Ann. Limnol. - Int. J. Lim. 53 (2017) 35–45

DOI: 10.1051/limn/2016034

Available online at:
www.limnology-journal.org

Forecasting population dynamics of the black Amur bream (*Megalobrama terminalis*) in a large subtropical river using a univariate approach

Fangmin Shuai[1,2,3], Sovan Lek[3], Xinhui Li[1,2]*, Qianfu Liu[1,2], Yuefei Li[1,2] and Jie Li[1,2]

[1] Pearl River Fisheries Research Institute, CAFS, Guangzhou, 510380, China
[2] Experimental Station for Scientific Observation on Fishery Resources and Environment in the Middle and Lower Reaches of the Pearl River, Zhaoqing, 26100, Ministry of Agriculture, People's Republic of China
[3] Toulouse III – University Paul Sabatier, Toulouse, Cedex 31062, France

Received 25 January 2016; Accepted 07 November 2016

Abstract – Understanding the stocks and trends of fish species using modern information technology is crucial for the sustainable use and protection of fishery resources. *Megalobrama terminalis* (Cyprinidae) is endemic to the large subtropical Pearl River (China) and is a commercially important species. Its population has however been suffering from long-term degradation. In this paper, a seasonal autoregressive integrated moving average (ARIMA) model and redundancy analysis (RDA) were proposed to predict larval abundance and its influence, using larva data collected every 2 days from 2006 to 2013. The ARIMA model provided good forecasting performance and estimated that the population trends will follow a relatively stable cycling trend in the near future. The cross-correlation function model further identified that discharge acted as a trigger for population growth; the effect of discharge on the number of larvae will last at least 5 days. However, the predicted breeding period will decrease significantly compared to 2006–2013. Such variability has the potential to cause a decrease in larva numbers that could destabilize the population dynamics of this species. We conclude that the ARIMA model approach is an especially promising tool for effectively predicting the population trend, which could be helpful in formulating realistic policies for effective fishery management.

Key words: ARIMA model / cross-correlation function / *Megalobrama terminalis* / population dynamics / forecasting

Introduction

Global fishery resources are being increasingly threatened by environmental stressors and habitat deterioration, such as loss of spawning grounds and the obstruction of migration pathways, that result from dam construction, pollution and overfishing (Sala *et al*., 2000; Novacek and Cleland, 2001; Dulvy *et al*., 2003; Morais, 2008; Stenseth and Rouyer, 2008). Small and isolated fish populations are especially susceptible to stochastic changes in population size (Frankham, 1996, 2005). Understanding fish population dynamics and trends, including the variation in the biomass of reproductively mature individuals and in the number of offspring ultimately contributing to recruitment, is crucial for refining stocks and protecting fishery resources (Fromentin and Powers, 2005; Anderson *et al*., 2008; Mouthon and Daufresne, 2008; Mangel *et al*., 2010; Hunt *et al*., 2011).

The genus *Megalobrama* (Dybowsky, 1872; Cyprinidae) includes five species that are widely distributed throughout China, Russia and Vietnam. Among these species, *Megalobrama terminalis* is endemic and dominant in the large subtropical Pearl River. *M. terminalis* is a large fish of high commercial importance due to its palatability and resulting popularity with consumers. However, its local population has been suffering from long-term degradation due to overfishing and habitat loss. High variability of fish populations usually causes a series of problems, such as harm to the stability of the community, which is undesirable for conservation of biodiversity.

Because *M. terminalis* is a semi-migratory fish (Chen and Lu, 2006), it is argued that hydrological changes are among the most important factors affecting its population dynamics. At the same time, recruitment is crucial for

*Corresponding author: lxhui01@aliyun.com

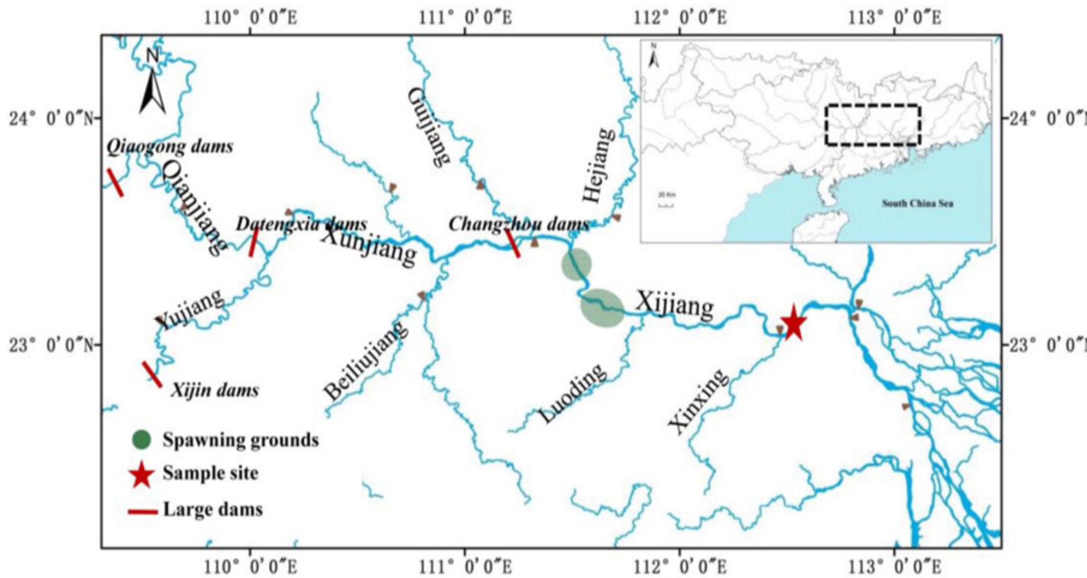

Fig. 1. Location of the Pearl River watersheds in southern China. The circles mark the spawning grounds of the *M. terminalis*. The star marks the site of larvae collection. The elongated rectangular marks indicate the sites of large dams (with capacity > 10 000 kW).

population survival, and spawning by riverine fish depends on specific flow events (Jobling, 1995; Probst *et al.*, 2009). The degree of variability in the flow regime is likely to drive fish reproductive strategies at various temporal and spatial scales (Humphries *et al.*, 1999; Humphries and Lakel, 2000), thereby affecting fish population dynamics. Since fish larval abundance and species composition largely reflect the population and dynamics of the adult fish, if the species identification has been established then larval sampling surveys are a more effective method of obtaining information on the population compared with the analysis of the adult fish (Koslow *et al.*, 2011; Sassa and Hirota, 2013). In particular, larval abundance can lead to shifts in the community structure and changes in species interactions (Copp, 1993; Copp *et al.*, 2010). Important basic notions, such as population dynamics and the mechanisms resulting from these dynamics in this species, such as how discharge affects its population, have thus far not been investigated, despite its ecological and economic significance in the Pearl River.

Therefore, there is a great need to understand the stocks and population dynamics of *M. terminalis*. The purpose of this study was to: (a) identify the status of *M. terminalis* represented by the sequence of observations in the Pearl River; (b) identify the factors affecting population variability; and (c) describe future trends in this species to achieve early management knowledge by advanced mathematical methods.

Materials and methods

Study area

Our study area was located in a traditional larval collecting zone of the Zhaoqing section (23°2′40″N, 112°27′5″E), of the Pearl River, the longest in southern China (≈2400 km). The mean annual discharge can reach 3.3×10^{11} m^3, with high flow in the summer and low flow in the winter. The spawning grounds of *M. terminalis* are distributed in the middle reaches of the Xijiang River (Fig. 1). The Zhaoqing section represents the only pathway for *M. terminalis* larvae to enter the Pearl River Delta network (Tan *et al.*, 2010).

Study species

M. terminalis (Richardson, 1846) is a dominant species and a typical migratory fish of the Pearl River and its tributaries, with individual development occurring in the middle and lower reaches of the river. Fish migrate to their fixed spawning grounds (approximately 150 km away from their living area) after reaching sexual maturity at the age of 2 for males and 3 years for females. They congregate for spawning and lay their sticky eggs on the sand and rocks (Feng *et al.*, 1986).

Data collection

Fish larva samples were collected from the study site from January 2006 to December 2013 using a drift net with a rectangular mouth in the form of an iron frame loop (1.0 $m.L^{-1}$ and 1.5 $m.W^{-1}$) fitted with a rectangular pyramid net (0.8 $m.L^{-1}$ × 0.4 $m.W^{-1}$ × 0.4 $m.D^{-1}$; 0.5 mm mesh) and a filter collection bucket. A flow meter was mounted on the mouth of the net to estimate the volume of water filtered, and thus to calculate larval density. Daily hydrological data of discharge for the period were provided by the Pearl River Water Conservancy Commission and were used to analyse the influence of hydrology on the occurrence of *M. terminalis* larvae in the river. Each year of the study, samples were collected three times a day (06:00–08:00, 13:00–15:00, 19:00–21:00), every other day. Upon collection, larvae were immediately fixed in 5% formalin and later identified to the species level. The relative positions of the dorsal and anal fins, spines and fin rays, as well as vertebra counts were used to identify fish larvae.

Data concerning discharge and temperature were provided by the Pearl River Water Conservancy Commission. Atmospheric pressure and precipitation were collected from http://www.weatheronline.co. The chemical oxygen demand (COD), NH_3-N, dissolved oxygen (DO) and pH were provided by the China National Environmental Monitoring Centre. All environment data were organized on a 2-day basis to match the larval collecting time.

The breeding period was defined as the interval of days between the first breeding day and the last breeding day in a given year. The date of maximum yield was defined as the date at which the most larvae were collected each year. In this study, we used the Spearman's rank correlation to test the breeding period changes and the accumulated daily discharge difference changes in these years. To obtain information about the population status of *M. terminalis* in the community, the entire catch collected by drift nets, shrimp pots and angling in the Zhaoqing section of the Pearl River every month between 2009 and 2013 was examined. All fish were identified and measured for total body length and weight, and gonad stage was also recorded.

Data analysis

Redundancy analysis (RDA)

RDA is widely used by ecologists and combines regression and principal component analysis (PCA). It can be used to model the relationship between the response variables and explanatory variables by means of multiple linear regressions (MLRs) and eigenvalue decomposition of fitted values (Makarenkov and Legendre, 2002; Angeler *et al.*, 2009). It extends MLR by allowing regression of multiple response variables on multiple explanatory variables and consistently outperformed the other statistical tests using all data (Legendre and Legendre, 2012). ANOVA permutation tests (replicated randomly 1000 times) were performed to evaluate the model's performance and significance of constraints. In this study, RDA was applied to determine how environmental variables affect the occurrence pattern and to find out which environmental variables were most related to species occurrence, based on abundance.

In this study, RDA analysis was applied to determine how environmental variables affect the abundance of *M. terminalis* larvae and to find out which environmental variables were most related to spawning based on abundance. Before analysis, larval data were subjected to Hellinger pre-transformation procedures and the environment data were $\log_e(y+1)$ transformed (Legendre and Gallagher, 2001).

Time-series analyses

To determine whether the number of larvae and their variation was affected by river discharge, the cross-correlation function (CCF) was used to compute how discharge affects the abundance of larvae over a range of time lags. The CCF quantifies the degree of similarity or correlation between two time-series as a function of the time shift (*i.e.*, the delay or "lag") between the two time-series. The CCF has been widely used in the analysis of multivariate and spatial time-series and proven useful when analysing complex non-linear dynamics (Paradis *et al.*, 2000). In the relationship between two time-series (y_t and x_t), the series y_t may be related to past lags of the x-series. The CCF is helpful for identifying lags of the x-variable that might be useful predictors of y_t. In our analysis process, CCF is defined as the set of sample correlations between $x_t + h$ and y_t for $h = 0, \pm 1, \pm 2, \pm 3$, and so on. A negative value for h is a correlation between the x-variable at a time before t and the y-variable at time t. When one or more $x_t + h$, with h positive, are predictors of y_t it is sometimes said that x lags y (Chatfield, 2000).

In this study, the x-variable is the discharge data and the y-variable is the fish larva data. Data were $\log_e(y+1)$ transformed before analysis (Legendre and Gallagher, 2001). We filled in some missing values (during bad weather days when no samples were taken) by interpolation Fourier transformation before analysis.

Seasonal ARIMA models

The complexity and non-linearity of increasingly available ecological data requires modern analytical approaches and statistical tools that can accurately analyse the behaviour of fish population dynamics, resulting in increasing applications of univariate autoregressive integrated moving average (ARIMA) models (Chatfield, 2000; Box *et al.*, 2013). ARIMA models have been successfully applied in fishery science for decades (Georgakarakos *et al.*, 2002, 2006; Vilizzi and Copp, 2005; Koutroumanidis *et al.*, 2006; Tsitsika *et al.*, 2007; Manjarres-Martinez *et al.*, 2010). These efficient models can provide accurate operational forecasts of annual commercial catches (Gutierrez-Estrada *et al.*, 2007; Kim *et al.*, 2015) and have become an important tool for forecasting fish populations. Furthermore, the estimate helps to alert managers to fluctuating values for a target species, enabling the formulation of realistic policies for effective fishery management (Jeong *et al.*, 2008).

The influenza time-series that we analysed in this study is characterized by a strong autocorrelation, a property that commonly violates ordinary linear regression. Thus, in order to account for the autocorrelation behaviour, we employed a class of time-series technique namely ARIMA

(Koutroumanidis *et al.*, 2006; Tsitsika *et al.*, 2007). ARIMA models are the most general class of models for forecasting a time-series. An ARIMA model can be viewed as a "filter" that tries to separate the signal from the noise, and the signal is then extrapolated into the future to obtain forecasts. ARIMA is based on the assumption that the response series is stationary, *i.e.* the mean and variances of the series are independent of time. Stationarity can be achieved by differencing the series, or transforming the variable so as to stabilize the variance or mean. In our analysis, we took the logarithmic transformation to reduce the variances of the fish larvae time-series, and subsequently differenced the series until it was stationary. Once the response series was stationary, we examined the autocorrelation function (ACF) and partial autocorrelation function (PACF) to determine the initial autoregressive (AR) and moving average (MA) order (Zhang, 2003; Box *et al.*, 2013). An ARIMA model is notated as ARIMA(p,d,q), where p indicates the AR order, d is the value of differencing orders, and q the MA order (Box *et al.*, 2013; Yu *et al.*, 2014).

Because the abundance of fish larvae presents obvious seasonality with high abundances in summer in the Pearl River, a seasonal ARIMA model was formed by including additional seasonal terms. Seasonal ARIMA models are referred to as ARIMA$(p,d,q)(P,D,Q)_{\mathrm{m}}$ where P, D and Q indicate the seasonal order of AR, differencing, and MA, respectively (Yu *et al.*, 2014).

In this study, we converted all data to weekly time-series to forecast population trends, the seasonality period in our study was 52. We filled in some missing values (no sampling during very bad weather days) by interpolation Fourier transformation before analysis. We selected the appropriate prediction model based on the ACF and PACF, as well as the smallest Akaike's information criterion (AIC) value.

All analyses were performed using R Statistical Software (R Development Core Team, 2011).

Results

Status of *M. terminalis* in the community

Based on the catch data from 238 different fishing vessels between 2009 and 2013, a total 1471 individuals were collected, comprising 45 taxa representing 13 families and eight orders. *M. terminalis* was present in 177 catches. This revealed that *M. terminalis* was the most dominant species in the fish community at our study site (Table 1).

Reproductive characteristics

Based on the data collected between 2006 and 2013, the spawning period of *M. terminalis* in the Pearl River extended from April to October (Fig. 2). The earliest occurrence of larva was on March 31, 2006 and the latest was on November 1, 2007. The breeding period decreased

Table 1. The 20 most dominant species in the middle and lower reaches of the Pearl River.

Taxon/species	Abundance (individuals)	Frequency
Cypriniformes		
Cyprinidae		
Megalobrama terminalis	**1471**	**177**
Squaliobarbus curriculus	1162	96
Cirrhina moitorella	909	106
Cyprinus carpio	96	47
Hmiculter leucisxulus	701	26
Hypophthalmichthys molitrix	85	36
Parabramis pekinensis	100	40
Xenocypris davidi	223	25
Ctenopharyngodon idellus	77	21
Erythroculter recurviceps	48	24
Aristichthys nobilis	12	10
Elopichthys bambusa	6	5
Megalobrama amblycephala	15	10
Squalidus argentatus	31	6
Siluriform		
Bagridae		
Pelteobagrus fulvidraco	237	51
Clupeiformes		
Clupeidae		
Clupanodon thrissa	126	12
Perciformes		
Serranidae		
Lateolabrax japonicus	28	16
Siluriformes		
Bagridae		
Mystus guttatus	35	15
Pelteobagrus vachelli	36	7
Clupeiformes		
Konosirus punctatus	78	4

Note: *Clupanodon thrissa* and *Konosirus punctatus* are estuarine fishes. Frequency = times present in the catches.

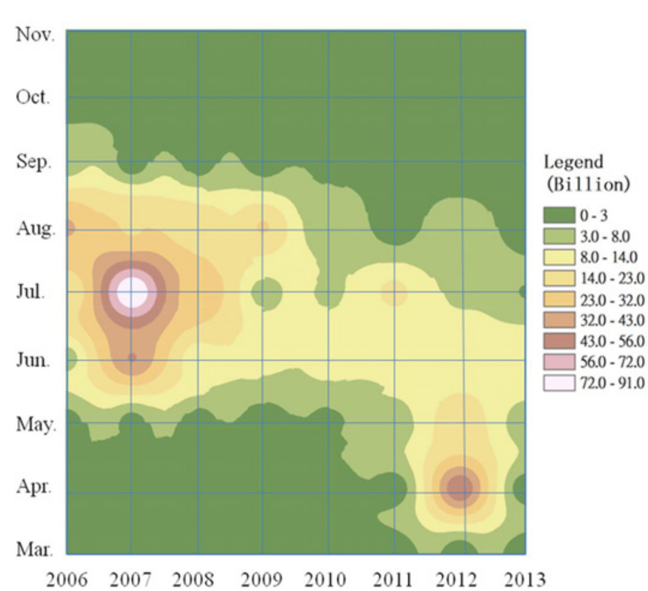

Fig. 2. Breeding characteristics of *M. terminalis* in the Pearl River. The colours represent different abundances.

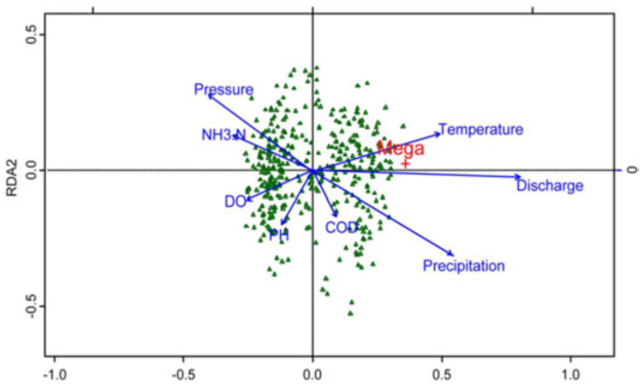

Fig. 3. Redundancy analysis triplot of the Hellinger-transformed *M. terminalis* larvae abundance data constrained by environmental variables, scaling 2. Green triangles are the samples. Environmental variable scores are represented by blue arrows. The red symbol is the *M. terminalis*.

significantly from 2006 to 2013 (Spearman's ρ, one-tailed, $P < 0.01$). The time of the spawning peak occurred earlier and earlier (Spearman's ρ, one-tailed, $P < 0.01$). The maximum number of larvae was collected in July 2007 during our study period. The peak in *M. terminalis* spawning occurred between June and August, accounting for 80% of the annual spawning total. However, the peak time tended to advance year to year (Fig. 2).

Relations between *M. terminalis* abundance and environmental factors

The RDA model, which is a direct gradient analysis technique, summarizes the linear relationships between the abundance of *M. terminalis* larvae and environmental factors (Fig. 3). The combined effect of the first two canonical axes explains 87.7% of the total variance of the data. The *P* value (ANOVA test) of the first two canonical axes was sufficiently low to denote a good sample separation along the axis. The scaling 2 triplot showed that discharge, precipitation and temperature were highly correlated with each other, and negatively associated with pressure and NH_3-N. They had important roles in the occurrence of the *M. terminalis* along the RDA1 axis, which accounts for 76% of the total variance. The second axis has only one characteristic variable, *i.e.* pressure, which shows some contribution to this axis (Table 2).

Using the stepwise procedure, we selected the best explanatory variables whose partial contribution optimally explains the largest portion of the variance of the response data by selecting the highest R^2 if that variable is also significant (permutation test) at a preselected significance level. Results show that discharge, precipitation and temperature explain the largest portion of variance. These three variables highly autocorrelated to each other. We therefore selected discharge as the best explanatory variable for the abundance of *M. terminalis* larvae and this was used in the next analysis.

Influence of hydrological conditions on abundance of larvae

We calculated the CCF of the hydrological data and the *M. terminalis* larvae data and found a significant positive correlation between them, over the course of the study (Fig. 4). A negative value for h means that there is a correlation between the discharge-variable at a time before t and the larvae-variable at time t, *i.e.* the discharge series leads the amount of *M. terminalis* larvae series. They are significantly positively correlated at the lag time from 0 to 4, and the correlation between them gradually decreases with increasing lag time (Fig. 4). This indicated that the discharge not only greatly affects the correlation between the amounts of larvae with the same day, but also affects that of the amount with the day after, or even a few days after. The discharge acted as a trigger, and the amount of larvae was a response to the discharge.

Forecasting population dynamics

The *M. terminalis* data are not stationary and present a high degree of seasonality (augmented Dickey–Fuller test, $P > 0.05$). The series was therefore decomposed into the trend effect, seasonal effects and random variability. There appears to be a slight downwards trend in the abundance of larvae over the years. There is a recurring pattern and steady seasonality within each year (*i.e.*, highest abundance occurs during the summer months, with a minor peak in autumn). Although some stochastic processes add to the seasonal cycle, the irregular errors are a stochastic process and their distribution fluctuates around zero.

We set up a suitable prediction model based on the ACF and PACF. The significant spike at lag 1 in the ACF suggests a regression AR(1) component. A significant spike at lag 2 in the PACF, indicating an additional non-seasonal term MA(2) component, needs to be included in the model. Combining the AIC value, we selected ARIMA$(1,1,2)(0,1,1)_{52}$ as our prediction model.

Forecasts from the model for the next 6 years are shown in Figure 5. We found that the abundance of larvae changed markedly year by year. Years 2015 and 2018 would have a high value, meaning that there will be high abundance of *M. terminalis* larvae during these 2 years. 2016 and 2019 will have low abundance. However, the abundance of larvae shows periodic and inter-annual variability. Periodic occurrence with high larval abundance may be every 3 years (Fig. 5). Overall, *M. terminalis* resources should remain in a stable cycling state in the near future, and this is very important for fishery resource protection and aquatic ecosystem balance. However, the predicted time of the most intense spawning will occur

Table 2. Summary of the RDA analysis.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
F	79.2613	24.3152	9.6522	3.8576	1.5624	0.8338
P value	0.001***	0.009*	0.135	0.267	0.529	0.687
Eigenvalue	0.2637	0.0671	0.0325	0.0029	0.0021	0.0016
Proportion explained	0.6937	0.1947	0.0672	0.0131	0.0103	0.0082
Cumulative proportion	0.6937	0.8884	0.9556	0.9687	0.9890	0.9972
Discharge	0.8237	− 0.1876	− 0.1026	− 0.0839	− 0.0218	− 0.0174
Precipitation	0.7347	− 0.4328	− 0.3265	− 0.1432	0.1762	− 0.0831
Temperature	0.6531	0.3236	0.1782	0.2581	0.1037	0.0826
Pressure	− 0.6237	0.3628	− 0.2368	0.1137	0.0892	0.0238
NH3.N	− 0.5318	0.3361	− 0.3217	0.1312	0.0539	0.0215
DO	− 0.4037	− 0.2679	0.1615	0.0732	0.0682	0.0107
pH	− 0.3871	− 0.4138	0.2162	0.1785	0.0539	0.0361
COD	0.3217	− 0.1359	− 0.0625	− 0.0317	− 0.0128	0.0063

$^{**}P < 0.005$; $^{***}P < 0.001$.

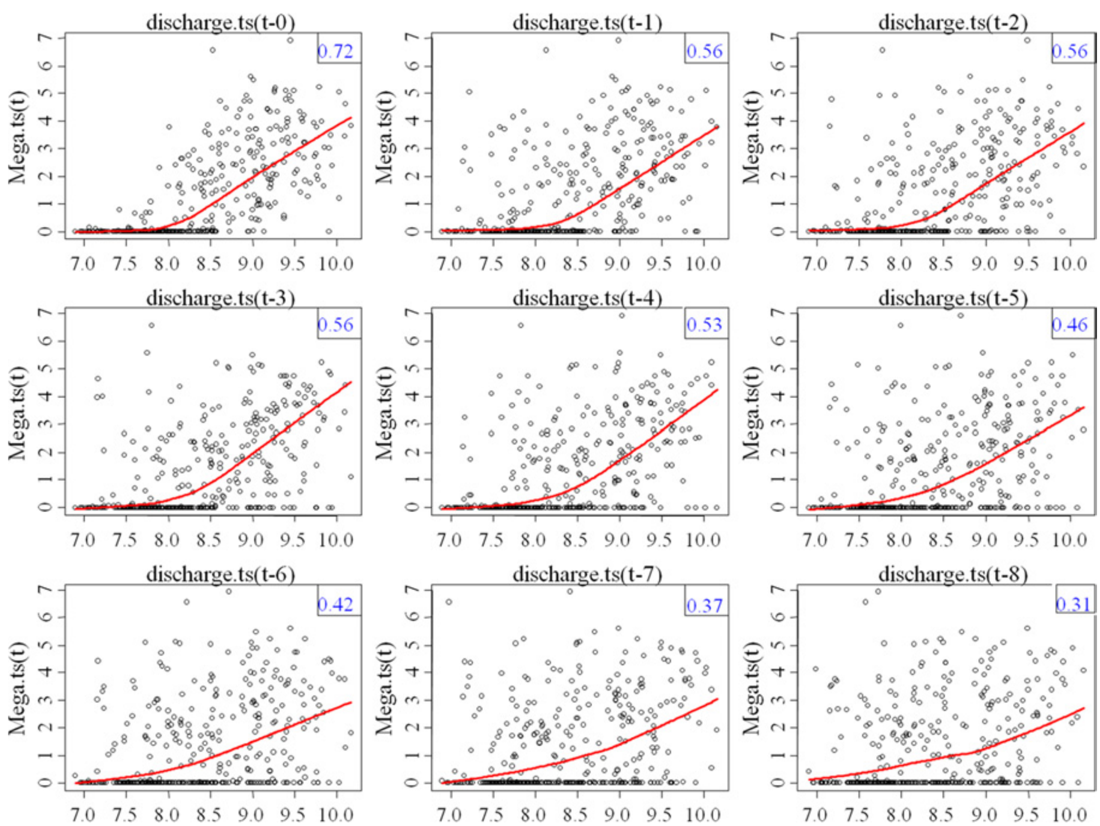

Fig. 4. The cross-correlations of lagged scatter plots between discharge ($t + h$) and the abundance of *M. terminalis* (t). In each plot, *M. terminalis* is on the vertical and a past lag of discharge is on the horizontal. Cross-correlation values are given on each plot and the prediction as a red line. A negative value for h is a correlation between the discharge at a time before t and the larvae at time t. The most dominant cross-correlations occur when $h = 0$.

earlier each year (Spearman's ρ, one-tailed, $P < 0.01$) (Fig. 6). In addition, the duration of the breeding period will decrease significantly compared to 2006–2013 (one-way ANOVA, $P < 0.05$).

The residuals for the fitted model and the forecast errors are shown in Figure 7. Nearly all the spikes are within the significance limits, and as a result the residuals appear to be white noise. A Ljung–Box test also shows that the residuals have no remaining autocorrelations, and the forecast errors exhibit a normal distribution, all of which shows that the model works fairly well.

Discussion

Understanding population dynamics and identifying the importance of environmental factors in the regulation of animal populations is a central issue in ecology

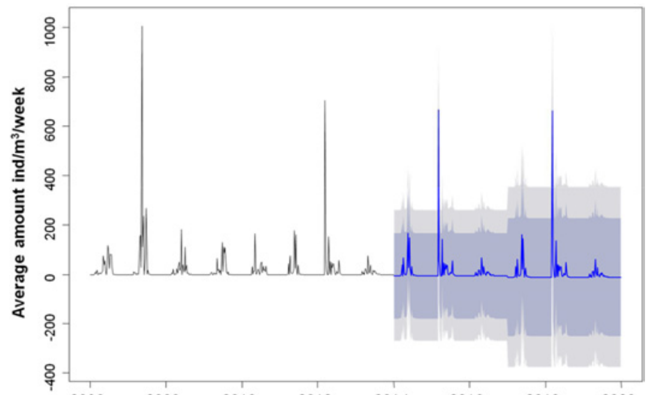

Fig. 5. Forecasts for *M. terminalis* larval abundance from 2014 to 2019. The bright blue line is the forecast, the dark grey and light grey areas are 80 and 95% confidence areas, respectively.

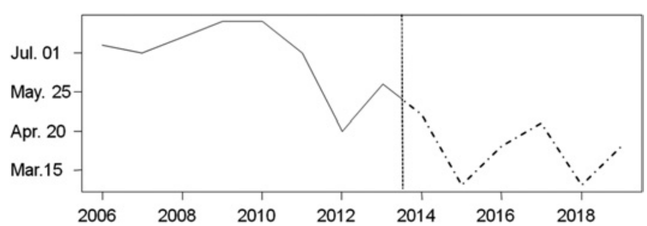

Fig. 6. The days on which the maximum number of larvae occurred. The left side of the dotted line is the actual data collection, and the right side are predicted data.

(Mougeot *et al*., 2003; Ozgul *et al*., 2010; Mullowney *et al*., 2014), and is also of particular significance in the case of fishery resources. Perhaps no question in population biology has generated more attention and debate over the past century than why populations fluctuate. The question remains relevant today because the causes of fluctuations have important implications for the management and conservation of natural resources (Shelton and Mangel, 2011). *M. terminalis* is a very important commercial fish in the Pearl River, and understanding the population dynamics of the species is crucial to both resource protection and utilization.

Our results show that the *M. terminalis* population will follow a relatively stable cycling trend in the coming years, under current environmental conditions. This is very important for fishery resource protection and aquatic ecosystem balance. This trend is mainly attributed to the implementation of fishing moratoria and laws protecting spawning grounds. Laws are crucial for stock recovery of species. A fishing moratorium was implemented for the first time in the Pearl River on April 1, 2011. Fishermen were not allowed to fish for *M. terminalis* during the spawning season. In addition, laws protect the spawning grounds in Zhaoqing and Qingpitong, two important sections of the Xijiang River. This has resulted in a decline in catch rates. However, the predicted time of the most intense spawning will occur earlier each year, and the length of the breeding period will decrease significantly compared to 2006–2013. Such variability has the potential to cause a decrease in larva numbers, which could destabilize the population dynamics of this species.

Existing research shows that temperature is crucial for fish breeding (Anguis and Canavate, 2005) and has a great influence on population dynamics (Martins *et al*., 2012) since temperature will stimulate the gonads (Crossin *et al*., 2008; Fincham *et al*., 2013). These findings are consistent with our results. *M. terminalis* larval occurrence was mainly affected by discharge, precipitation and temperature in the Pearl River. The reproduction of the riverine fishes is linked to specific flow events and flood pulses, which appear to trigger spawning (Humphries *et al*., 1999). Hydrological changes are among the most important factors affecting regeneration and reproduction of fish populations, especially for fish with drifting eggs. Some species, such as bream, lay their sticky eggs on the sand and rocks. They require specific complex hydrogeological conditions that will facilitate adherence of eggs.

Our results also show that discharge acted as a trigger that greatly impacted the abundance of *M. terminalis* larvae. The effect of discharge on the amount of larvae will last at least 5 days. This may be due to the specific spawning habitat requirements of *M. terminalis* (Feng *et al*., 1986; Scheidegger and Bain, 1995; Merigoux and Ponton, 1999; Humphries and Lakel, 2000). After fertilization, they need the flood to drive rolling from upstream to downstream, and to prevent the eggs from being buried by mud. During the process of rolling, eggs develop into larvae. The earliest day of the flood advances year by year, this is consistent with the fact that the time of most intense spawning will occur earlier and earlier (Pearson's correlation, one-tailed, $P < 0.05$). This was potentially induced by the construction of dams in the upstream reaches of the Pearl River, such as the Changzhou Dam. This has the potential to cause a decrease in larva numbers that could destabilize the population dynamics of this species. Their period of high larval occurrence may be every 3 years, but from 2007 to 2012, a 5-year period occurred because of the construction of the Changzhou Dam in 2007. *M. terminalis* needs several years to adjust to these dams. Most economically important fish species in the Pearl River are affected by inter-annual discharge variability (Tan *et al*., 2010).

There is evidence that quantifiable relationships exist between hydrology and density of young fish: high flow before and during spawning were positively correlated with recruitment (Unfer *et al*., 2011; Vilizzi, 2012). River regulation typically leads to a reduction in fishery resources and the diversity of fish communities (Pringle *et al*., 2000; Gehrke and Harris, 2001; Hu *et al*., 2008; Bice and Zampatti, 2011). The catch in several major rivers in China has been affected by dam construction, such as the Three Gorges Dam, Gezhouba Dam on the Yangtze River, Changzhou Dam on the Pearl River and so on (Yi *et al*., 2010). Dam construction in rivers has become a common phenomenon; there are eight large dams (with capacities larger than 10 000 kW) on the Pearl River basin, not to mention the smaller dams. These dams affect

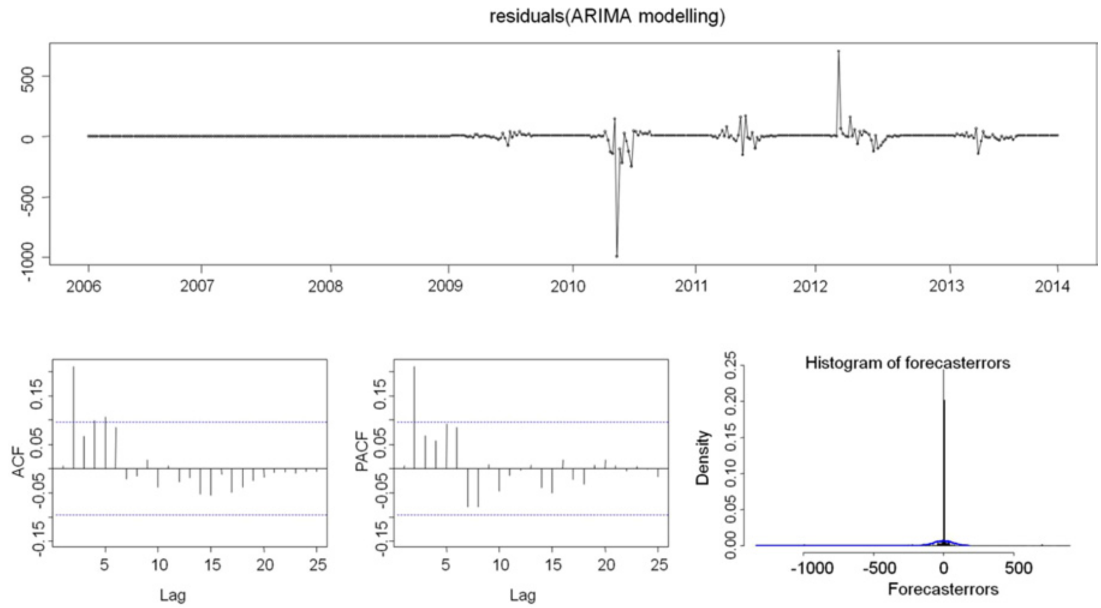

Fig. 7. Residuals and forecast errors from the fitted $\text{ARIMA}(1,1,2)(0,1,1)_{52}$ model for the *M. terminalis* larvae trends.

natural hydrology and flow, and thus impact the biodiversity of fishes in which spawning depends on changes in hydrological pulse (Martin and Paller, 2008). In addition, the spawning period is occurring earlier each year. This may be related to global warming, but confirmation of this hypothesis requires further investigation. In order to protect the *M. terminalis* population and its spawning grounds, some wading engineering should be banned by river managers, such as dam construction, waterway regulation and so on.

Ecological time-series data are typically non-linear, highly irregular and involve seasonality. For such data, first-order autoregressive and traditional statistical models such as correlation analysis may miss important features of the data (Cazelles and Stone, 2003). The ARIMA model is a powerful tool with which to analyse time-series data and the CCF is also a priority method to identify how environments affect organisms, for instance how discharge affects fish larva abundance. Many methods exist for forecasting seasonal time-series data, such as exponential smoothing, autoregressive neural networks (ANN), autoregressive recurrent neural networks (ARNN) and so on (Kim *et al.*, 2015). An ARIMA model based on autocorrelations, taking account of how "noisy" the series is, is an adaptive and extrapolative method that can provide more accurate projections than those using asymmetry and weights. With enough elements regressed and averaged, the ARIMA model can fit an approximation to almost any time-series and has definite merits for data interpretation (Kim *et al.*, 2015), and has been successfully applied in ecology, including for river systems (Kim, 2016) and studies of insects (Castro-Rebolledo and Donato-Rondon, 2015). Compared with the most common habitat suitability and species distribution models, such as the ecological niche factor analysis (ENFA) (Brotons *et al.*, 2004), niche-based models (NBMs) (Gama *et al.*, 2016), generalized linear models (GLM) (Hirzel *et al.*, 2001) and Maxent model (Brotons *et al.* 2004), the ARIMA model has advantages in terms of population trend predictions, because it combines species abundance data in the analysis. This enables the study of non-stationary spatial or time-dependent data characteristics. While the habitat suitability and species distribution models mainly use presence data or presence/absence data, they will miss important features of the data (Cazelles and Stone, 2003), and are unable to retrieve the moment when the links are the most pre-eminent.

Our data were collected three times a day every other day from January 2006 to December 2013: such a high-resolution monitoring database is rarely found in ecology. These data would be valuable in the development of ARIMA models for autoregressive prediction. Therefore, the characteristics of *M. terminalis* population dynamics identified by a seasonal ARIMA model in this study can be used to improve fishery resource protection and river management in the Pearl River. We believe that river flow, both as discharge and flood pulses, controls larval abundance in the Pearl River. In order to confidently identify and understand in greater detail how environmental factors might influence annual patterns in the *M. terminalis* population, long-term monitoring of all fish larval abundances and other environmental factors (such as redox potential (ORP), total dissolved solids (TDS) and transparency), along with alien species population data, and anthropogenic disturbance data (such as aquaculture, dam construction, agriculture and human settlement) in the Pearl River are needed.

Acknowledgements. We are grateful to the LOTUS Unlimited Erasmus Mundus that gave the first author post-doc mobility. We are also grateful to the Zhaoqing Detachment of the Guangdong Fishing Administrative Brigade for their assistance in the field. We thank Peter Winterton for his assistance in writing this manuscript. This study was supported by the National Natural Science Foundation of China (grant no. 31400354), the Special Scientific Research Funds for Central Non-profit Institutes and the Chinese Academy of Fishery Sciences (grant no. 2015B01PT01). This study was supported by the Guangxi Natural Science Foundation of China (grant no. 2013GXNSFEA053003) and the Special Fund for Agro-Scientific Research in the Public Interest (grant no. 201303048).

References

Anderson C.N., Hsieh C.H., Sandin S.A., Hewitt R., Hollowed A., Beddington, J., May R.M. and Sugihara G., 2008. Why fishing magnifies fluctuations in fish abundance. *Nature*, *452*, 835–839.

Angeler D.G., Viedma O. and Moreno J.M., 2009. Statistical performance and information content of time lag analysis and redundancy analysis in time series modeling. *Ecology*, *90*, 3245–3257.

Anguis V. and Canavate J.P., 2005. Spawning of captive Senegal sole (*Solea senegalensis*) under a naturally fluctuating temperature regime. *Aquaculture*, *243*, 133–145.

Bice C.M. and Zampatti B.P., 2011. Engineered water level management facilitates recruitment of non-native common carp, *Cyprinus carpio*, in a regulated lowland river. *Ecol. Eng.*, *37*, 1901–1904.

Box G.E., Jenkins G.M. and Reinsel G.C., 2013. Time Series Analysis: Forecasting and Control, John Wiley & Sons, Hoboken, New Jersey.

Brotons L., Thuiller W., Araújo M.B. and Hirzel A.H., 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, *27*, 437–448.

Castro-Rebolledo M.I. and Donato-Rondon J.Ch., 2015. Emergence patterns in tropical insects: the role of water discharge frequency in an Andean Stream. *Ann. Limnol. - Int. J. Lim.*, *51*, 147–155.

Cazelles B. and Stone L., 2003. Detection of imperfect population synchrony in an uncertain world. *J. Anim. Ecol.*, *72*, 953–968.

Chatfield C., 2000. Time Series Forecasting, Chapman & Hall/CRC, London.

Chen, R.G., Lu, Z.F., 2006. Guangxi Freshwater Fishes, Guangxi People's Publishing House, Guangxi, pp. 165–167.

Copp G.H., 1993. Microhabitat use of fish larvae and 0+ juveniles in a small abandoned channel of the upper River Rhône, France. *Folia Zool.*, *42*, 153–164.

Copp G.H., Kovac V. and Siryova S., 2010. Microhabitat use by stream-dwelling spirlin *Alburnoides bipunctatus* and accompanying species: implications for conservation. *Folia Zool.*, *59*, 240–256.

Crossin G.T., Hinch S.G., Cooke S.J., Welch D.W., Patterson D.A., Jones S.R.M. *et al.*, 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. *Can. J. Zool.*, *86*, 127–140.

Dulvy N.K., Sadovy Y. and Reynolds J.D., 2003. Extinction vulnerability in marine populations. *Fish Fish.*, *4*, 25–64.

Feng Q.X., Wang J.C. and You B.Z., 1986. The investigation report of Guangdong bream spawning grounds. *Freshwat. Fish.*, *6*, 1–5 (in Chinese).

Fincham J.I., Rijnsdorp A.D. and Engelhard G.H., 2013. Shifts in the timing of spawning in sole linked to warming sea temperatures. *J. Sea Res.*, *75*, 69–76.

Frankham R., 1996. Relationship of genetic variation to population size in wildlife. *Conserv. Biol.*, *10*, 1500–1508.

Frankham R., 2005. Genetics and extinction. *Biol. Conserv.*, *126*, 131–140.

Fromentin J.M. and Powers J.E., 2005. Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. *Fish Fish.*, *6*, 281–306.

Gama M., Crespo D., Dolbeth M. and Anastácioa P., 2016. Predicting global habitat suitability for *Corbicula fluminea* using species distribution models: the importance of different environmental datasets. *Ecol. Model.*, *319*, 163–169.

Gehrke P.C. and Harris J.H., 2001. Regional-scale effects of flow regulation on lowland riverine fish communities in New South Wales, Australia. *Regul. River*, *17*, 369–391.

Georgakarakos S., Haralabous J., Valavanis V., Arvanitidis C., Koutsoubas D. and Kapantagakis A., 2002. Loliginid and ommastrephid stock prediction in Greek waters using time series analysis techniques. *Bull. Mar. Sci.*, *71*, 269–287.

Georgakarakos S., Koutsoubas D. and Valavanis V., 2006. Time series analysis and forecasting techniques applied on loliginid and ommastrephid landings in Greek waters. *Fish. Res.*, *78*, 55–71.

Gutierrez-Estrada J.C., Silva C., Yanez E., Rodriguez N. and Pulido-Calvo I., 2007. Monthly catch forecasting of anchovy *Engraulis ringens* in the north area of Chile: non-linear univariate approach. *Fish. Res.*, *86*, 188–200.

Hirzel A.H., Helfer V. and Metral F., 2001. Assessing habitat-suitability models with a virtual species. *Ecol. Model.*, *145*, 111–121.

Hu W.W., Wang G.X., Deng W. and Li S.N., 2008. The influence of dams on ecohydrological conditions in the Huaihe River basin, China. *Ecol. Eng.*, *33*, 233–241.

Humphries P. and Lakel P.S., 2000. Fish larvae and the management of regulated rivers. *Regul. River.*, *16*, 421–432.

Humphries P., King A.J. and Koehn J.D., 1999. Fish, flows and floodplains: links between freshwater fish and their environment in the Murray–Darling River system, Australia. *Environ. Biol. Fish.*, *56*, 129–151.

Hunt T.L., Douglas J.W., Allen M.S., Gwinn D.C., Tonkin Z., Lyon J. and Pickworth A., 2011. Evaluation of population decline and fishing sustainability of the endangered Australian freshwater fish *Macquaria australasica*. *Fisheries Manag. Ecol.*, *18*, 513–520.

Jeong K.S., Kim D.K., Jung J.M., Kim M.C. and Joo G.J., 2008. Non-linear autoregressive modelling by Temporal Recurrent Neural Networks for the prediction of freshwater phytoplankton dynamics. *Ecol. Model.*, *211*, 292–300.

Jobling M., 1995. Environmental Biology of Fishes, Chapman and Hall Publishers, London, 455 p.

Kim J.Y., Jeong H.C., Kim H. and Kang S., 2015. Forecasting the monthly abundance of anchovies in the South Sea of Korea using a univariate approach. *Fish. Res.*, *161*, 293–302.

Kim S., 2016. A multiple process univariate model for the prediction of chlorophyll-a concentration in river systems. *Ann. Limnol. - Int. J. Lim.*, *52*, 137–150.

Koslow J.A., Goericke R., Lara-Lopez A. and Watson W., 2011. Impact of declining intermediate-water oxygen on deepwater fishes in the California Current. *Mar. Ecol. Prog. Ser.*, *436*, 207–218.

Koutroumanidis T., Iliadis L. and Sylaios G.K., 2006. Time-series modelling of fishery landings using ARIMA models and Fuzzy Expected Intervals software. *Environ. Modell. Softw.*, *21*, 1711–1721.

Legendre P. and Gallagher E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*, 271–280.

Legendre P. and Legendre L.F.J., 2012. Numerical Ecology, Elsevier, Amsterdam, pp. 117–121.

Makarenkov V. and Legendre P., 2002. Nonlinear redundancy analysis and canonical correspondence analysis based on polynomial regression. *Ecology*, *83*, 1146–1161.

Mangel M., Brodziak J. and DiNardo G., 2010. Reproductive ecology and scientific inference of steepness: a fundamental metric of population dynamics and strategic fisheries management. *Fish Fish.*, *11*, 89–104.

Manjarres-Martinez L.M., Gutierrez-Estrada J.C., Mazenet-Gonzalez J. and Soriguer M.C., 2010. Seasonal patterns of three fish species in a Caribbean coastal gill-net fishery Biologically induced or climate-related aggregations? *Fish. Res.*, *106*, 358–367.

Martin F.D. and Paller M.H., 2008. Ichthyoplankton transport in relation to floodplain width and inundation and tributary creek discharge in the lower Savannah River of Georgia and South Carolina. *Hydrobiologia*, *598*, 139–148.

Martins E.G., Hinch S.G., Patterson D.A., Hague M.J., Cooke S.J. and Miller K.M. *et al*., 2012. High river temperature reduces survival of sockeye salmon (*Oncorhynchus nerka*) approaching spawning grounds and exacerbates female mortality. *Can. J. Fish. Aquat. Sci.*, *69*, 330–342.

Merigoux S. and Ponton D., 1999. Spatio-temporal distribution of young fish in tributaries of natural and flow regulated sections of a neotropical river in French Guiana. *Freshwat. Biol.*, *42*, 177–198.

Morais P., 2008. Review on the major ecosystem impacts caused by damming and watershed development in an Iberian basin (SW-Europe): focus on the Guadiana estuary. *Ann. Limnol. - Int. J. Lim.*, *44*, 105–117.

Mougeot F., Redpath S.M. and Hudson P.J., 2003. The effect of aggressiveness on the population dynamics of a territorial bird. *Nature*, *421*, 737–739.

Mouthon J. and Daufresne M., 2008. Population dynamics and life cycle of *Pisidium amnicum* (Muller) (Bivalvia: Sphaeriidae) and *Valvata piscinalis* (Muller) (Gastropoda: Prosobranchia) in the Saone river, a nine-year study. *Ann. Limnol. - Int. J. Lim.*, *44*, 241–251.

Mullowney D.R., Dawe E.G., Colbourne E.B. and Rose G.A., 2014. A review of factors contributing to the decline of Newfoundland and Labrador snow crab (*Chionoecetes opilio*). *Rev. Fish. Biol. Fisher.*, *24*, 639–657.

Novacek M.J. and Cleland E.E., 2001. The current biodiversity extinction event: scenarios for mitigation and recovery. *Proc. Natl. Acad. Sci. USA*, *98*, 5466–5470.

Ozgul A., Child D.Z., Oli M.K., Armitage K.B., Blumstein D.T., Olson L.E., Tuljapurkar S. and Coulson T., 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, *466*, 482–485.

Paradis E., Baillie S.R., Sutherland W.J. and Gregory R.D., 2000. Spatial synchrony in populations of birds: effects of habitat, population trend, and spatial scale. *Ecology*, *81*, 2112–2125.

Pringle C.M., Freeman M.C. and Freeman B.J., 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: tropical-temperate comparisons the massive scope of large dams and other hydrologic modifications in the temperate New World has resulted in distinct regional trends of biotic impoverishment. While neotropical rivers have fewer dams and limited data upon which to make regional generalizations, they are ecologically vulnerable to increasing hydropower development and biotic patterns are emerging. *BioScience*, *50*, 807–823.

Probst W.N., Stoll S., Peters L., Fischer P. and Eckmann R., 2009. Lake water level increase during spring affects the breeding success of bream *Abramis brama* (L.). *Hydrobiologia*, *632*, 211–224.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical computing, Vienna, Austria. Available online at: http://www.R-project.org

Sala O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M., Poff N.L., Sykes M.T., Walker B.H., Walker M. and Wall D.H., 2000. Global biodiversity scenarios for the year 2100. *Science*, *287*, 1770–1774.

Sassa C. and Hirota Y., 2013. Seasonal occurrence of mesopelagic fish larvae on the onshore side of the Kuroshio off southern Japan. *Deep-Sea Res. Pt. I.*, *81*, 49–61.

Scheidegger K.J. and Bain M.B., 1995. Larval fish distribution and microhabitat use in free-flowing and regulated rivers. *Copeia*, 125–135.

Shelton A.O. and Mangel M., 2011. Fluctuations of fish populations and the magnifying effects of fishing. *Proc. Natl. Acad. Sci. USA*, *108*, 7075–7080.

Stenseth N.C. and Rouyer T., 2008. Ecology: destabilized fish stocks. *Nature*, *452*, 825–826.

Tan X.C., Li X.H., Lek S., Li Y., Wang C., Li J. and Luo J.R., 2010. Annual dynamics of the abundance of fish larvae and its relationship with hydrological variation in the Pearl River. *Environ. Biol. Fish.*, *88*, 217–225.

Tsitsika E.V., Maravelias C.D. and Haralabous J., 2007. Modeling and forecasting pelagic fish production using univariate and multivariate ARIMA models. *Fish. Sci.*, *73*, 979–988.

Unfer G., Hauer C. and Lautsch E., 2011. The influence of hydrology on the recruitment of brown trout in an Alpine river, the Ybbs River, Austria. *Ecol. Freshwat. Fish.*, *20*, 438–448.

Vilizzi L., 2012. Abundance trends in floodplain fish larvae: the role of annual flow characteristics in the absence of overbank flooding. *Fundam. Appl. Limnol.*, *181*, 215–227.

Vilizzi L. and Copp G.H., 2005. An analysis of 0 + barbel (Barbus barbus) response to discharge fluctuations in a flume. *River. Res. Appl.*, *21*, 421–438.

Yi Y.J., Wang Z.Y. and Yang Z.F., 2010. Impact of the Gezhouba and Three Gorges Dams on habitat suitability of carps in the Yangtze River. *J. Hydrol.*, *387*, 283–291.

Yu L., Zhou L., Tan L., Jiang H., Wang Y., Wei S. and Nie S., 2014. Application of a New Hybrid Model with Seasonal Auto-Regressive Integrated Moving Average (ARIMA) and Nonlinear Auto-Regressive Neural Network (NARNN) in Forecasting Incidence Cases of HFMD in Shenzhen, China. *PLoS ONE*, *9*, e98241.

Zhang G.P., 2003. Time series forecasting using a hybrid ARIMA and neural network model. *Neurocomputing*, *50*, 159–175.