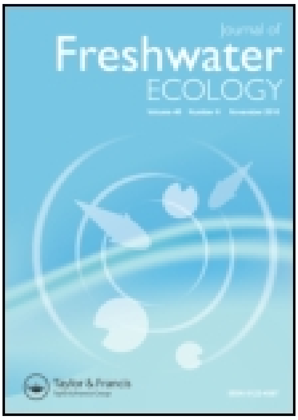

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Synchronization of fishes' temporal feeding patterns with weather in mid-Missouri

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Synchronization of fishes' temporal feeding patterns with weather in mid-Missouri

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Daily food consumption was estimated over 30 successive days in summer for bluegill (*Lepomis macrochirus*) in a 13 ha impoundment, and simultaneously for green sunfish (*Lepomis cyanellus*) in a second-order mid-Missouri stream from the same watershed. Using temperature data from the Sanborn Field Station for the same period, a relationship between daily food consumption rate of the two fish species and synoptic-scale weather patterns or cycles was established using cross spectral analysis which is not found in the previous literature. Previous analyses of the two species in their respective aquatic environments showed that their daily consumption rates over 30-day periods were rhythmic and peaked on a time scale of 2 and 14 days. A spectral analysis of the temperature data from that period showed that there were statistically significant temperature variations on the time scale of 2, 6, and 15 days. The latter two periods are related to well-known synoptic meteorological rhythms (the passage of cyclones and large-scale vacillation in the jet stream). This same technique, method of cycles, when applied to the fishes' consumption rate data showed that the spectral peaks occurred similar to those in the temperature analysis. Then, a similar analysis was performed on data taken from a 6-month feed study in another part of the world (Finland), in order to determine whether our results were robust. This result was positive as well. Thus, it is hypothesized here that the food consumption patterns of these two fishes are linked to variations in the local synoptic and large-scale weather conditions.

Keywords: fish feeding; deprivation periods; synoptic weather; cross-spectral analysis; vacillation

Introduction

In meteorology, there are two well-known synoptic-scale and planetary-scale periods that are used for medium and long-range forecasting. These periods can be found in any long-time series (defined as at least one month) of daily or hourly temperature and pressure records. The first of these cycles is generally referred to as the synoptic period. There is a strong anecdotal evidence that temperature, pressure, and precipitation in the mid-to-high latitudes typically vary on a 2–7-day cycle (depending on the region and season) in association with the regular passage of

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low- and high-pressure systems (e.g., Ahrens 2009). This is especially true in the Midwestern region of the United States. Also, in this context, we refer to medium range forecasting as 3–5 days and long-range forecasting as 7–10 days. The forecasts are based on models (computer and observational) rooted in atmospheric dynamic and thermodynamic principles.

Additionally, the largest (planetary) scale weather patterns (e.g., temperature, pressure, and winds) have a well-known 10–14-day oscillation period, which is roughly the limit of dynamic predictability (e.g., Lorenz 1963, 1969). This period (vacillation) is the natural period that derives from the scale analysis of solutions to the equations of motion, these being dependent on the size and rotation rate of our planet. This phenomenon was described statistically in the atmospheric mass field by, for example, Hansen (1986) and Sutera (1986), and results in a change in amplitude of the large-scale atmospheric waves from a more zonal configuration (low amplitude) to one that is more meridional (high amplitude).

It is also well-known that daily consumption rates of fish vary, to an extent, in accordance with temperature (e.g., Bajer et al. 2004; Whitledge et al. 2006) and possibly in relation to pressure changes in the atmosphere as well. What is less well known, however, is whether daily feeding rates of fish are rhythmic and whether these in fact correspond to cycles in weather. Finally, the broader question remains as to whether or not these periods vary/differ among the distinct regions wherein the fish are found. This may relate to the ability of fishes to observe or detect their prey, as well as to behavioral responses of the prey itself. The linkage to weather may be indirect, as the changes in temperature, pressure (and thus wind), as well as the occurrence of precipitation, may generate turbidity in water bodies and lead to changes in the stability of the water temperature profile in a water body.

In a previous study of the feeding habits of fish, Whitledge and Hayward (2000) estimated the daily food consumption of bluegill (*Lepomis macrochirus*) and green sunfish (*Lepomis cyanellus*) over a 30-day period in the summer. They found that these species reached feeding peaks following 2 - and 14-day periods of low feeding in a small impoundment and small stream within the same watershed in Central Missouri. They further demonstrated that the 2 - and 14-day intervals, after which peak fish consumption rates were observed in the lake and stream, likewise produced the highest growth rates ($p < 0.05$) in the laboratory, when bluegills and also yellow perch (from Missouri, but outside the study watershed) were feed-restricted for 2 - or 14-day periods and then fed liberally for 2 weeks.

Then, the goal of this study is to demonstrate that the feeding and growth periods of fish may be linked to local weather variability. This linkage is made by applying dynamic time series analysis methods (method of cycles) and statistical methods for a study performed in Missouri as well as a study performed previously in Finland. These methods were not used in the previous study, and cross spectral analysis was not found in the literature for this type of study. It may then be possible to use this information to more efficiently manage fish growth and populations for economic benefits, such as farming fish in stock ponds (recreational fishing) or for food.

Methods

Description of data

Bluegill and green sunfish daily food consumption data over the 30-day period from 15 July to 15 August, as reported by Whitledge and Hayward (2000), were used herein. These data were provided in units of grams of feed per gram of body weight. The temperature (°F) and precipitation (inches) data had been archived and were provided by the Missouri Climate Center (http://www.mcc.missouri.edu). These were converted to metric units (°C and mm). In most studies, metric units are used with meteorological data, however, surface weather information in the United States is routinely archived in English units. Additionally, feeding data from a study conducted in 2002 in Helsinki, Finland, were analyzed and compared to weather data obtained from Finnish Meteorological Institute at the Helsinki Kaisaniemi site. These temperature data were given in degrees Celsius and precipitation data in millimeters.

Analysis and experimental design

Whitledge and Hayward (2000) studied bluegill daily consumption patterns over 30 days in a 13 ha impoundment in Central Missouri; green sunfish daily consumption was likewise evaluated in a small Central Missouri stream located in the same watershed. The 30-day consumption patterns for both species were similar. The control fish (hybrid bluegills and yellow perch) were from different water bodies in Missouri (i.e., not from the original impoundment and stream) and were housed individually in enclosures within tanks, and fed daily without restriction. The treatment fish (same two species) also housed individually, were 'food deprived' for either (2, 4, 6, 10, or 14 days) and then fed liberally for multiple weeks.

In order to analyze the weather and daily food consumption data, Fourier transforms were applied to the time-series data. Fourier transforms are used routinely to convert data in Cartesian space (x, y, z, t) to wave space. Plots of wave power versus wave number can then be analyzed in order to extract dominant periods from a time series. These spectral peaks can then be tested for statistical significance against a red or white noise continuum (e.g., Wilks et al. 2006) depending on whether it could be expected *a priori* that low frequency (red) or no particular frequencies (white) would be dominant. Here we have tested versus the white spectrum primarily as it would not be expected *a priori* that certain frequencies would dominate in our region.

Occasionally, this type of analysis is referred to as the 'method of cycles' (e.g., Mokhov et al. 2004; Birk et al. 2010). The underlying assumption is that the system being studied behaves like a regular pendulum or is cyclical (or at least quasi-cyclical). These systems can be represented by differential equations of the following form:

$$X'' + \lambda^2 X = 0 \tag{1}$$

In this equation, X represents any variable which could vary in time or space. Here we use temperature, precipitation, and daily food consumption data all of which vary in time. This type of equation is called a Sturm–Louville-type equation (e.g., Kreyszig 1988) and it describes the 'motion' of an undamped oscillating system in mathematical space. These equations can be solved using empirical orthogonal functions (e.g., Fourier series or wavelet transforms).

A cross-spectral analysis (e.g., Wilks 2006) was then performed using the daily food consumption rate and the temperature time series. This analysis involves the convolving of the two spectra and then examining the resultant spectrum.

These spectral peaks were also tested for statistical significance using the same techniques used for the original spectra. Lastly, in the Finnish weather data, given that the annual cycle is likely to dominate the Fourier analysis, the annual cycle was removed from the data set. This was done by fitting a cubic regression line to the temperature data and then subtracting this cubic function from the daily mean.

Results

Daily food consumption

Figure 1 shows the daily food consumption rate for both bluegill and green sunfish as adapted from Whitledge and Hayward (2000). The 14-day period found in their study using statistical methods is somewhat evident in the figure visually as peaks in the consumption rates appear near the beginning of the period and during the latter half of the period. There may be visual evidence of a shorter time period; however, this is more difficult to discern without further analysis. In both samples, there was a downward trend in the feeding rates that was steeper in the green sunfish samples but only slight in the bluegill samples. Neither trend was significant since the sample was relatively small.

Temperature and precipitation data

During the period from 15 July to 15 August 1996, temperatures were generally below the 1981– 2010 normal except for brief periods from 18–20 July to 5–7 August (Figure 2a). The months of July and August 1996 were 1.6°C and 0.6°C below normal, respectively, and were embedded within a cooler than normal summer, although the summer was not unusually cool using the criteria of Lupo et al. (2003).

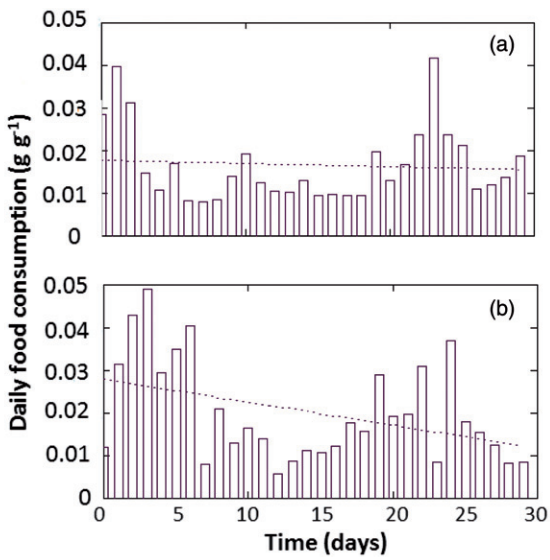

Figure 1. The daily food consumption data ($g\,kg^{-1}$) for (a) bluegill (*Lepomis macrochirus*), and (b) green sunfish (*Lepomis cyanellus*) for 15 July to 15 August 1996. The dashed line is a linear regression line.

The linear trend line was slightly negative during the period, which would be expected as late July is the warmest time of the year for Central Missouri. However, it is evident that there was a quasi-cyclical pattern to the temperature record.

The summer of 1996 was also below the normal for precipitation but not unusually so (see Hagen et al. 2009). During the summer months, 60, 89, and 45 mm of rain fell during June, July, and August, which represented shortfalls of 46, 12, and 44 mm for each month, respectively. Most of the precipitation fell during the latter part of July (Figure 2b). Then, after 30 July, there was very little precipitation. This type of precipitation distribution is common in the Midwest; that is, 2–3 weeks of wet weather, followed by a similar period of dryness, and may be linked to the Madden Julian Oscillation in the tropics (Mo 2000). Additionally, Ratley et al. (2002) demonstrated that the time period between major rains during the summer in this region is generally 10 days to 3 weeks, which is at least twice as great as similar periods during the other seasons.

Finally, temperature and precipitation data from Helsinki, Finland, are also shown for the period of 1 July to 31 December 2002 (Figure 3). In the temperature plot, there was not only a general decline which would be expected with the annual cycle but also shorter-term cycles were visible (Figure 4). The precipitation data showed that in 2002, August and September were relatively dry and the last part of the year experienced regular precipitation events.

Spectral analysis

In Figure 5(a), the power spectrum data derived from the bluegill daily consumption rate data showed significant peaks at wave numbers 3, 7, and 15, which roughly

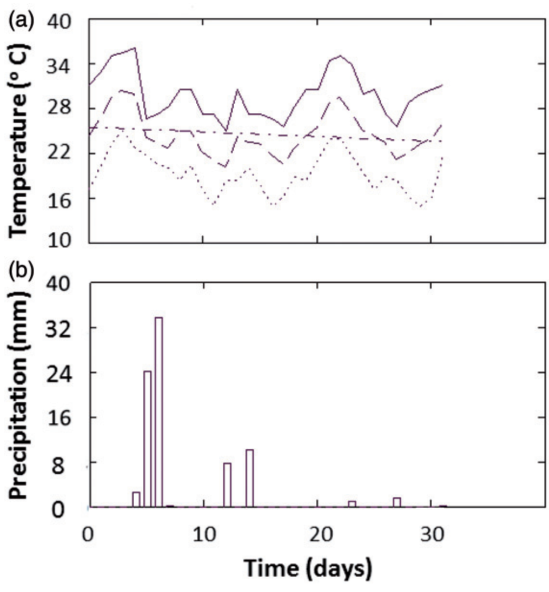

Figure 2. The daily (a) temperature (°C) and (b) precipitation (mm) record from Sanborn Field in Columbia, MO, USA, from 15 July to 15 August 1996. The solid (top), dotted (bottom), and dashed (middle) lines are the daily maximum, minimum, and mean temperatures, respectively. The dashed straight line is the linear trend (regression) line.

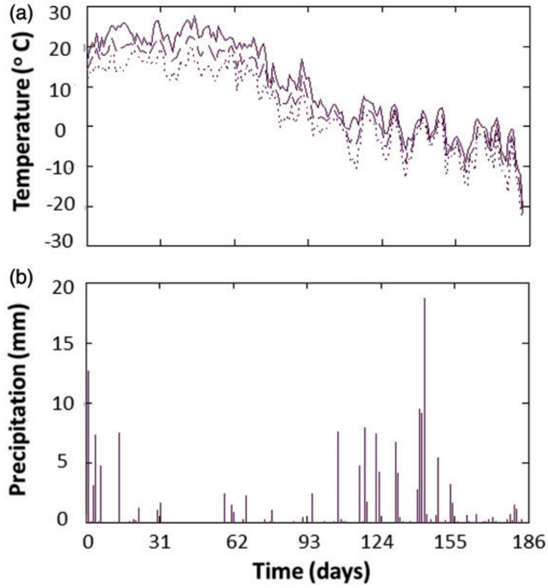

Figure 3. As in Figure 2, except that the data are for Helsinki, Finland, from 1 July to 31 December 2002. There is no trend line in Fig. 3a.

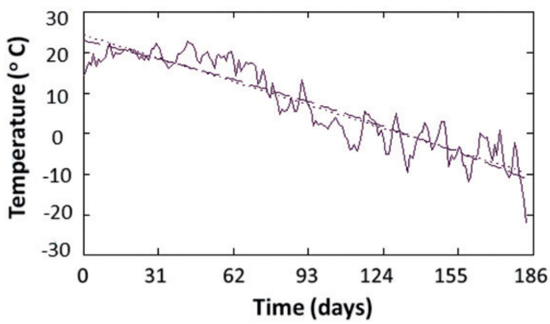

Figure 4. As in Figure 3a, except that only mean temperature is shown. The dotted (dashed) line is a quadratic (cubic) regression function.

correspond to periods of 10, 4, and 2 days, respectively. For the green sunfish (Figure 5b) these peaks occurred at wave numbers 2, 11, and 13, which correspond to periods of 15, 3, and 2 days, respectively. An examination of the temperature and precipitation data (Figure 5c) coincident with the time period of the fish feed deprivation study, demonstrates that there were significant peaks in the temperature data at wave numbers 2, 5, and 13, which correspond to 15-, 6-, and 2-day periods, respectively. It is difficult to discern what patterns may exist in the precipitation data in that the spectral power is weak at most wave numbers (Figure 5d).

A cross-spectral analysis was then performed using, for example, the green sunfish and temperature time series. Figure 6 represents the convolution of the temperature data with the daily food consumption data. It is apparent that there are two strong peaks; one close to wave numbers 2 and 3, and another near wave numbers 10 and 11. These strong peaks are significant at the 95% confidence level.

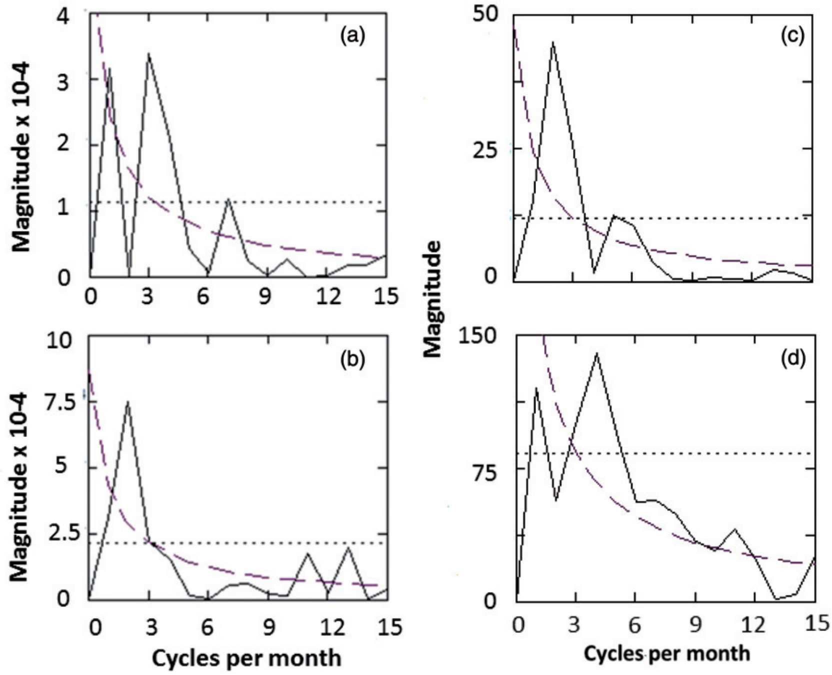

Figure 5. Power spectra for (a) bluegill daily consumption rate, (b) green sunfish daily consumption rate, (c) Sanborn field temperature, and (d) precipitation data for the same time period with the ordinate displaying the relative magnitude or power of the Fourier coefficient and the abscissa is the number of cycles per month. The dotted (dashed) line is the 95% confidence level following Wilks (2006) and assuming the spectrum is white (red).

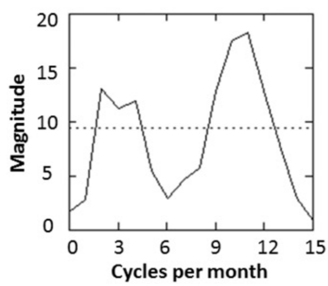

Figure 6. As in Figure 5, except shown is the cross-spectral analysis of the green sunfish and temperature data. The dotted line is the 95% confidence level.

Furthermore, in order to show that this analysis demonstrates correspondence between the daily consumption rate and weather, we compared the results of Nikki et al. (2004) who showed that in Finland, the best feed deprivation period for eliciting compensatory growth was approximately 4 days. In their study the food deprivation experiments were performed at 2, 4, 8, and 14 days with rainbow trout (*Onchorhynchus mykiss*). Weather data provided by the Finnish Meteorological Institute (Figure 7) demonstrates that there were significant cycles near wave numbers 2, 3.5, 4, and 5 (per month). Non-integer wave numbers can be inferred here

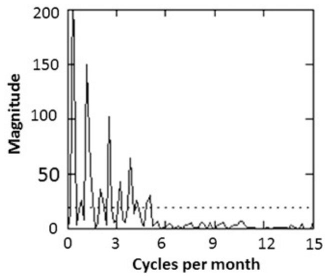

Figure 7. As in Figure 5, except that the temperature record for is shown for Helsinki, Finland.

because the data set was much longer and then was converted into waves per month. The wave numbers cited here correspond to periods of 15, 9, 7, and 6 days.

Discussion

In order to substantiate the relationship between the climate and the daily consumption rate data, the cross-spectral analysis was performed using both the species separately. This analysis does correspond to the results of Whitledge and Hayward (2000) in demonstrating the dominance of peaks at the long and short end of the spectrum for the green sunfish (Figure 6). Additionally, the same analysis was performed for the bluegill data and resulted in a similar figure (not shown).

Here, the spectral peaks for the consumption rates roughly corresponded with the temperature spectral peaks in the 10–15 -, 3–6 -, and 2-day ranges. These daily food consumption results in Missouri, for the most part, correspond to those of Whitledge and Hayward (2000), who found preferred feeding and growth periods following 2 and 14 days of feed deprivation. Whitledge and Hayward (2000) also found a noticeable lack of correlation to growth rates (in their study measured in grams per day using the initial and final weights of their fish) and consumption rates at the 5–9-day deprivation periods. Here, no significant spectral peaks for cycles four–six were found, and these would correspond to the Whitledge and Hayward (2000) periods. It should be noted that only 30 days of data were analyzed here. A time series of 30 days is short and may result in aliasing error in that the power spectra provide information at discrete wave numbers. Then the 14-day deprivation period found by Whitledge and Hayward (2000) would not result in an integer wave number in a 30-day time frame. This may explain why the bluegill feed data did not precisely match at the 14-day deprivation period.

In the temperature time series, the 15-day period is related to changes in the atmospheric long-wave pattern associated with vacillation. The 6-day period is the synoptic period, or the passage of shorter-scale waves in the atmosphere, whereas the 2-day period may be associated with mesoscale pulses resulting from convection elsewhere in the Midwestern United States, or other subgrid-scale processes. It should be noted that this conjecture would be difficult to substantiate without a more dense observation network covering the Midwest during the summer of 1996. However, there is strong correspondence between the preferred feeding period and the temperature time series.

It is difficult here to find exact correspondence between the Finnish temperature data and the data from Nikki et al. (2004). Examining Figure 3, it was likely that there was some variation in the duration of the synoptic cycle, especially as the time period here spans the summer season and goes into the winter season. The synoptic cycle in the summer can be expected to be longer (e.g., Ratley et al. 2002). Also, the 4-day period from Nikki et al. (2004) was close to the 6-day period here, but their study did not test 6 days explicitly. The advantage of the longer study here is that it provided a larger, more robust, data set that should, in theory, provide a stronger statistical relationship. However, the shorter study of Whitledge and Hayward (2000), particularly during the summer season, should provide a data set that is potentially free of longer-term cycles, as well as changes in the synoptic cycle that may accompany a change of seasons. The Helsinki temperature record here, nonetheless, showed the potential for correspondence with the daily food consumption data from the study of Nikki et al. (2004), in spite of the testing periods used for each.

Conclusions

Results showed strong peaks, in the daily consumption rate for fish and temperature spectra at low wave numbers (2–4) and high wave numbers (10–11), corresponding to those found by Whitledge and Hayward (2000) who made direct laboratory observations of the magnitude of fishes' compensatory growth responses, to varying periods (days) of feeding deprivation. The peaks found in this study were significant at the 95% confidence level. The growth rates were significantly higher in treatment groups that involved 2- and 14-day deprivation periods versus the control group (Whitledge and Hayward 2000), indicating potential broad scale influences of weather events on fish food consumption and growth. Additionally, at feed-deprivation periods that were not identified by Whitledge and Hayward (2000), the spectral peaks in each analysis were weak. Then, a cross-spectral analysis of the temperature and fish-feed data also corresponded strongly to the 2- and 14-day feed-deprivation periods of Whitledge and Hayward (2000). Finally, in order to provide a comparison to the analysis in our region, a brief analysis of weather information from Helsinki, Finland, was conducted and compared with the study of Nikki et al. (2004).

Thus, there is some evidence here that weather plays a role, albeit indirectly, in the feeding habits and growth of fishes. While there has long been anecdotal evidence that fish feeding habits correspond to the weather and more precisely cycles within the weather, this is the first study that the authors are aware of which demonstrates, through the use of spectral techniques, that fish growth rates may likewise correspond to the local weather. Then in future studies, it may be possible to perform field work in which farmed fish or stock fish are fed in concert with local weather variability using the results gained here in order to determine whether these fish grow larger.

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