.31 | 0.190 | 0.52 | -0.01 (0.01) | 1.32 | 0.186 | 0.51 |
| Brackish/freshwater | -0.48 (0.55) | 0.88 | 0.381 | 0.38 | -1.00 (0.62) | 1.62 | 0.104 | 0.60 | -0.83 (0.73) | 1.14 | 0.255 | 0.45 |
| Catchment : lake area ratio | -0.07 (0.25) | 0.27 | 0.789 | 0.29 | -0.19 (0.26) | 0.74 | 0.462 | 0.34 | -0.02 (0.07) | 0.07 | 0.946 | 0.28 |
| Total phosphorus | 5.54 (4.91) | 1.13 | 0.260 | 0.42 | 1.84 (5.30) | 0.35 | 0.729 | 0.29 | 3.75 (0.61) | 0.61 | 0.544 | 0.32 |
| Concrete bank protection (%) | 0.00 (0.01) | 0.17 | 0.869 | 0.29 | -0.01 (0.01) | 1.55 | 0.122 | 0.56 | -0.01 (1.25) | 1.25 | 0.213 | 0.47 |
| FGR of exotic piscivores | -0.43 (0.17) | 2.47 | 0.013 | 0.87 | -0.44 (0.19) | 2.36 | 0.018 | 0.83 | -0.52 (0.22) | 2.40 | 0.017 | 0.84 |
| B) CPUE stability, CV⁻¹ | | | | | | | | | | | | |
| Intercept | 1.00 (0.64) | 1.57 | 0.117 | | 0.51 (0.43) | 1.20 | 0.231 | | 0.47 (0.36) | 1.33 | 1.85 | |
| Lake area | 0.26 (0.09) | 2.92 | 0.004 | 0.93 | 0.24 (0.07) | 3.35 | 0.001 | 0.98 | 0.18 (0.06) | 3.18 | 0.001 | 0.96 |
| Maximum depth | 0.00 (0.00) | 1.25 | 0.213 | 0.48 | 0.00 (0.00) | 0.97 | 0.333 | 0.39 | 0.00 (0.00) | 0.56 | 0.574 | 0.32 |
| Brackish/freshwater | -0.35 (0.32) | 1.09 | 0.277 | 0.43 | -0.06 (0.24) | 0.23 | 0.822 | 0.29 | -0.05 (0.19) | 0.26 | 0.797 | 0.29 |
| Catchment : lake area ratio | 0.19 (0.14) | 1.38 | 0.167 | 0.49 | 0.14 (0.11) | 1.26 | 0.209 | 0.45 | 0.13 (0.09) | 1.48 | 0.139 | 0.52 |
| Total phosphorus | 2.66 (2.98) | 0.90 | 0.371 | 0.37 | 2.08 (2.32) | 0.90 | 0.368 | 0.37 | 2.69 (1.83) | 1.47 | 0.143 | 0.52 |
| Concrete bank protection (%) | 0.00 (0.00) | 0.87 | 0.382 | 0.38 | 0.00 (0.00) | 0.04 | 0.968 | 0.29 | 0.00 (0.00) | 0.27 | 0.787 | 0.29 |
| FGR of exotic piscivores | -0.24 (0.10) | 2.27 | 0.023 | 0.81 | -0.12 (0.08) | 1.63 | 0.103 | 0.58 | -0.11 (0.06) | 1.81 | 0.071 | 0.64 |
| C) CPUE stability: SD_{cr} | | | | | | | | | | | | |
| Intercept | -3.05 (0.50) | 6.15 | 0.00 | | -2.55 (0.44) | 5.75 | 0.000 | | -2.47 (0.39) | 6.34 | 0.000 | |
| Lake area | -0.05 (0.08) | 0.70 | 0.481 | 0.34 | -0.11 (0.07) | 1.44 | 0.149 | 0.52 | -0.09 (0.07) | 1.39 | 0.166 | 0.50 |
| Maximum depth | 0.00 (0.00) | 1.44 | 0.151 | 0.54 | 0.00 (0.00) | 1.33 | 0.185 | 0.49 | 0.00 (0.00) | 1.20 | 0.230 | 0.46 |
| Brackish/freshwater | 0.36 (0.29) | 1.24 | 0.216 | 0.47 | 0.17 (0.28) | 0.63 | 0.530 | 0.34 | 0.24 (0.25) | 0.96 | 0.336 | 0.39 |
| Catchment : lake area ratio | -0.09 (0.12) | 0.70 | 0.483 | 0.33 | -0.11 (0.12) | 0.91 | 0.364 | 0.37 | -0.05 (0.11) | 0.46 | 0.645 | 0.30 |
| Total phosphorus | -2.02 (2.47) | 0.82 | 0.415 | 0.35 | -2.55 (2.45) | 0.92 | 0.360 | 0.37 | -2.41 (2.18) | 1.11 | 0.268 | 0.41 |
| Concrete bank protection (%) | 0.00 (0.00) | 0.08 | 0.940 | 0.29 | 0.00 (0.00) | 0.56 | 0.579 | 0.32 | 0.00 (0.00) | 0.67 | 0.505 | 0.34 |
| FGR of exotic piscivores | 0.17 (0.09) | 1.86 | <i>0.063</i> | 0.67 | 0.15 (0.09) | 1.77 | <i>0.077</i> | 0.64 | 0.13 (0.08) | 1.60 | 0.110 | 0.58 |

Notes: FGR is functional group richness. The predictors identified as important (RVI > 0.7) are highlighted in bold. P values are based on Wald test Z score. Values of P < 0.05 are boldface, values of P < 0.1 are italic.

affected the SD_{cr}. For CV⁻¹ and SD_{cr} in the three time periods (except SD_{cr} over 30 year), the variance of the random variable in the best model was smaller than that of the residual (Appendix G), indicating that the effects of the random factor were small.

Although we conducted additional statistical analyses to examine the effect of the interaction between the FGR of exotic piscivores and the lake area or depth and the interaction between the FGR of exotic piscivores and the percent coverage of concrete bank protection, the relative importance value of these interaction terms were very low (0.08–0.48) for all analysis periods.

DISCUSSION

By compiling two sets of long-term fishery statistics and using Bayesian state-space models, we documented trajectories and recent declines in the CPUE for entire communities in Japanese lakes. Although aggregated CPUE should be carefully interpreted as an indicator of community biomass (e.g., as noted by Maunder et al.

2006), the decline is particularly serious because it implies that entire communities, rather than single stocks, have changed across Japanese lakes. Furthermore, our macroecological analyses clearly indicate that the FGR of exotic piscivores was the most important predictor of the change and stability of the CPUE among the drivers we considered. To the best of our knowledge, this study is the first to document long-term trends in inland fishery resources and to show that increasing numbers of exotic piscivores reduce those resources and their temporal stability. Our analysis provides the missing baseline for inland fishery resources, which is necessary for future management and restoration, and highlights the need to evaluate the trends and current status of inland fishery resources at a global scale.

Current trends and drivers of the changes in CPUE

The FGR of exotic piscivores was the most consistently well-supported predictor variable for CPUE and these two variables were negatively correlated (Table 1,

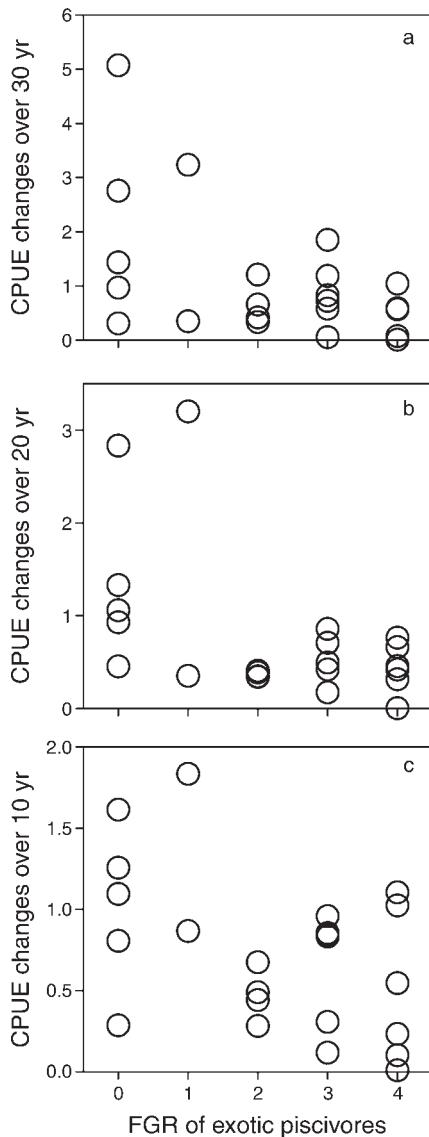


FIG. 3. The relationships between the CPUE changes and the functional group richness (FGR) of exotic piscivores in 23 Japanese lakes over the past (a) 30, (b) 20, and (c) 10 years. To consider uncertainty, the data on the CPUE changes represent median values for 100 replications (see *Methods: Quantifying CPUE changes and stabilities*).

Fig. 3). Recognizing that statistical relationships do not necessarily imply causality, particularly in larger-scale studies, the negative impacts of exotic piscivores on the CPUE are supported by evidence from field experiments and surveys. The negative relationship between the richness of exotic piscivores and the richness of native fish species has been reported previously (Findlay et al. 2000). Hughes and Herlihy (2012) demonstrated that the abundance of exotic piscivores is associated with the abundance of native fish species. Some previous studies conducted in Japan have shown that exotic piscivores decrease the richness or abundance of native fish species,

including commercially important fish species (Azuma and Motomura 1998, Nakai 1999, Kitano 2004, Matsuzaki et al. 2011, Tsunoda and Mitsuo 2012).

Considering that the FGR was a better predictor than species richness (data not shown), the addition of new functional groups may negatively impact the CPUE. The invasion of exotic piscivores as new functional groups into ecosystems has a direct negative effect on native prey species and community-wide indirect effects on native species at lower trophic levels, the food-web structure, and ecosystem stability and functions (Vander Zanden et al. 1999, Maezono et al. 2005, Eby et al. 2006, Strayer 2012). Matsuzaki et al. (2013) found that invasive exotic fish species in Japan are functionally dissimilar from native species and that their introduction can change functional group composition considerably. Thus, the introduction of exotic piscivores may decrease inland fishery resources over the period of several decades, and increases in the number of such species or the FGR of exotic piscivores may cause further reductions in those resources.

Drivers of the stability of CPUE

Two temporal stability indices for the CPUE, as well as the CPUE itself, were associated with the FGR of exotic piscivores in at least one of the past 10-, 20- or 30-year periods (Table 1, Fig. 4). The introduction of piscivores can increase the length of the food chain because there are few native piscivores in Japan. Systems with longer food chains are less stable than those with shorter food chains (Post 2002). Long et al. (2011) demonstrated experimentally that increasing the food chain length by adding predators destabilizes the abundance of lower trophic levels through the trophic cascade effect. Food web stability is also enhanced by the coexistence of many weak interactions with a few strong interactions (Methratta and Link 2006). Adding piscivores to food webs in Japanese lakes, where native piscivores are scarce, might increase the number of strong trophic links and change the variation in the strength of trophic links, which can reduce food web stability.

In addition to the FGR of exotic piscivores, lake area was the strongest predictor of CV^{-1} in the three periods. There are at least two possible explanations for this result. First, larger lakes tend to have greater habitat heterogeneity and more potential prey refugia. In larger lakes, limited access across subhabitats (e.g., littoral–pelagic) may reduce prey availability and increase the stability of food webs (Tunney et al. 2012). Second, lakes with larger areas are reported to be more diverse in various taxa, such as mollusks, zooplankton, and fish (Browne 1981, Hoffmann and Dodson 2005). The diversity in resource species may stabilize the consumer populations by increasing the availability of resources or ensuring the long-term availability of edible species (Petchey 2000, Narwani and Mazumder 2010). From a management perspective, small lakes should be a high priority with regard to reducing the probability of crashes in stocks and

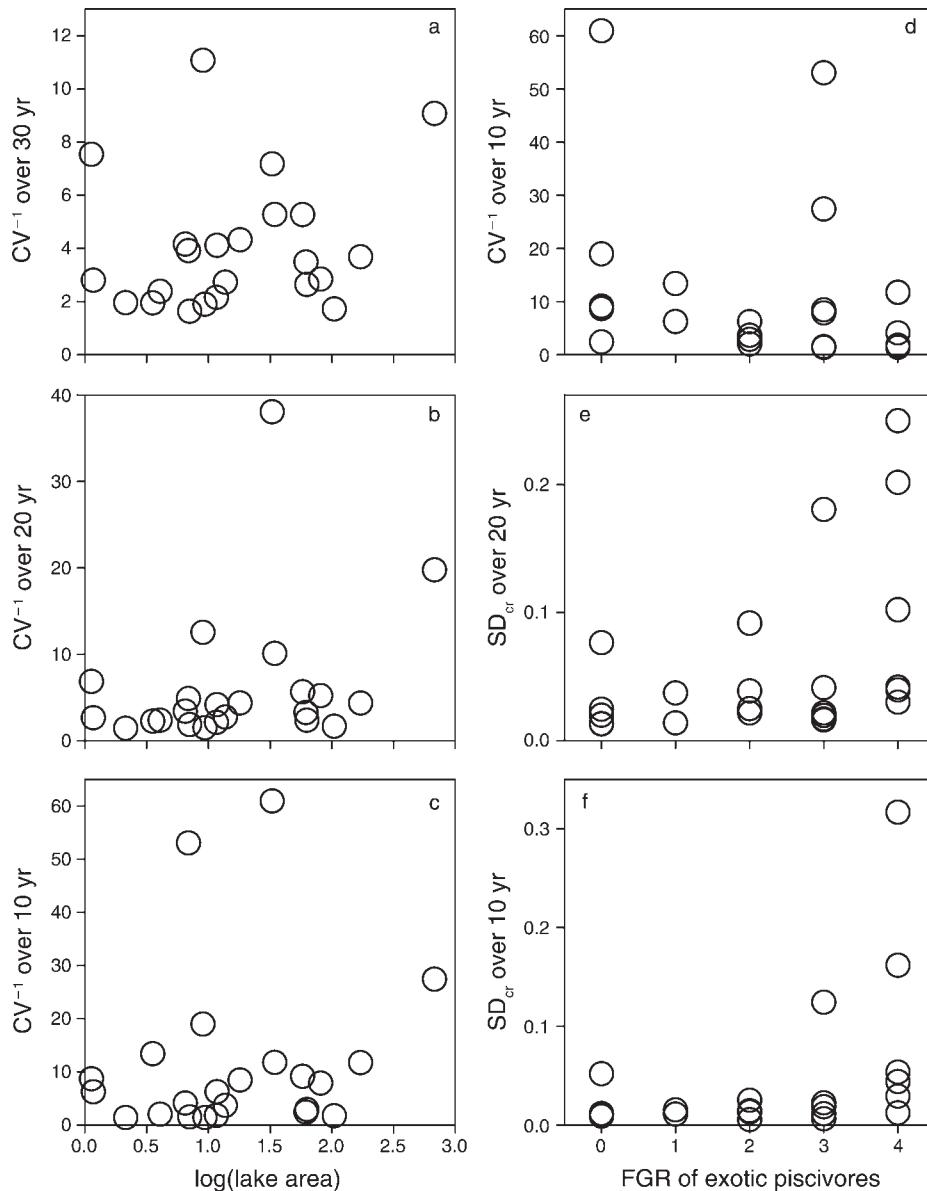


FIG. 4. The relationships between the temporal stability index (CV^{-1}) and log-transformed lake area in 23 Japanese lakes over the past (a) 30, (b) 20, and (c) 10 years, as well as (d) the relationships between CV^{-1} and the functional group richness (FGR) of exotic piscivores over the past 10 years. Relationships between the temporal stability index (SD_{et}) and the functional group richness (FGR) of exotic piscivores are shown over the past (e) 20 and (f) 10 years. To consider uncertainty, the data on the CPUE changes represent median values for 100 replications (see *Methods: Quantifying CPUE changes and stabilities*).

the attendant serious consequences for fisheries because their CPUEs are more vulnerable to temporal fluctuations.

Caveats, limitations, and future issues

Although our analyses showed that the FGR of exotic piscivores is an important driver for of the declines observed in CPUE, we recognize that there may be other factors that were not considered in this study but could be important in regulating the CPUE. Although the overall magnitude of change is clear, there remains uncertainty regarding the trajectories of

individual species; the use of aggregated CPUE metrics may mask the effects of compensatory interactions between species. For example, the species assemblage could be driven by commercial harvest (McClanahan 2010). Furthermore, social factors, such as a shift in consumer preference, could affect the species composition of the catch. Fish prices are a function of supply and demand, and thus may be an important part of a comprehensive understanding of the status and trend of the resources (Matsuda et al. 2009, McClanahan 2010).

Changes in fishing gear and vessel characteristics (e.g., larger boats, large engines, and lighter nets) could influence the trends in the CPUE (Lotze and Milewski 2004, McClanahan et al. 2008). However, we believe that these changes can be discounted. Although the data are limited in most lakes, in Lake Biwa and Kasumigaura (the first and second largest lakes in Japan, respectively), major gear changes, such as the start of trawl fishing, occurred during Japan's period of high economic growth (i.e., 1960s; Shiga Statistics Association of Agricultural and Forestry 1962, Fisheries Office of Kasumigaura and Kitaura in Ibaraki Prefecture 2013). The changes in the proportion of powered boats, which we used to represent fishing efficiency, could be associated with these major gear changes, at least partly (Appendix E). If this is true for other lakes, further research on this aspect is needed.

Allan et al. (2005) reported the effects of overfishing on inland fishery resources in developing countries in Asia and Africa. While the estimated total fishing efforts have declined in 19 of 23 lakes over the last 30 years (Appendix B) and the total number of powered fishing boats on all lakes has not changed (Appendix D), the CPUE did not increase in most lakes. Although our interpretation of these patterns is somewhat speculative, we propose that the effects of harvesting or overfishing on the CPUE of entire communities seems likely to be relatively small over time, especially since the 1980s. Multiple types of data must be collected, and multiple indicators must be used to assess the status of fish stocks and ecosystems (Methratta and Link 2006).

Because we relied on information on the presence or absence of exotic piscivores and did not consider their abundance or the timing of their introductions, we cannot properly understand the long-term effects of exotic piscivores on commercial fish and invertebrates. The effects that invading species have on a system increase with the abundance of these species and are more important when the invading species are functionally different from the native species. These effects can vary over time; thus, both the acute and chronic effects of invasions are important (Strayer et al. 2006). The effects of the FGR of exotic piscivores on the stability of CPUE tended to have greater relative importance for the 10- and 20-year periods than for the 30-year period (Table 1). Although accurate information regarding the timing of all exotic piscivores is available only for certain lakes, the dynamics of their impacts over time are worth exploring further in future studies. It is also unclear how multiple species of exotic piscivores influence populations of commercial fish and invertebrates. In addition to direct predation, the competitive impacts of exotic piscivores on native fish and invertebrate populations may be more important mechanisms (Vander Zanden et al. 1999). Stable isotope analysis can clarify the food web structure and identify the mechanisms of the effects of exotic piscivores (Vander Zanden et al. 1999, Miyake and Miyashita 2011).

Management implications

Our results clearly suggest that it would be highly desirable to prevent further invasions by exotic piscivores and to conduct intensive and continuous removal efforts in the invaded lakes. The Ministry of the Environment of Japan and some local governments began preventing and removing fish designated as IAS by the Ministry of the Environment of Japan on 1 February 2006. Under the IAS Act, releasing, keeping, selling, transferring, translocating, and importing live IAS are strictly regulated. However, few local governments quantitatively monitor the changes in native or commercially important species following these removal schemes. Because removal of exotic piscivores should be performed continuously for long periods of time to suppress the impacts of these fish, such monitoring is strongly encouraged to make management actions more adaptive and effective and to promote and maintain conservation incentives for local people. Because the removal of exotic piscivores occasionally results in undesirable changes to native communities (Maezono et al. 2005), any restoration plan should consider the possibility of unexpected secondary impacts. It is also important to develop effective removal methods for other piscivores because the methods used in Japan are limited in applicability to largemouth bass and bluegill (Katano and Matsuzaki 2012).

Although ecosystem-based resource management of marine ecosystems has received considerable attention, less attention has been paid to regulating the use of inland fishery resources. Thus, both fishery-dependent and fishery-independent data are rare and unevenly distributed. Furthermore, the MAFF has recently reduced the number of lakes monitored under both ASFAP and CF databases due to financial constraints. This situation may impede fishery sustainability and freshwater biodiversity conservation. It is too costly and virtually impossible for the government to further increase monitoring (Matsuda et al. 2009). Therefore, simple ecosystem indicators may be desirable when the data available for management purposes are limited (Jennings 2005). The framework developed in this study may help in assessing the current status using at least three types of fishery statistics data (total fishery production, total fishing effort, and the number of powered and nonpowered boats). A long-term strategy that maintains current fishery statistics and census schemes, such as the ASFAP and CF, without reducing the number of monitoring metrics and target lakes should be constructed to manage and restore inland fishery resources in Japan.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–G and the Supplement are available online: <http://dx.doi.org/10.1890/13-2182.1.sm>