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Title
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Permalink
https://escholarship.org/uc/item/1nn44319

Journal
Ecology, 87(8)

ISSN
0012-9658

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Publication Date
2006-08-01

DOI
10.1890/0012-9658(2006)87[1932:brteft]2.0.co;2

Peer reviewed

REPORTS

BIOLOGICAL RESPONSES TO ENVIRONMENTAL FORCING:
THE LINEAR TRACKING WINDOW HYPOTHESIS

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Abstract. Determining the relative contributions of intrinsic and extrinsic processes to the regulation of biological populations has been a recurrent ecological issue. Recent discussions concerning ecosystem "regime shifts" again raise the question of whether population fluctuations are mainly controlled by external forcing. Results of nonlinear time series analyses indicate that pelagic populations typically do not passively track stochastic environmental variables. Rather, population dynamics are better described as nonlinear amplification of physical forcing by biological interactions. However, we illustrate that in some cases populations do show linear tracking of the physical environment. To explain why population dynamics can sometimes be linear, we propose the linear tracking window hypothesis: populations are most likely to track the stochastic environmental forcing when their generation time matches the characteristic time scale of the environmental signal. While our observations follow this hypothesis well, our results indicate that the linear tracking window is a necessary but not a sufficient condition.

Key words: ecosystem shifts; environmental forcing; generation time; linear tracking; nonlinear responses; population dynamics.

INTRODUCTION

Understanding the mechanisms that cause fluctuations of natural populations has been a persistent theme in ecology. As early as the Nicholson–Andrewartha and Birch controversy, intrinsic dynamics (e.g., density dependence; Nicholson 1933) and external forcing (e.g., weather; Andrewartha and Birch 1954) have been debated as fundamental causative agents controlling fluctuations of natural populations. The relative contribution of these two sources of variability has been stridently debated ever since (Turchin 2003). Although ecologists have agreed that neither exclusive view provides a satisfactory explanation for observed fluctuations in populations (Ellner and Turchin 1995, Turchin 1999), this conceptual consensus does not provide guidance as to the conditions in which one or the other predominates (Dixon et al. 2001).

Recently, similar discussions have arisen in the aquatic sciences community, known as the regime shift debate. The popular concept of a regime shift (sensu Isaacs 1976) is that an ocean climate condition can persist for a protracted period and then undergo a relatively rapid shift to another state (cf. Scheffer et al. 2001). This notion comes from long-term observations of large-scale climate indices, for example, the North Pacific Index (NPI; Trenberth and Hurrell 1994), the Pacific Decadal Oscillation (PDO; Mantua et al. 1997), and the North Atlantic Oscillation (NAO; Hurrell 1995), among others. A variety of biological records have been suggested to correspond to the alleged climatic regimes (Beamish et al. 1997, Francis et al. 1998, Brinton and Townsend 2003, Lavaniegos and Ohman 2003, Peterson and Schwing 2003, deYoung et al. 2004). These observations suggest that marine ecosystems have shifted from one state to another as a result of the changes in underlying climatic factors (Benson and Trites 2002).

However, it has also been argued that these apparent regime shifts in climate time series might simply be realizations of autocorrelated red noise rather than singular events generated from nonlinear dynamics (Wunsch 1999, Pierce 2001, Rudnick and Davis 2003). Whether such climatic state shifts are best described as abrupt, nonlinear changes, as well as the characteristics of biological responses to environmental changes, is actively debated. To address these questions, Hsieh et al. (2005*a*) examined nonlinearity of a suite of physical and biological variables associated with the regime shift debate in the North Pacific and showed that the physical

variables are in fact linear. The claimed regime shifts in climate did not happen in the past century. However, the biological variables consistently show a nonlinear signature. This is true across several time scales, ranging from weekly to annual. Biological populations did not simply track the linear environmental variable passively; rather, their responses to linear external forcing were nonlinear.

Here we extend the analysis of Hsieh et al. (2005*a*) by asking whether all population responses to environmental forcing are nonlinear for three well-defined time scales (daily, monthly, and annual) in nature. We focus on the generation time of a population, as this has been suggested to be an important factor determining population dynamics in response to external forcing (Pimm 1991). We explicitly examine whether nonlinearity of a biological time series is related to the organism's generation time, here approximated as the time between first appearance of an egg and appearance of eggs of the progeny generation for metazoans and the time between first appearance of mother and daughter cells for unicellular organisms.

MATERIALS AND METHODS

We followed the procedures of Hsieh et al. (2005*a*) for data analysis and briefly describe them here. We base the nonlinear time series methods on state space reconstruction with lagged coordinate embeddings (Takens 1981). To embed a series of scalar measurements, vectors in the state space are formed from time delayed values of the scalar measurements: X_t, $\{x_t, x_{t-\tau}, x_{t-2\tau}, \ldots, x_{t-(E-1)\tau}\}$, where E is the embedding dimension, and τ is the lag ($\tau = 1$ in all our analyses). We first use the simplex-projection to identify the best embedding dimension (E) (Sugihara and May 1990), and then use this embedding in the S-map procedure to assess the nonlinearity of the time series (Sugihara 1994). For both methods, we evaluate model performance on an out-of-sample basis: each time series is divided in half, so that the first half is used to build the model and the second half is used to test it. The idea behind determining nonlinearity of a time series is to examine whether or not there is a significant improvement in out-of-sample forecast performance with an equivalent nonlinear vs. a linear forecast model. We call it "equivalent" because whether the model is linear or nonlinear depends only on one parameter, θ. When θ = 0, the model is linear; when θ > 0, the model is nonlinear. We then investigate a series of models with 0 ≤ θ ≤ 3 and select the best model based on the out-of-sample forecast skill.

After selecting the best model, we test the significance of improvement of nonlinear forecast skill over the linear model. In Hsieh et al. (2005*a*), the correlation coefficient (ρ) between predictions and observations was used to represent model predictability, and nonlinearity was measured as the increase in correlation (Δρ) of a nonlinear over a linear model. The prior study used the parametric Fisher's *Z* statistic to test the significance of

Δρ (Kleinbaum et al. 1998). The drawback of this approach is that does not take the serial correlation within the time series into consideration. Therefore, Δρ is a biased measurement of nonlinearity, and an alternative approach needs to be developed to account for the autocorrelation in performing the hypothesis test. To overcome this difficulty, in the current work we use mean absolute error (MAE) to represent model predictability, as well as the decrease in forecast error (ΔMAE) to measure nonlinearity (Sugihara et al. 1996). We use a nonparametric randomization procedure to test the significance of ΔMAE. This procedure is carried out as follows: First, calculate ΔMAE from the S-map procedure, denoted as the statistic *T*. Second, randomly shuffle the original time series, repeat the S-map test on the shuffled time series, and obtain a bootstrapped null ΔMAE, *T**. After repeating this procedure 1000 times, we determine the probability that *T** is superior to *T*.

We analyze biological time series of diatoms, dinoflagellates, copepods, euphausiids, and fishes sampled in the Northeast Pacific and copepods sampled in the North Sea (northeastern Atlantic), categorized according to their approximate generation time (see the Appendix). Diatoms and dinoflagellates, including daily data (1919–1922) and weekly data (1918–1939), were from W. E. Allen's collection from the Scripps pier in La Jolla, California (Hewes and Thomas 2002). Among those phytoplankton specimens, many were identified only to the genus level. Therefore, we collapsed data from the species to the genus level (except for *Pseudonitzschia australis*, *Ceratium fusus*, and *Prorocentrum micans* that were enumerated consistently), and selected the taxa that appeared frequently (at least two-thirds of the sampling period) to assure data quality (see the Appendix). For Northeast Pacific copepods, we used time series from night samples of the 24 species (adult females only) that occurred most frequently (≥20 of 31 continuous sampling years, 1951–1966 and 1985–1999, omitting the intervening years containing gaps in sampling) during spring cruises of the California Cooperative Oceanic Fisheries Investigations (CalCO-FI) in the southern sector of the California Current (Rebstock 2002). For Northeast Pacific euphausiids, we used night samples of the eight most abundant species sampled during spring CalCOFI cruises in the southern sector of the California Current as reported in Brinton and Townsend (2003), as well as the next eight abundant species sampled at the same place and time and analyzed in the same manner, but not previously published. Higher trophic levels were represented by annual data of 29 coastal and neritic fish species sampled as ichthyoplankton in the CalCOFI surveys, categorized according to their age-at-maturation (Hsieh et al. 2005*b*), as well as by annual commercial landings of five species of Pacific salmon (Washington and Oregon Department of Fish and Wildlife 2004: Table 3). For North Sea copepods from the Continuous Plankton Recorder survey, we used eight species that spanned the longest period and

TABLE 1. Analyses of physical time series.

Physical data and time period	Best E	Best MAE	ΔMAE	Nonlinear?	Sample size	P
Daily						
SIO SST (1919–1922)	20+	0.699	0.002	no	1461	0.213
Weekly						
SIO SST (1921–2002)	20+	0.607	0.000	no	4226	1.000
Monthly						
SIO SST (1921–2002)	20+	0.721	0.000	no	984	1.000
PDO (1900–2004)	20+	0.525	0.000	no	1248	1.000
NPI (1899–2004)	20+	0.374	0.000	no	1260	1.000
SOI (1933–2003)	20+	0.766	0.000	no	852	1.000
NAO (1950–2004)	20+	0.633	0.000	no	660	1.000
Annual						
SIO SST, composite (1921–2002)	20	0.520	0.004	no	984	0.207
PDO, composite (1900–2004)	10	0.708	0.003	no	1248	0.143
NPI, composite (1899–2004)	16	0.617	0.000	no	1260	1.000
SOI, composite (1933–2003)	13	0.706	0.000	no	852	1.000
NAO, composite (1950–2004)	10	0.581	0.000	no	660	1.000

Notes: Key to variables: E, embedding dimension; Best MAE, the best forecast skill (mean absolute error); ΔMAE, the difference between MAE of the linear model and Best MAE. A positive ΔMAE measures the difference in forecasting skill of the best nonlinear model as compared to the linear model. Significance of ΔMAE is tested by a randomization procedure. All physical time series at the time scales relevant to the biological data (Table 2) show linear stochastic properties. Key to abbreviations: SIO SST, Scripps pier sea surface temperature; PDO, the Pacific Decadal Oscillation; NPI, the North Pacific Index; SOI, the Southern Oscillation Index; NAO, the North Atlantic Oscillation.

showed no error values (due to missing data) in the WinCPR database (Vezzulli et al. 2005). Because the time series based on annual data points for individual species are too short to analyze by the nonlinear method employed here, composite time series were formed by concatenating all species' time series within a given taxon (Hsieh et al. 2005a). The North Sea copepods from the monthly and annual sampling frequency were both analyzed as composites to be consistent with the CalCOFI copepods.

We reproduced the analyses of the physical time series used in Hsieh et al (2005a), but tested them with the new randomization procedure. In addition, we analyzed the daily Scripps pier sea surface temperature (SST) during 1919–1922, corresponding to the daily phytoplankton data from W. E. Allen's series, as well as the NAO index during 1950–2004.

RESULTS AND DISCUSSION

Analysis of the physical time series (Table 1) reinforces the conclusion that these physical time series are consistently linear, when sampled on time scales from daily to annual. Although there surely are nonlinearities in the underlying physical processes (Sugihara et al. 1999), the time series of the measured quantities are best described by a linear model. In contrast to the physical time series, most of the biological data sets we examined exhibited a nonlinear signature (Table 2). These results are consistent with Hsieh et al. (2005a), indicating nonlinear biological responses to linear environmental forcing. However, specific biological time series showed clear linear characteristics. This was true for euphausiids (krill), whether all species were considered together or species

were partitioned according to biogeographic origins (Table 2). Among all taxa for which annual sampling was analyzed, only the euphausiids showed a linear signature; organisms with both shorter generation times (calanoid copepods) and longer generation times (many species of fishes sampled as either larvae or adults) showed nonlinear characteristics. The other taxa that displayed linear characteristics were phytoplankton (*Pseudo-nitzschia australis*, *Navicula* spp., and *Gymno-dinium* spp.) and North Sea copepods. The phytoplankton species showed a linear signature only in the daily time series. When these same phytoplankton species were examined at increasingly longer time periods, including weekly and monthly averages, their time series displayed nonlinear signatures (Table 2). Furthermore, the North Sea copepods showed a linear signature only when treated from monthly samples (analyzed as a composite), but not when the same data were examined by annual averages (Table 2).

Why do the euphausiid annual data, North Sea copepod monthly data, and some phytoplankton daily data differ from other populations by showing a linear signature? The procedure for summing several species cannot be the explanation, because the same phytoplankton showed a nonlinear response at longer time intervals. Based on consideration of the organisms' generation time, we propose the linear tracking window (LTW) hypothesis: populations are most likely to track stochastic environmental forcing when their generation time matches the characteristic time scale of the environmental signal. This characteristic time scale can be considered as dominant periodicities in the physical environment. To identify dominant periodicities in the California Current, we used spectral analysis to inves-

TABLE 2. Analyses of biological time series.

Biological data	Best E	Best MAE	ΔMAE	Nonlinear?	Sample size	P
Daily						
Pseudo-nitzschia australis	9	0.169	0.000	no	852	1.000
Navicula spp.	13	0.486	0.000	no	852	1.000
Gymnodinium spp.	20	0.399	0.003	no	755	0.123
Chaetoceros spp.	3	0.099	0.135	yes	852	0.001
Coscinodiscus spp.	6	0.348	0.008	yes	852	0.048
Ceratium fusus	3	0.445	0.008	yes	852	0.019
Prorocentrum micans	4	0.358	0.022	yes	728	0.001
Weekly						
Pseudo-nitzschia australis	3	0.281	0.101	yes	886	0.001
Navicula spp.	3	0.466	0.031	yes	886	0.001
Gymnodinium spp.	6	0.507	0.020	yes	901	0.002
Chaetoceros spp.	3	0.340	0.085	yes	886	0.001
Coscinodiscus spp.	3	0.398	0.050	yes	886	0.001
Ceratium fusus	5	0.408	0.017	yes	901	0.043
Prorocentrum micans	3	0.189	0.008	yes	901	0.046
Monthly						
Pseudo-nitzschia australis	3	0.379	0.180	yes	203	0.001
Navicula spp.	4	0.611	0.046	yes	203	0.002
Gymnodinium spp.	2	0.516	0.064	yes	207	0.001
Chaetoceros spp.	5	0.466	0.026	yes	203	0.031
Coscinodiscus spp.	4	0.748	0.118	yes	203	0.001
Ceratium fusus	5	0.620	0.039	yes	207	0.001
Prorocentrum micans	3	0.388	0.033	yes	207	0.043
CPR copepods, composite	15	0.525	0.002	no	3840	0.452
Annual						
CPR copepods, composite	5	0.703	0.018	yes	320	0.001
CalCOFI copepods, composite	6	0.532	0.010	yes	744	0.001
CalCOFI northern copepods, composite	6	0.548	0.022	yes	279	0.001
CalCOFI southern copepods, composite	6	0.531	0.010	yes	434	0.001
CalCOFI euphausiids, composite	9	0.615	0.003	no	832	0.325
CalCOFI northern euphausiids, composite	6	0.740	0.000	no	260	1.000
CalCOFI southern euphausiids, composite	9	0.637	0.001	no	572	0.451
CalCOFI fish (age 1 to 2), composite	6	0.558	0.016	yes	315	0.018
CalCOFI fish (age 2.5 to 3.5), composite	7	0.588	0.014	yes	385	0.001
CalCOFI fish (age 4 and above), composite	7	0.591	0.023	yes	315	0.001
Pacific salmon	4	0.486	0.043	yes	315	0.001

Notes: Variables and abbreviations are as defined in Table 1. Note that the sampling period for daily phytoplankton data (1919–1922) is different from that of weekly and monthly phytoplankton data (1918–1939). Monthly phytoplankton data are averages of weekly samples. Monthly CPR (Continuous Plankton Recorder) copepod data (Vezzuli et al. 2005) are spatial averages over the North Sea, and annual data are averages of the monthly samples.

tigate Scripps pier temperature records averaged at monthly intervals during 1916–2004. We used temperature to represent environmental forcing because it is a good proxy of other physical processes in the southern California Current system, and it is the only available long-term physical variable. The power spectrum shows a distinct annual peak (Fig. 1), corresponding to a dominant seasonal signal. Variations on other time scales are well documented from the Scripps pier records, including monthly (lunar; Pineda 1991, 1995), daily (diel; Pineda 1991, 1994), and still higher frequency variations, which we cannot resolve with the data available here.

Generation time is a time scale that integrates the processes of reproduction, growth, and mortality acting over the entire life history to account for variations in abundance. Therefore, the LTW is defined according to the correspondence between the characteristic biological and environmental time scale (Fig. 2). When the

generation time of a population is longer than the environmental time scale they experience, they will not be able to track environmental changes closely because the biological processes cannot respond as fast as the physical forcing. Conversely, when their generation time is shorter than the characteristic environmental time scale, the dynamics of a population are the result of integration of several generations and therefore they do not track the environmental variables well. Only when their generation time matches the characteristic time scale of the environmental signal can the population have a chance to show linear tracking. For the data of varying time scales we examined, our results correspond well to the LTW hypothesis: in the Northeast Pacific, only euphausiids with generation times corresponding to seasonal forcing in the environment and phytoplankton with generation times corresponding to diel variability fall into the "linear" window and track environmental variations (Fig. 2). In the Northeast Atlantic, we have
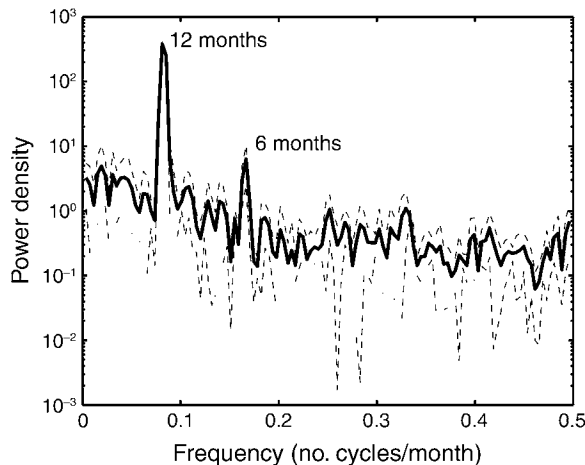
FIG. 1. Power spectrum of the Scripps pier sea surface temperature record (solid line) with 95% confidence limits (dashed lines), based on monthly averages from 1916 to 2002, showing significant energy at the annual scale. The peak at the six-month scale is the semiannual or biennial harmonic.

not identified specific spectral peaks in the environment, but copepods with generation times that average one month (apart from the dormant season) are often exposed to conditions whose within-season variability has approximately a monthly time scale during their growing season, and therefore they show a linear signature in the monthly time series. In each of these cases, the fluctuation of the organisms' abundance from one generation to another is the result of linear tracking of the characteristic environmental signal.

While we only examined the data at a daily, weekly, monthly, and annual scale, we do not suggest that these are the only important time scales related to population dynamics. However, these scales are easy to understand and are observable in nature. To understand a system, it is essential to identify the variables and processes that define the primary environmental time scale relevant to the particular populations of interest. These biologically relevant processes can be determined not only by the strength of the environmental signal but also by its timing or variability. For example, phenological changes can influence population trajectories (Mackas et al. 1998). We recognize that the environment can sometimes be described by broad spectral peaks of variability, rather than a few preferred time scales, and in such circumstances the LTW condition could be less important. Furthermore, the populations themselves may have different time scales of response for different component processes (e.g., ingestion, growth, development, mating, etc.). For long-lived organisms, there can be critical life history phases, which are most susceptible to variations in environmental forcing. Nevertheless, we find generation time a very useful integrative measure that establishes a biologically relevant time scale for the cumulative influence of many individual components

acting over the course of a generation, and is also readily comparable across taxa. Despite these simplifications, the LTW hypothesis explains the observed patterns rather well (Fig. 2).

In considering the LTW hypothesis, the biological response to environmental forcing can be considered as a transfer function. There can be many time scales in the environment and the population, and the transfer function is not constant across time scales. Although evidence suggests that the transfer functions are primarily nonlinear (Belgrano et al. 2004, Hsieh et al. 2005a), we argue that the transfer function can be linear in those circumstances when the population generation time matches the characteristic environmental time scale. This arises because the biological response, measured as a change in abundance of individuals over time, is linked to changes in the physical environment acting over the entire life history of the organisms. The integration of all biological processes that lead to a change in abundance of individuals is then coupled to the environmental forcing. Nevertheless, it is important to point out that the LTW is a necessary but not sufficient condition; Fig. 2 exhibits that not all data
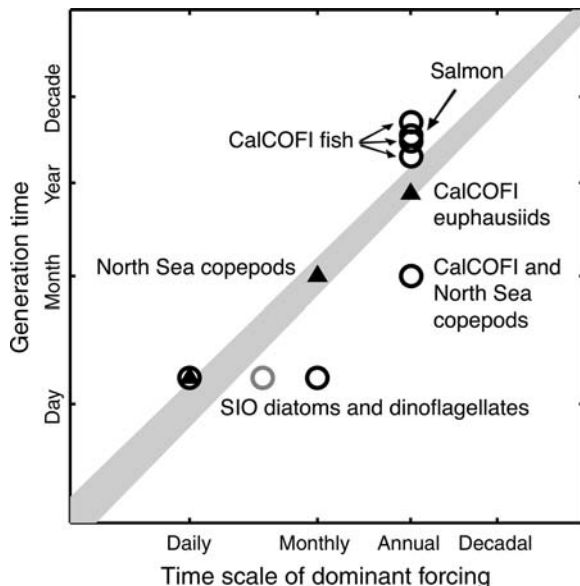

FIG. 2. Schematic illustration of the linear tracking window (LTW) hypothesis. The gray band represents the 1:1 window in which biological generation times match the dominant time scale of environmental variability. Only populations falling in this window are expected to show a linear signature, i.e., passive tracking of the environmental variable. The x-axis indicates the time scale of dominant forcing and also corresponds to the sampling (observation) frequencies that were available and analyzed. Note the logarithmic scale of both axes. Open circles illustrate data sets showing a nonlinear signature, nearly all of which fall outside the linear tracking window; filled triangles represent data sets showing a linear signature, which occur only within the tracking window. The gray open circle represents the phytoplankton data as weekly averages that do not correspond to any time scale of dominant environmental forcing.

falling in the LTW show a linear signature. Some populations might not linearly track the environmental forcing even when their generation time matches the dominant time scale.

The LTW hypothesis matches the population generation time with the dominant environmental time scale. To properly assess whether a population shows linear tracking in the LTW, it is thus necessary to identify the dominant environmental time scales where the population lives. In addition, it would be desirable to sample the population with a sampling interval considerably finer than that of the generation time to examine dynamics at many time scales by resampling the data at different time intervals (each test is independent), including tests inside and outside the LTW.

The preconditions of correspondence of generation times and dominant environmental forcing in the LTW are not often met for populations at a wide spectrum of time scales of interest to ecologists. In addition, since the LTW is a necessary but not sufficient condition for a population to track the environmental signal linearly, nonlinear dynamics tend to dominate in natural populations. Because natural populations often do not passively track environmental variables, using simple linear relationships between climate indices and biological populations to forecast these populations is not likely to succeed (Ohman et al. 2004). It is worth pointing out that our results do not identify how, mechanistically, organisms respond to any particular environmental signal. Mechanisms such as density dependence (Ohman and Hirche 2001, Achord et al. 2003, Belgrano et al. 2004) and/or nonlinear amplification of physical forcing (Dixon et al. 1999) are possible explanations of the time series that demonstrate nonlinear characteristics. Another mechanism proposed by Peters et al. (2004) suggests that when sequential, scale-dependent thresholds are crossed, abrupt changes can occur in population response or ecosystem state. Further research is required to achieve a mechanistic understanding of the interplay of environmental forcing and biological responses and, in addition, long-term surveys must continue to characterize the dynamics in nature.

In summary, we demonstrate that natural populations often do not track the linear environmental signal passively. We also show that in certain circumstances populations can linearly track the environmental signal, and these cases can be explained by the linear tracking window (LTW) hypothesis. Biological time scale (generation time) is an important variable determining how populations respond to external forcing. Dominant environmental time scales can be system specific (although the daily, monthly, and annual cycles may be ubiquitous) and need to be identified to understand biological–physical interactions. The LTW hypothesis can be further tested in other ecosystems.

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APPENDIX

Biological data employed in the analysis (*Ecological Archives* E087-121-A1).