Ecological Modelling 383 (2018) 98–105

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Silver carp larva abundance in response to river flow rate revealed by cross-wavelet modelling

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ARTICLE INFO

Keywords:
Cross wavelet modelling
Fish larvae
Discharge
Time series analysis
Pearl River

ABSTRACT

The complexity and non-linearity of increasingly available fisheries data, requires modern analytical approaches and statistical tools that can accommodate the temporal and scale structures of natural systems. Traditional analyses often assume uncorrelated or weakly correlated temporal structure in fisheries data time series. We propose that frequency and scale domain methods, in the form of wavelet transforms, can serve as useful probes in early investigations of fisheries data, finding out the mechanisms underlying the changes in the diversity and abundance of fishes. We used cross-wavelet analysis with phase angle and coherency parameters to study the effect of discharge on the occurrence of silver carp larvae in a large subtropical river. Simulation studies show that the spectral signature given by the cross-wavelet method provided a useful approach for statistically detecting and characterizing temporal dependency in the occurrence of fish larvae. In addition, our simulations provide an objective, quantitative basis for understanding how river flow rate acts as a trigger for the occurrence of larvae. And our results can be used to ecological operation silver carp larvae were found when discharge was greater than $10^4\,m^3\,s^{-1}$. The flood peak persists for some days (at least 2 days) and can induce a peak in larval abundance. Our analyses also show that flood duration and the flood total volume decreased from 2006 to 2013. Moreover the flood occurred earlier each year. This may be why the period of most intense spawning (the day of maximum larvae collected) was earlier each year. We conclude with a discussion about the role wavelet analysis may have in appropriately guiding flexible probabilistic models connecting fisheries with environmental covariates. The wavelet approach is an especially promising tool for analyzing ecological data, such as the relationship between hydrological conditions and fish larva occurrence.

1. Introduction

Intensive regulation of large rivers has altered natural hydrological regimes with profound consequences for aquatic biota (Puckridge et al., 1998; Nilsson et al., 2005). The impacts of flow regulating structures (e.g. dams and weirs) and changes to natural flow regimes on fish have been discussed worldwide (Gehrke et al., 1995; Pringle et al., 2000; Hu et al., 2008). River regulation typically leads to a reduction in fisheries resources and in fish community diversity (Bice and Zampatti, 2011). The mechanisms underlying the varying diversity and abundance of fish has long been a perplexing problem for fish ecologists. Numerous mechanisms and models have been proposed to account for the decrease in fish resources, including the impacts of human activities and climate change (Minns, 2009; Barange and Cheung, 2010). One of these theories states that freshwater fish population decreases are mainly attributed to the construction of dams which change the continuum of the rivers leading to changes of hydrology and flow, and which also affects fish migration and reproduction (Sanchez et al., 2011).

The reproduction of riverine fishes can be linked to specific flow events. The degree of variability of the flow regime, at various temporal and spatial scales, probably drives the reproductive strategies of riverine fishes (Humphries and Lake, 2000). Some research shows that hydrological changes are among the most important factors for reproduction of the silver carp. High flows before and during the

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https://doi.org/10.1016/j.ecolmodel.2018.05.020
Received 28 November 2017; Received in revised form 26 April 2018; Accepted 21 May 2018
Available online 26 May 2018

spawning period were positively correlated with fish spawning (Unfer et al., 2010; Vilizzi, 2012), most likely because of their specific habitat requirements (Humphries and Lake, 2000). Overbank flood pulses and in-channel flow pulses can enhance riverine fish production (Hardie et al., 2007), especially for bream (Probst et al., 2009). Earlier studies (Costa-Pierce, 1992; Jankovic, 1998; Kocovsky et al., 2012) reported that flood events, as seen through water levels, are important for spawning and for larval survival of the Asian carps. Although considerable effort has been made to understand the effect of the flow rate on spawning, these mechanism are still not very clear, and in general there is an astonishing lack of consensus about the mechanisms behind the manner in which water discharge acts as a trigger for the occurrence of larvae.

Time series analysis is a fundamental issue in ecology (Ghil et al., 2011). The signals contained in time series datasets often reflect the results of the superimposition of various natural mechanisms. These mechanisms may have different time characteristics and different scale patterns. "Since the spawning type of most fish were single spawning, and the spawning period are concentrated in a special time. The number of larvae will be very large on a certain day and may be very small or even to zero on the second day. So the fisheries time-series data, especially the larvae data, are non-linear and irregular. For such data, first-order autoregressive and traditional statistical models such as correlation analysis, principal component analysis, linear regression, redundancy analysis or any similar statistical tools, may miss important features of the data because they can't do frequency decomposition (Cazelles and Stone, 2003), they are unable to retrieve the moment when the links are the most pre-eminent. The classical standard approaches to investigate such data by frequency decomposition is Fourier analysis. However, a disadvantage of Fourier analysis is that the window width is changeless and thus the time resolution is constant for all frequencies investigated. Here, wavelet analysis has proven to be superior: to analyze the time series locally in time and in scale. Another advantage of wavelet analysis is the flexible choice of the mother wavelet according to the characteristics of the time series investigated. Thus, to analyze local correlations, cross-wavelet analysis may be seen as a very powerful technique.

Wavelet analysis (also called wavelet theory or just wavelets) provides a way to conduct multi-resolution analysis in non-linear domains (Grinsted, 2004) by visualising the decomposition of a signal into translated and dilated patterns which give the local contribution of a wavelet to the signal (Grenfell et al., 2001). Wavelets are specially adapted to the characterization of local structures, and has been successfully applied in ecology (Polansky et al., 2010; Wang et al., 2010; Recknagel et al., 2013), including studies of disease (Grenfell et al., 2001; Cazelles et al., 2007) and population dynamics (Cazelles et al., 2008).

If the objective of a study is to find a relationship between two time series, it is possible to compute the cross wavelet coefficient (equivalent to the covariance). For two time series, it is also possible to provide the phase angle and the coherence. This tool is very interesting and novel for ecological data series, such as those used to analyze the effect of hydrological phenomena on the production of fish larvae. With typical non-linear and highly irregular fisheries time-series data, wavelet analysis has the unique advantage of being able to find out how two time-series data are related in which period or which scale, and can find out which is the dependent and which is the independent variable. This cannot be done by traditional statistical methods such as correlation analysis.

To our knowledge, no research has yet employed wavelets to analyze hydrological changes and fish larvae occurrence at the high temporal resolution of the data considered here. Such studies are important both to understand the mechanisms of fish spawning and for fisheries management. Wavelet analysis is less common in fisheries studies (but see Grados et al., 2012). The objectives of this paper are: 1) to find out the occurrence characteristics and the ecological conditions for silver carp larvae based on larval and hydrological data from 8 years of continuous monitoring in the Pearl River (China), 2) to evaluate their relationship by using cross-wavelet analysis, and 3) to model how water discharge acts as a trigger for the occurrence of larvae. Our study paves the way for future research on this subject. We believe that this work provides theoretical guidance for fisheries protection and management.

2. Materials and methods

2.1. Study species

The silver carp, Hypophthalmichthys molitrix Cuvier and Valencinnes (Cyprinidae, Hypophthalmichthyinae), one of the traditional big four domestic carps, is a large, commercially important fish in China. With its high productivity, silver carp has been introduced to many other countries for various reasons (Milstein et al. 2006). However, the size of the wild silver carp population in China has decreased sharply in recent years. The main reasons are the loss of spawning grounds or obstruction of fish migration caused by dam constructions, changes of river flow regime, overfishing (Hu et al., 2008; Duan et al., 2009; Tan et al., 2010). Silver carp is a typical filtering-feeding fish and widely dispersed in the Pearl River basin. Silver carp in the Pearl River mature at about age 3 and spawn once a year, typically migrating from middle and lower reaches to spawning ground in the upper reaches and tributaries. The eggs are buoyant and drift downstream as they develop.

2.2. Study sites

The Pearl River is the longest river in southern China (2400 km) and flows into the South China Sea with a mean annual discharge of 3.3×10^{11} m^3. The catchment area is about 453,690 km^2. The seasonal flow regime of the Pearl River is evident, with high flows during summer, with low flows during spring and winter. The Pearl River supports 381 fish species, 262 freshwater species and 119 estuarine species (Tan et al., 2010).

The spawning grounds of silver carp are shown in Fig. 1. At the beginning of the flood season, silver carp spawn and their larvae drift down into the delta (Tan et al., 2010). Our study site (23°2′40″N, 112°27′5″E) is located along the Zhaoqing section in the Pearl River, ~ 100 km upstream of the Pearl River estuary (Fig. 1). This location is a necessary place for larvae and drifting eggs transported to the Pearl River Delta. In addition, the water flow in this section is relatively slow, which facilitates the larvae collection.

2.3. Data collection

Samples were collected three times a day (06:00–08:00, 13:00–15:00, and 19:00–21:00) and once every 2 days at the whole year. Larval fish samples were collected with Jiang nets of 0.5 mm mesh. The Jiang net were 2 m in total length and consists of a rectangle mouth formed by an iron frame loop with an area of 1.5 m^2 (1.0 m high and 1.5 m wide), with a rectangular pyramid net and a filter collection bucket (0.8 m × 0.4 m × 0.4 m). A flow meter was mounted in the mouth of the net to measure the volume of water filtered in order to calculate larval density (number·m^{-3}). The nets were deployed in water 2.5 m deep, space in 10 m far from the shore for sampling.

Larval fish samples collected were immediately fixed with 5% formalin. Caudal vein, melanophores distribution, snout shape, relative position of the dorsal and anal fins, spines, the fin ray, and vertebrae counts are used to identify fish larvae. To gain insight into fish stock composition, larval fish collections were performed in this location from the year 2006 to 2013.

Water discharge data were obtained from the Pearl River Water Conservancy Commission. We defined the spawning period as the days between the first and last spawning days in any one year. The most intense spawning period was noted as the day of maximum larval