Environmental noise affects the fluctuations of Atlantic large pelagics

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Abstract:

Environmental variables affect many processes of fish biology and their fluctuations are thought to be one of the main factors in variability of fish stocks. Recent work has shown that the variability of the environment in the frequency domain (i.e., the environmental noise) can interact with endogenous processes (e.g., density dependence) and affect fluctuations of animal populations. In this study, we investigate whether fluctuations of large pelagics' time series are affected by environmental noise and whether life-history traits of species modulate this response. By analysing several environmental variables and a large dataset of tuna and billfish catch per unit effort (CPUE) time series from the Atlantic, we show that in environments dominated by long-term fluctuations (i.e., red noise) CPUE time series were less variable and displayed smoother fluctuations. Furthermore, larger, slower-growing and later-maturing species were found to be more sensitive to changes of environmental noise than species with a shorter turnover rate. Our results suggest that environmental noise interacts with fish biology; understanding how it is integrated into biological processes might provide important insights to understand the responses of fish stocks dynamics to exploitation and environmental changes.

1. Introduction

Many environmental variables, particularly in marine environments, exhibit highly autocorrelated fluctuations that are well described by power law models; these variables are said to display $1/f^{\beta}$ noise (Steele, 1985; Vasseur and Yodzis, 2004). In this formulation, the scaling exponent (β) describes the relative importance of the different frequencies in the variance of the signal and it is usually estimated as the slope of the power spectrum in log-coordinates (Halley, 1996; Royer and Fromentin, 2007). Consequently, when the spectral densities of low frequencies are greater than the spectral densities of high frequencies, the scaling exponent becomes negative; the more negative the scaling exponent, the more important the low frequencies. Unlike for white noise in which the low and high frequencies have the same importance ($\beta = 0$), the variance of marine environmental variables (e.g. sea surface temperature) is rather dominated by low frequencies. Such signals are said to display "reddened spectra" with reference to visible light (Steele, 1985). Such reddened spectra are not restricted to environmental variables. Using long-term ecological time series, including fisheries data, other studies exhibited an increase of population variability with census time, the so-called "more time more variation" effect, which also describes reddened spectra (Pimm and Redfearn, 1988; Cyr, 1997; Inchausti and Halley, 2002; Halley and Stergiou, 2005).

Importantly, red noise could enhance the probability of extinction of populations because of higher probability of consecutive adverse conditions (Lawton, 1988; Miramontes and Rohani, 1998; Lundberg et al., 2000; Akçakaya et al., 2003). However, this issue turned into a more complex question as results on population extinction proved to depend upon complex interactions between environmental noise and endogenous processes, such as the strength of density dependence (Ripa and Lundberg, 1996, 2000; Morales, 1999; Jonzén et al., 2002;

Lundberg and Ripa, 2002). Because marine environments generally display more reddened noise than terrestrial ones, and because exploitation reduces the population size, modifies its demographic structure and can further alter trophic interactions (e.g. Jennings and Kaiser, 1998; Vasseur and Yodzis, 2004), exploited fish stocks can be particularly prone to environmental noise. Given its potential implications for management, conservation, as well as for conceptual reasons, understanding if environmental noise can affect fluctuations of fish stocks is of particular interest.

To address this issue, we investigated whether fluctuations in long time series of large pelagic fish displayed different properties among marine environments characterized by contrasting environmental noises. In addition, since environmental noise interacts with endogenous processes and since the biological characteristics of species can affect the response to environmental noise (e.g. Petchey, 2000), we further aimed at investigating how life-history traits can modulate the response of species to environmental noise. In concrete terms, we confronted the statistical properties of 75 catch per unit effort (CPUE) time series of nine species of tuna and billfish, with four oceanographic variables in 11 Atlantic areas. Tuna and billfish are highly migratory species displaying a broad range of life histories and a large geographic repartition thus, constituting a well-suited case study to investigate the effects of environmental noise on fish stock fluctuations.

2. Materials and Methods

2.1. Atlantic tuna and billfish time series

We obtained the dataset using long-term catch and effort spatially disaggregated data from the International Commission for the Conservation of Atlantic Tunas (ICCAT) and from the Institut pour la Recherche et le Développement (IRD). In order to be able to compare environments and species, the time series of annual catch per unit effort (CPUE) for each species were produced in a common and neutral spatial grid. To do so, we chose the Longhurst provinces that are based on the classification of the world oceans into biomes displaying homogeneous and specific environmental properties (Longhurst, 2001), as in Rouyer et al. (2008). We then obtained suitable time series to compare among areas and species, but with the shortcoming of not accounting for interannual migration (e.g. bluefin tuna *Thunnus thynnus*). Note, however, that the analyses are based on annual (and not monthly) CPUE that allows us to cope with seasonal migrations between areas. To minimise potential bias due to interannual migrations, we used the Longhurst provinces, which are large and homogeneous from a biochemical and oceanographic perspective. Finally, we removed time series that were either too short, plagued with missing values or poorly informative (i.e. flat pattern) using the advice from experts on these fisheries.

The final dataset was validated with 75 time series from nine tuna and billfish species in 11 Longhurst provinces (Fig. 1). The most important source of catch data (i.e. 70% of the time series) came from Japanese longline fisheries because they were amongst the oldest ones operating in the Atlantic and because their catches concern all the species throughout the whole Atlantic. These data were available from 1956 to 2004. Other time series mostly came from European baitboat and purse-seiner fleets and were mainly available over the 1969–2004 period.

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The length of the time series in the final dataset ranged between 22 and 49 years and displayed a mean length of 42 years (see Rouyer et al., 2008 for a more complete description of the dataset). Skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) tunas constitute the bulk of the catches of tropical tuna (Fonteneau, 1997) whereas the billfishes, i.e., white marlin (*Tetrapterus albidus*), blue marlin (*Makaira nigricans*) and sailfish (*Istiophorus platypterus*) are generally bycatch of these tropical fisheries and are, thus, of interest since they are affected differently by changes in fishing strategy and techniques (Serafy et al., 2004). Albacore tuna (*Thunnus alalunga*) and swordfish (*Xyphias gladius*) are considered subtropical species, but they are also common in temperate waters whereas bluefin tuna are the only strict temperate tuna (Fromentin and Fonteneau, 2001).

2.2. Environmental variables

Various environmental factors are known to affect key biological and ecological processes of tuna and billfish populations (e.g., Lehodey, 1997; Royer et al., 2004; Prince and Goodyear, 2006). Many environmental variables might thus be relevant. The spatio-temporal range and resolution as well as the occurrence of missing values, while taking into account redundancy and correlation between variables, directed our final choice.

The most studied geophysical variable, sea-surface temperature (SST) was retained as it influences numerous key parameters of fish biology, such as growth and distribution. We also retained the longitudinal (U) and latitudinal (V) wind stress components because of their impacts on local and regional oceanographic processes that may affect biological processes, especially recruitment success and distribution (e.g. Bakun, 1996). Finally, sea-surface salinity (SAL) was also retained, as gradients of this hydrological variable are often associated with the distribution

range, abundance of larvae and displacements of tuna species (e.g. Lang et al., 1993; Lehodey et al., 1998; Maury et al., 2001).

Since models can be limited in their ability to represent the entire range of frequencies at any given spatial scale, we used in priority *in-situ* measurements being re-analysed and validated from various institutional datasets (Fromentin et al., 2005). SST was extracted from the NOAA Extended Reconstructed Sea Surface Temperature, which is reconstructed on the basis of *in-situ* measurements from the ICOADS dataset coupled with improved statistical methods (Available at http://www.cdc.noaa.gov/cdc/data.noaa.ersst.html). This variable consists of a monthly time series defined on a $2.0° \times 2.0°$ global grid and whose temporal extent ranges from 1800 to 2005. The U and V wind velocity components came from the 40-year re-analysis (ERA40) provided by the European Centre for Medium-Range Weather Forecasts (ECMWF, Available at http://data.ecmwf.int/data/d/era40_mnth/). This dataset consists of a monthly time series defined in a $2.5° \times 2.5°$ global grid and whose temporal extent ranges from 09/1957 to 08/2002. Finally, the SAL data were extracted from the Simple Ocean Data Assimilation (SODA, University of Maryland) global analysis dataset (Available at http://ingrid.cwb.gov.tw/SOURCES/.UMD/.Carton/.goa/.beta7/); available on a $1° \times 1°$ global grid from 01/1950 to 12/2001 on a monthly basis. For each environmental variable, time series were extracted from each available pixel in each province.

2.3. Life-history traits

To investigate how different life histories may modulate species responses to environmental noise, we retained three traits for each species. We used size-based rather than age-based traits because the former are more reliable and more easily available across species.

We retained the maximum length (Lm) as larger fishes have generally a longer life span and more numerous age classes, which can affect population fluctuations due to generation overlapping (Petchey, 2000; Fromentin and Fonteneau, 2001; Bjørnstad et al., 2004). To depict the size at maturity and rate of growth, we retained the length at maturity (L50), defined as the length at which 50% of individuals are mature, as well as the growth parameter from the von Bertalanffy curve (K). Lm is known to be correlated with L50 (here c = 0.77) and K (here c = -0.81), but if Lm allows for an efficient discrimination of traits for species with large size differences (e.g. skipjack and bluefin tunas), species with similar Lm can display substantial differences in both K and L50 (e.g. blue-marlin and swordfish; Table 1). We consequently conserved the three parameters to reflect these differences. A Principal Component Analysis (PCA) was also carried out to obtain an index that combines all life-history traits (see Fromentin and Fonteneau 2001), but the effects of individual traits were also considered. The parameter estimates were mainly extracted from Fromentin and Fonteneau (2001) and from the ICCAT manual (2008), although other references were extracted from the literature to complement the dataset (Table 1).

2.4. Colour of the environmental noise

The "colour of noise" displayed by the environmental time series was commonly estimated as the spectral exponent of a $1/f^{\beta}$ model fitted to the power spectrum and in log-coordinates (Halley, 1996; Vasseur and Yodzis, 2004). As the spectral estimates display a high variance we used the multitaper method to obtain robust estimates; this method has already been widely applied on the analysis of geophysical signals such as atmospheric and oceanic data (Thomson, 1982; Ghil and Vautard, 1991; Percival and Walden, 1993). This method attempts to reduce the variance of spectral estimates by using a small set of orthogonal tapers that allows one to compute a set of independent estimates of the power spectrum. Averaging over these independent estimates yields a better and more stable estimate than do single taper methods (Thomson, 1990).

For each variable, we first extracted the time series and computed its power spectrum. Because the estimation of the power spectrum is sensitive to the length of the time series and since we aimed at characterizing a general property of the environment, the power spectra were computed over the maximum time period available for each variable. This allowed us to analyze the maximum range of frequencies available, and it also prevented biases due to potential changes in the frequency content through time. We then applied a robust regression on the power spectrum in log-coordinates to estimate the scaling exponent. The robust regression ensured that the estimates were not affected by peaks in the power spectrum, such as the peak due to seasonality. We obtained an estimate of the scaling exponent for each pixel of each environmental variable. Doing so, we produced four Atlantic maps (one for each variables; Fig.2). A PCA was then applied on a table of scaling exponents (pixels * environmental

variables) using a correlation matrix to combine the four environmental variables into one environmental signal (Fig. 2). Multivariate approaches, such as a PCA, are largely used for studying the spatial variability and the combined effect of geophysical variables (e.g. McFarlane et al., 2000; Pedraza and Ochoa, 2006). PCA finds an orthogonal set of axes and the first axis, uncorrelated to the others, is a linear combination of the different variables that maximizes the variance of the dataset. Investigating the correlation circle allowed us to check for the nonredundancy of variables, while the projection of the dataset onto the first axis produced an overall measure of environmental noise as a linear combination of the four environmental variables. This enabled us to integrate the information from four environmental variables to extract the principal mode of variability for environmental noise over the Atlantic. The significance of the first axis was assessed using the broken-stick model (MacArthur, 1957). The broken-stick model was originally proposed to describe the relative abundance of bird species in an environment, such that the relative abundance of n species are proportional to the size of the segments of a unit-length stick broken at $n - 1$ random locations. By analogy, Frontier (1976) applied it to the variance decomposition performed by the PCA by assuming that the total variance was randomly divided among different axes and that the percentage of variation explained by the PCA axes would be similar to the expected length of the pieces of a stick randomly broken. The test was performed by comparing the percentage of variance explained by the first axis to the prediction made by the broken stick model (see Frontier, 1976 and Legendre and Legendre, 1998 for technical details). As the fisheries time series were available at lower spatial resolution, the province, we randomly picked 1000 values into the distribution of the scaling exponents for each variable and each province. Those 1000 values were then averaged to obtain a robust estimate of the mean scaling exponent for the province.

2.5. Statistical properties of the CPUE time series

We selected the following three properties to describe different relevant aspects of the CPUE fluctuations and to study the effects of environmental noise.

2.5.1.Variance in the time domain: the population variability

The variance of population abundance in the time domain depicts the average magnitude of the fluctuations and is usually quantified through the coefficient of variation (CV). However, the CV is unit-free and independent of the mean, and thus can be biased by rare events and non-Gaussian distributions. As fisheries time series are often plagued with zero counts and often display non-Gaussian distributions, we instead used the population variability (PV) metric proposed by Heath (2006). This approach quantifies the variability as the percent difference between all combinations of the observed variable (here, CPUE) and is less sensitive to rare events and tailed variables compared to the CV (Heath, 2006).

For a time series of size *n*, the PV is defined as:

$$PV = \frac{2 \sum \left(1 - \frac{min(z_i, z_j)}{max(z_i, z_j)} \right)}{n(n-1)} \ , \tag{1}$$

where z represents the list of all the possible pairwise combinations (i,j) of values in the time series, with i≠j.

2.5.2. Detection of density dependence: the Partial Rate Correlation Function

The strength of density-dependent processes has been shown to interact with environmental noise (e.g. Petchey et al., 1997; Cuddington and Yodzis, 1999). Following Berryman and Turchin (2001), we thus computed the Partial Rate Correlation Function (PRCF) at lag one to quantify the strength of direct density dependence in fisheries time series.

The PRCF at lag one of the time series x(t) is estimated as the correlation between the series of per capita rate of change $R(t) = l(t) - l(t-1)$ and the lagged density $l(t-1)$, with $l(t) = \log(x(t)+1)$:

$$PRCF = \frac{\sum \left(l(t) - \bar{l}\right)\left(R(t) - \bar{R}\right)}{\sqrt{\sum \left(l(t) - \bar{l}\right)^2 \sum \left(R(t) - \bar{R}\right)^2}} \; . \tag{2}$$

2.5.3. Variance in the frequency domain: the scaling exponent

The colour of noise or the scaling exponent (BETA) of each fisheries time series was also estimated to quantify its variance in the frequency domain. However, estimating the scaling exponent of fisheries time series can hardly be applied using a simple spectral analysis because these time series are often too short to get a reliable estimate of the power spectrum. Therefore, we used the more robust multiple segmenting method proposed by Miramontes and Rohani (2002). This method splits the time series into small segments and computes the spectral exponent on each of these pseudoreplicates. An accurate estimate for the spectral exponent of the whole time series can then be obtained from the relationship between segment length and spectral exponent estimates.

The CPUE statistics were then plotted against environmental noise after removing the potential effect of gear (Rouyer et al. 2008). This was achieved by taking the residuals of a linear model explaining each statistic as a function of a factorial effect of gears.

2.6. Effects of life-history traits

We investigated whether the relationships between each of the statistics and environmental noise were related to life-history traits of species. To do so, we first estimated for each species the slope of the linear regression between the three statistics (PRCF, BETA and PV)

and the environmental noise of each environmental variable, using jackknife and bootstrap

resampling techniques. This allowed us to dampen the effects of outliers and to compensate for

the different number of time series available for each species. We then plotted the slopes for each

species against their life-history parameters to investigate potential interactions between life-

history traits and environmental noise.

All computations were performed using R (ver. 2.6.1, R Development Core Team, 2007;

Available at http://www.R-project.org).

3. Results

3.1. Environmental noise over the Atlantic

Mapping the estimated scaling exponent for each environmental variable as well as the first axis of the PCA on the environmental variables allowed us to investigate the spatial variability of environmental noise over the whole Atlantic in a synoptic way (Fig. 3).

These five maps displayed large homogeneous areas of lower/greater values, indicating that environmental noise was not randomly distributed over the Atlantic, and thus enabled us to identify areas with different stochastic properties. For instance, the tropical and subtropical areas (below 20°N) were dominated by low-frequency fluctuations for both the SST and wind stress, while the temperate areas displayed more balanced (more white) environmental signals (Fig. 3a–c). The salinity exhibited a different spatial pattern, as areas dominated by low frequencies were mostly located in the northeast and west equatorial Atlantic (Fig. 3d). The first component of the PCA that explained 55% of the total variance among the four environmental variables was significant according to the broken-stick model (Frontier, 1976; Legendre and Legendre, 1998). Therefore, we used it as a measure of environmental noise that integrates the different variables, and we refer to it as the Environmental Noise Index (ENI). SST, UST and VST contributed similarly and significantly to the ENI while SAL had little influence (the loadings were 0.54, 0.61, 0.58 and -0.04, respectively). The ENI was positive for the more reddened areas (i.e. more negative exponents) while it was negative for the less reddened areas (i.e. less negative exponents). So, the more positive the ENI, the more the area is dominated by low frequencies in SST, UST and VST. In general, the southeastern areas were clearly dominated by low frequencies than the northeastern ones (Fig. 3e). As the Longhurst provinces were fairly homogeneous, we averaged the estimated scaling exponents and the ENI over each province

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(Table 2) to enable comparisons with the statistical properties of the CPUE time series.

3.2. Relationships between environmental noise and CPUE statistics

To investigate the relationship between environmental noise and the three statistics computed for the CPUE time series (PRCF, BETA and PV), we plotted them against the ENI for each species.

First, the relationships displayed clear differences between species. Inspecting the PV against the ENI, showed clear decreasing trends for blue-marlin ($r^2 = 0.52$, $p = 0.07$), swordfish ($r^2 = 0.38$, $p = 0.05$), sailfish ($r^2 = 0.67$, $p = 0.09$) and white-marlin ($r^2 = 0.44$, $p = 0.22$) CPUE time series, whereas the trends were weaker and nonsignificant for bigeye ($r^2 = 0.07$, $p = 0.33$), skipjack ($r^2 = 0.1$, $p = 0.54$) and yellowfin ($r^2 = 0.0$, $p = 0.98$) tunas (Fig. 4). Note, that results for the bluefin tuna were not suitable for interpretation because of its geographic repartition. The bluefin tuna time series all issued from provinces that displayed similar environmental characteristics for both the scaling exponent and the ENI. This did not allow for comparisons with time series for other species that were available over a broader area and thus a larger range of scaling exponents. The BETA results were consistent with those obtained for the PV (Fig. 4). While blue marlin ($r^2 = 0.06$, $p = 0.6$), swordfish ($r^2 = 0.29$, $p = 0.09$) and white marlin ($r^2 = 0.93$, $p = 0.01$) displayed a decrease of the BETA with the ENI (albeit not always significant), yellowfin tuna ($r^2 = 0.01$, $p = 0.40$) and skipjack tuna ($r^2 = 0.15$, $p = 0.45$) displayed weaker or no relationships with the ENI. The results for the PRCF generally displayed a decrease in the negative feedback for environments dominated by long-term fluctuations (positive ENI; Fig. 4). Finally, some areas exhibited CPUE with a lower PV and PRCF as well as a more negative BETA, indicating a domination of smoother, reddened and less variable fluctuations than in other

areas (in contrast to more variable areas but with a more balanced spectrum between high and low frequencies). Note, that the sample size differs substantially among species and is also often small (e.g., sailfish: $n = 5$, bigeye tuna: $n = 15$), thus influencing p-values and impairing their comparison among species.

3.3. Effect of life-history traits

The first principal component from the correlation matrix between life-history traits explained 79% of the variance and was significant according to the broken-stick model. The first component scored negative for the larger, slower-growing and later-maturing species (bluefin tuna, blue marlin, sailfish, swordfish and white marlin) and scored positive for the smaller, faster-growing and earlier-maturing species (albacore, bigeye, skipjack and yellowfin tunas). Since this measure combines all the life-history traits across species, we refer to it as the combined traits index (CTI).

The slopes of the linear regressions between environmental noise and the different statistics were plotted against life-history parameters to investigate how life-history traits modulate the response of species to environmental noise. First, we considered the more general picture by plotting the slopes obtained from the CPUE statistics and the ENI, versus the CTI for each species. These results showed an increase of the slopes with the CTI for the relationships obtained with PV ($r^2 = 0.47$, $p = 0.059$) and the BETA ($r^2 = 0.27$, $p = 0.186$) whereas no clear relationship was found when considering the PRCF ($r^2 = 0.0$, $p = 0.93$). In other words, species with a negative CTI were characterized by a steeper decline of PV with ENI, whereas the slopes were almost flat for species with a positive CTI (Fig. 5a); so that the larger, the slower growing and the later maturing that a species is, the more important the decrease of CPUE variability with

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environmental noise. The slopes obtained between the PRCF and the ENI did not appear to be related to life-history traits as depicted by the CTI (Fig. 5b), whereas for the BETA (Fig. 5c), the results showed that larger, slower-growing and later-maturing species displayed more pronounced slopes. As for the PV, these species appeared more sensitive to changes of environmental noise and their CPUE displayed more reddened fluctuations in more reddened environments.

We then investigated the respective effect of different environmental variables by plotting the slopes obtained for each of the four environmental variables and CPUE statistics versus the CTI. The slopes of SST and PV for each species revealed a high and significant correlation with life-history traits ($r^2 = 0.81$, $p = 0.002$; Fig. 5d) and furthermore, the values of these slopes were large enough to denote biologically relevant changes. Again, larger, slower-growing and later-maturing species displayed a more important increase of variability with environmental noise than smaller, faster-growing and earlier-maturing ones. Unlike slopes obtained with the PRCF (Fig. 5e), the slopes obtained with the BETA were more affected by wind stress environmental variables (UST and VST) and species time series with a negative CTI becoming more reddened in more reddened areas (Fig. 5f). No clear pattern, however, emerged when considering SST and SAL. Finally, we investigated each individual life-history trait. The growth parameter (K) was found to correlate with the slopes obtained for each of the three statistics and environmental noise. In particular, the best correlations were found between K and the slopes obtained for PV versus SST ($r^2 = 0.66$, $p = 0.014$; Fig. 5g), PRCF versus UST ($r^2 = 0.39$, $p = 0.096$; Fig. 5h) and BETA versus UST ($r^2 = 0.66$, $p = 0.014$; Fig. 5i). The faster growing a species, the less the PV, the BETA and the PRCF of the CPUE were found to vary with environmental noise. In other words, the CPUE time series for faster-growing species did not show any change of property

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with environmental noise as the variability, frequency content and negative feedback remained stable across environments.

4. Discussion

In this study, we performed an extensive description of environmental noise to investigate how much CPUE fluctuations could be related to the colour of environmental noise. As ecological processes might not be equally sensitive to the same environmental cues, we considered several variables that were further integrated into one index (the ENI). Environmental noise was spatially structured withsome homogeneous and rather large areas displaying different stochastic profiles. Particularly, the southern areas (below 20°N) were found to display more reddened fluctuations than northern areas meaning that the variability of the environmental cues in southern areas are characterized by low-frequency signals (i.e. more long-term fluctuations).

Our results suggested that environmental noise might be related to changes in the fluctuations of fisheries time series, as three biological parameters were significantly correlated with environmental noise. Reddened areas were generally associated with a lower PV, a more negative BETA and a smaller PRCF, indicating that CPUE time series were less variable, smoother and with a less important negative feedback at lag one. However, a straight interpretation of these results remains difficult for several reasons. First, the BETA and the PRCF were significantly negatively correlated ($r^2 = 0.50$, p < 0.0001), which was partly expected on relatively short time series as the PRCF is related to the importance of the high-frequencies in the signal and is thus affected by the smoothness of the time series.. Therefore, a lower PRCF does not necessarily imply that the negative feedback is weaker, but that reddened fluctuations (i.e., a more negative BETA) can make difficult to detect it. This could partly explain the weak

relationship between life-history traits and the PRCF. Furthermore, our dataset was constituted

with CPUE data that are known to be far from reliable indicators of fish dynamics; they are

affected by many other processes, such as environmental fluctuations and fisheries dynamics that

may also interact with each other (Rouyer et al., 2008). In addition, some species display large

migrations between provinces (e.g. bluefin tuna). These factors cannot be accounted for in this

analysis and may partially bias the results (Hilborn and Walters, 2003; Serafy et al., 2004).

However, migrations are clearly expected to blur the results or reduce differences among regions,

and it is not possible to neglect the effects of fisheries dynamics on CPUE time series and to

conclude that relationships with environmental noise only relate to changes in underlying

biological processes.

The biological integration of environmental noise remains a key issue: biological

processes are sensitive to different time scales in the environment and species with contrasting

life histories can "perceive" the environmental colour differently (Bjørnstad et al., 1999, 2004;

Petchey, 2000; Fromentin and Fonteneau, 2001; Greenman and Benton, 2005). For instance,

marine biological processes such as larval survival and growth are sensitive to the physical

habitat and may act as filters for environmental noise (Petchey, 2000; Laakso et al., 2001, 2003).

Our results showed that the noise displayed by different environmental variables was differently

associated with the CPUE statistics. If the ENI summarized most of the variance in the different

variables, SST was found more relevant for the PV while the two wind stress variables (UST and

VST) were more relevant for the PRCF and the BETA (i.e., for the frequency content of CPUE).

The relationships obtained between the CPUE statistics and environmental noise varied

between species. This suggests that, in addition to fisheries dynamics (see Rouyer et al., 2008),

variations in CPUE time series may also reflect interactions between environmental properties

and endogenous processes (Luckinbill and Fenton, 1978; Lundberg et al., 2000; Petchey, 2000; Jonzén et al., 2002; Inchausti and Halley, 2003). Here, the different results were associated with different life-history traits. The CPUE statistics for the larger, slower-growing and later-maturing species (negative CTI: white-marlin, blue-marlin, sailfish, swordfish and bluefin tuna) showed variation with environmental noise, while no clear association was found for the smaller, faster-growing and earlier-maturing species (positive CTI: skipjack, yellowfin, albacore and bigeye tunas). Species with a negative CTI have multiple reproductive age classes and slower growth, allowing for the buffering of short-term environmental fluctuations that can ultimately lead to a reddening of the CPUE time-series (Fromentin and Fonteneau, 2001). In addition, the combination of multiple age classes and stochastic environmental variations can induce low-frequency variability in the spawning stock biomass of these species, which has been called 'cohort resonance' (Bjørnstad et al., 2004). On the contrary, species with a positive CTI are less prone to smooth out short-term environmental disturbances and to display a reddening of the dynamics due to cohort resonant effect. Recruitment dynamics might be central here, as these dynamics act as the integrative process through which environmental noise translates into biological processes. Understanding the recruitment dynamics of species with contrasting life-history traits (e.g. Goodwin et al. 2006) and subjected to coloured environments would probably constitute a key step for further mechanistic insights.

Our results show that fluctuations displayed by the CPUE are affected by environmental noise, but species that are more migratory, which are also larger, later maturing and slower growing, are more sensitive to red noise. It is important to note that the effect of environmental noise is more difficult to assess for resident tropical species since they experience less diverse environmental noise due to a more confined spatial distribution, mainly located in more reddened

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areas. This result is in agreement with Rouyer et al. (2008) who also showed that the patterns of variations for 169 time series of large pelagics fish were also strongly spatially structured at the scale of the entire Atlantic. The time series that originated from the northern areas were found to display a less important spatial homogeneity but were more affected by the NAO than CPUE from southern areas. However, this spatial structure reflected an important interaction with species distribution; the more migratory species inhabiting northern provinces and experiencing more different habitats displayed less homogeneity than species with a smaller distribution inhabiting the more reddened southern areas.

In addition, Royer and Fromentin (2007) hypothesised that the Mediterranean SST that are characterised by more short-term fluctuations, would have been more favourable on the long term for bluefin tuna recruitment success than the open ocean that is characterised by reddened noise. Combining these findings with those discussed above leads us to put forward that the spatial distribution as well as the life histories of tuna and billfish may be partly related to the environmental properties of their habitat. On the one hand, fishing is known to affect the variability of fish stocks through changes in demographic structure that affect the resilience and resistance of fish populations to environmental variation (Hsieh et al., 2006; Ottersen et al., 2006; Anderson et al. 2008, Stenseth and Rouyer, 2008). On the other hand, exploitation is also known to directly affect life-history traits through phenotypic plasticity (Rochet, 1998; Law, 2000; Ernande et al., 2004; Olsen et al., 2004). Different responses to environmental noise can then be expected between exploited and non-exploited species. Investigating how fishing affects the response of stocks to environmental noise through their life-history traits would then provide further insights to understand the consequences of exploitation in a changing environment.

Acknowledgments

REFERENCES

Akçakaya, H.R., Halley, J.M., Inchausti, P., 2003. Population-level mechanisms for reddened spectra in ecological time series. Journal of Animal Ecology 72, 698–702.

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

Arocha, F., Marcano, L., 2006. Life history characteristics of *Makaira nigricans*, *Tetrapturus albidus*, and *Istiophorus albicans* from the eastern Caribbean Sea and adjacent waters. In: Nielsen, J., Dodson, J., Friedland, K., Hamon, T., Hughes, N., Musick, J., Verspoor, E. (Eds.), Proceedings of the Fourth World Fisheries Congress: Reconciling Fisheries with Conservation. American Fisheries Society Symposium 49, Bethesda, Maryland, pp. 587–597.

Bakun, A., 1996. Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. California, USA: University of California Sea Grant, San Diego, in cooperation with Centro de Investigaciones Biologicas de Noroeste, La Paz, Baja California Sur, Mexico, pp. 323.

Berryman, A., Turchin, P., 2001. Identifying the density-dependent structure underlying ecological time series. Oikos 92, 265–270.

Bjørnstad, O.N., Fromentin, J.-M., Stenseth, N.C., Gjosaeter, J., 1999. Cycles and trends in cod populations. Ecology 96, 5066–5071.

Bjørnstad, O.N., Nisbet, R.M., Fromentin, J.-M., 2004. Trends and cohort resonant effects in age-structured populations. Journal of Animal Ecology 73, 1157–1167.

Cuddington, K.M., Yodzis, P., 1999. Black noise and population persistence. Proceedings of the Royal Society of London, B 266, 969–973.

Cyr, H., 1997. Does inter-annual variability in population density increase with time? Oikos 79, 549–558.

Ernande, B., Dieckmann U., Heino, M., 2003. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. Proceedings of the Royal Society of London, B 271, 415–423.

Fonteneau, A., 1997. Atlas des pêcheries thonières tropicales. Captures mondiales et environnement. ORSTOM editions (in French).

Fromentin, J.-M., Fonteneau, A., 2001. Fishing effects and life history traits: a case study comparing tropical versus temperate tunas. Fisheries Research 53, 133–150.

Fromentin, J.-M., Royer, F., Marsac, F., 2005. Open environmental databases for open-sea

fisheries biologists. ICCAT Collective Volume of Scientific Papers 58, 1756–1760.

Frontier, S., 1976. Etude de la decroissance des valeurs propres dans une analyse en composantes principales: comparaison avec le modèle de baton brisé. Journal of Experimental Marine Biology and Ecology 25, 67–75 (in French).

Ghil, M., Vautard, R., 1991. Interdecadal oscillations and the warming trend in global temperature time series. Nature 350, 324–327.

Goodyear, C.P., Arocha, F., 2001. Size composition of blue and white marlin taken in selected fisheries in the western North Atlantic. ICCAT Collective Volume of Scientific Papers 53, 249–257.

Greenman, J.V., Benton, T.G., 2005. The frequency spectrum of structured discrete time population models: its properties and their ecological implications. Oikos 110, 369–389.

Halley, J.M., 1996. Ecology, evolution and 1 /f noise. Trends in Ecology and Evolution 11, 33–38.

Halley, J.M., Stergiou, K.I., 2005. The implications of increasing variability of fish landings. Fish and Fisheries 6, 266–276.

Heath, J.P., 2006. Quantifying temporal variability in population abundances. Oikos 115, 573–581.

Hilborn, R., Walters, C.J., 2003. Quantitative Fisheries Stock Assessment. Springer, pp. 592.

Hsieh, C.H., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M., Sugihara, G., 2006. Fishing elevates variability in the abundance of exploited species. Nature 443, 859–862.

ICCAT, 2008. ICCAT manual. <http://www.iccat.int/pubs_FieldManual.htm>.

Inchausti, P., Halley, J., 2002. The long-term temporal variability and spectral colour of animal populations. Evolutionary Ecology Research 4, 1033–1048.

Inchausti, P., Halley, J., 2003.On the relation between temporal variability and persistence time in animal populations. Journal of Animal Ecology 72, 899–908.

Jennings, S., Kaiser, M., 1998. The effects of fishing on marine ecosystems. Advances in marine biology 34, 201–352.

Jonzén, N., Lundberg, P., Ranta, E., Kaitala, V., 2002. The irreducible uncertainty of the demography-environment interaction in ecology. Proceedings of Royal Society of London, B 269, 221–225.

Laakso, J., Kaitala, V., Ranta, E., 2001. How does environmental variation translate into

biological processes. Oikos 92, 119–122.

Laakso, J., Kaitala, V., Ranta, E., 2003. Non-linear biological responses to disturbance: consequences on population dynamics. Ecological Modelling 162, 247–258.

Lang, K.L., Grimes, C.B., Shaw, R.F., 1994. Variations in the age and growth of yellowfin tuna larvae, *Thunnus albacares*, collected about the Mississippi River plume. Environmental Biology of Fishes 39, 259–270.

Law, R., 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science 57, 659–668.

Lawton, J.H., 1988. More time means more variation. Nature 334, 563.

Legendre, P., Legendre, L., 1998, Numerical ecology, Elsevier, Amsterdam, pp. 409–411.

Lehodey, P., Bertignac, M., Hampton, J., Lewis, A., Picaut, J., 1997. El Niño Southern oscillation and tuna in the western Pacific. Nature 389, 715–718.

Lehodey, P., Andre, J.-M., Bertignac, M., Hampton, J., Stoens, A., Menkes, C., Memery, L., Grima, N., 1998. Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical bio-geochemical model. Fisheries Ocenography 7, 317–325.

Lessa, R., Duarte-Neto, P., 2004. Age and growth of yellowfin tuna (*Thunnus albacares*) in the western equatorial Atlantic, using dorsal fin spines. Fisheries Research 69, 157–170.

Longhurst, A.R., 2001. Ecological Geography of the Sea. Elsevier, Place of Publications.

Lunckinbill, L.S., Fenton, M.M., 1978. Regulation and environmental variability in experimental populations of protozoa. Ecology 59, 1271–1276.

Lundberg, P., Ranta, E., Ripa, J., Kaitala, V., 2000. Population variability in space and time. Trends in Ecology and Evolution 15, 460–464.

Lundberg, P., Ripa, J., 2002. Visibility of demography-modulating noise in population dynamics. Oikos 96, 379–382.

MacArthur, R.H., 1957. On the relative importance of bird species. Proceedings of the National Academy of Science of the United States of America, 43, 293–295.

Maury, O., Gascuel, D., Marsac, F., Fonteneau, A., De Rosa, A.-L., 2001. Hierarchical interpretation of nonlinear relationships linking yellowfin tuna (*Thunnus albacares*) distribution to the environment in the Atlantic Ocean. Canadian Journal of Fisheries and Aquatic Sciences 58, 458–469.

McFarlane, G.A., King, J.R., Beamish, R.J., 2000. Have there been recent changes in climate?

Ask the fish. Progress in Oceanography 47, 147–169.

Miramontes, O., Rohani, P., 1998. Intrinsically generated coloured noise in laboratory insect populations. Proceedings of the Royal Society of London, B 265, 785–792.

Miramontes, O., Rohani, P., 2002. Estimating 1/f scaling exponents in short time series. Physica D 166, 147–154.

Morales, J.M., 1999. Viability in a pink environment: why "white noise" models can be dangerous. Ecology Letters 2, 228–232.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B., Dieckmann, U., 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428, 932–935.

Ottersen, G., Hjermann, D.ø., Stenseth, N.C., 2006. Changes in the spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. Fisheries Oceanography 15, 230–243.

Pedraza, M.J., Diaz Ochoa, J.A., 2006. Sea level height, sea surface temperature, and tuna yields in the Panama bight during El Niño. Advances in Geosciences 6, 155–159.

Percival, D.B., Walden, A., 1993. Spectral analysis for physical applications – multitaper and conventional univariate techniques. Cambridge University, Cambridge, UK.

Petchey, O.L., Gonzalez, A., Wilson, H.B., 1997. Effects on population persistence: the interaction between environmental noise colour, intraspecific competition and space. Proceedings of the Royal Society of London B 264, 1841–1847.

Petchey, O.L., 2000. Environmental colour affects aspects of single-species population dynamics. Proceedings of the Royal Society of London B 267, 747–754.

Pimm, S., Redfearn, A., 1988. The variability of animal populations. Nature 334, 613–614.

Porch, C.E., 2003. Preliminary assessment of Atlantic white marlin (*Tetrapturus albidus*) using a state-space implementation of an age-structured production model. ICCAT Collective Volume of Scientific Papers 55, 559–577.

Prince, E.D., Goodyear, C.P., 2006. Hypoxia-based habitat compression of tropical pelagic fishes. Fisheries Oceanography 15, 451–464.

R Development Core Team, 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. http://www.R-project.org

Ripa, J., Lundberg, P., 1996. Noise colour and the risk of population extinctions. Proceedings of

the Royal Society of London, B 263, 1751–1753.

Ripa, J., Lundberg, P., 2000. The route to extinction in variable environments. Oikos 90, 89–96.

Rochet, M.-J., 1998. Short-term effects of fishing on life history traits of fishes. ICES Journal of Marine Science 55, 371–391.

Rouyer, T., Fromentin, J.-M., Ménard, F., Cazelles, B., Briand, K., Pianet, R., Planque, B., Stenseth, N.C., 2008. Complex interplays between population dynamics, environmental forcing and exploitation in fisheries. Proceedings of the National Academy of Science of the United States of America 105, 5420–5425.

Royer, F., Fromentin, J.-M., Gaspar, P., 2004. Association between bluefin tuna schools and oceanic features in the western Mediterranean. Marine Ecology Progress Series 269, 249–263.

Royer, F., Fromentin, J.-M., 2007. Environmental noise in spawning areas: the case of Atlantic bluefin tuna (*Thunnus thynnus*). Fisheries Oceanography 16, 202–206.

Serafy, J.E., Diaz, G.A., Prince, E.D., Orbesen, E.S., Legault, C.M., 2004. Atlantic blue marlin, *Makaira nigrican*s, and white marlin, *Tetrapterus albidus*, by-catch of the Japanese pelagic longline fishery, 1960-2000. Marine Fisheries Review 66, 9–20.

Steele, J.H., 1985. A comparison of terrestrial and marine ecological systems. Nature 313, 355–358.

Stenseth, N.C., Rouyer, T., 2008. Destabilized fish stocks. Nature 452, 825–826.

Thomson, D.J., 1982. Spectrum estimation and harmonic analysis. IEEE Proceedings 70, 1055–1096.

Thomson, D.J., 1990. Time series analysis of Holocene climate data. Philosophical Transactions of the Royal Society A 330, 601–616.

Vasseur, D.A., Yodzis, P., 2004. The color of environmental noise. Ecology 85, 1146–1152.
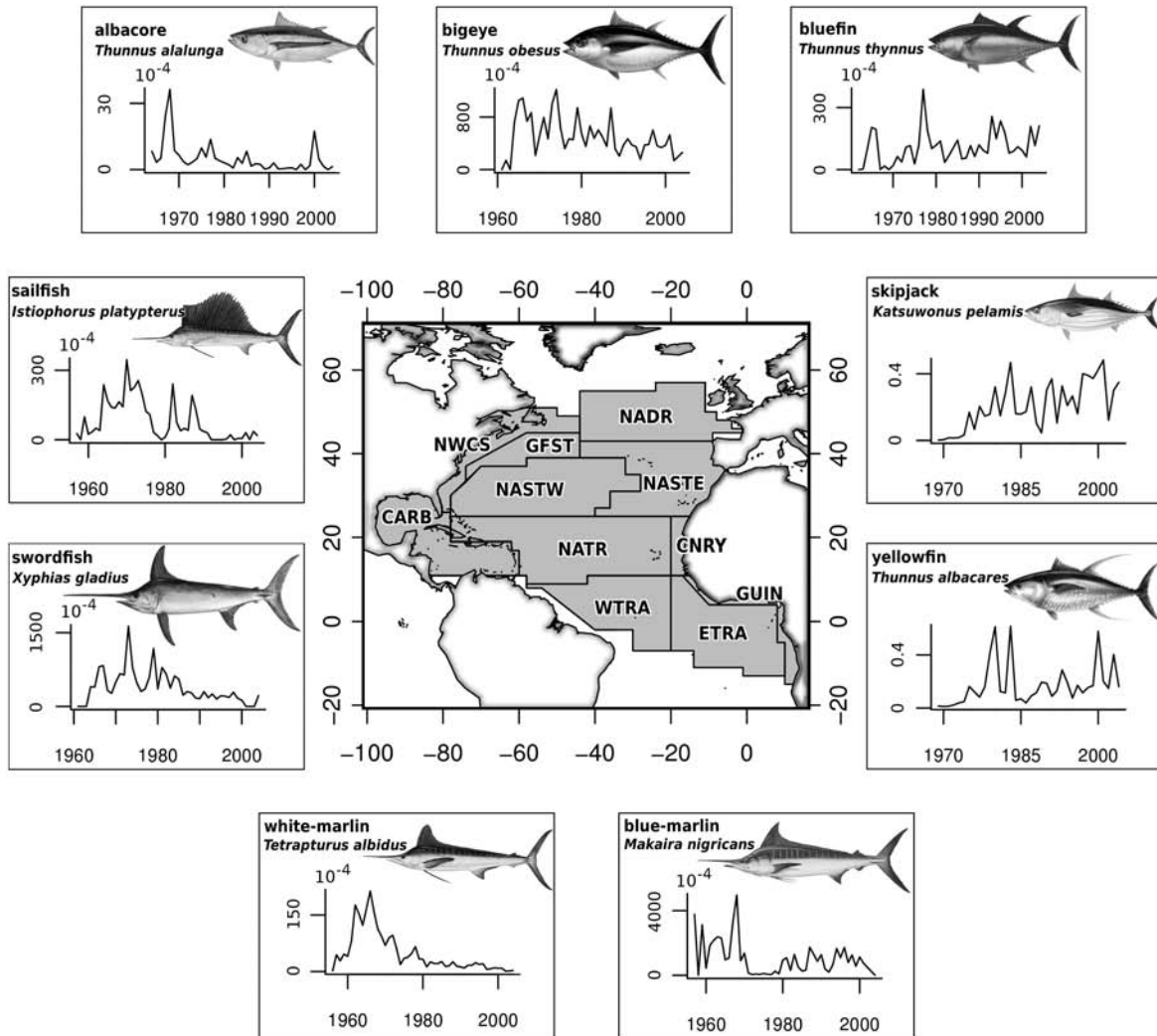
FIGURE CAPTIONS

Fig. 1. Geographical provinces used in this study (Longhurst Provinces) and some illustrative

time series for the species studied. The dataset is constituted by 75 CPUE time series from nine

different species over 11 different areas in the Atlantic (see Section 2.1).
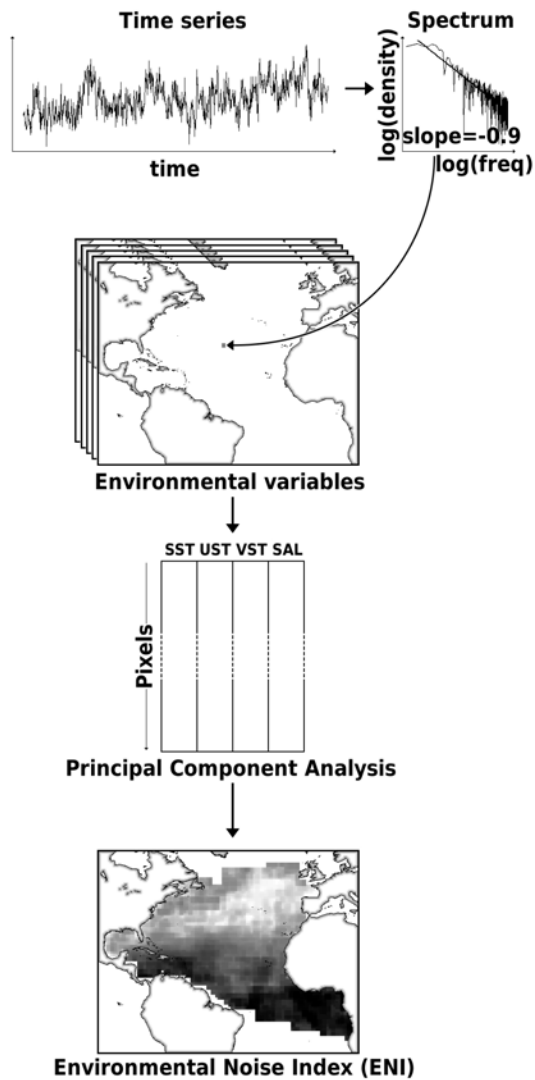
Fig. 2: Methodological procedure used to construct the Environmental Noise Index (ENI). First

the power spectrum was computed on the time series extracted for each available pixel of each

environmental variable. The scaling exponent is then estimated and consigned in a large pixel *

variable table. A PCA is then performed on this table and the first component is mapped and used

as the ENI, which represents an index of environmental noise combining the four environmental
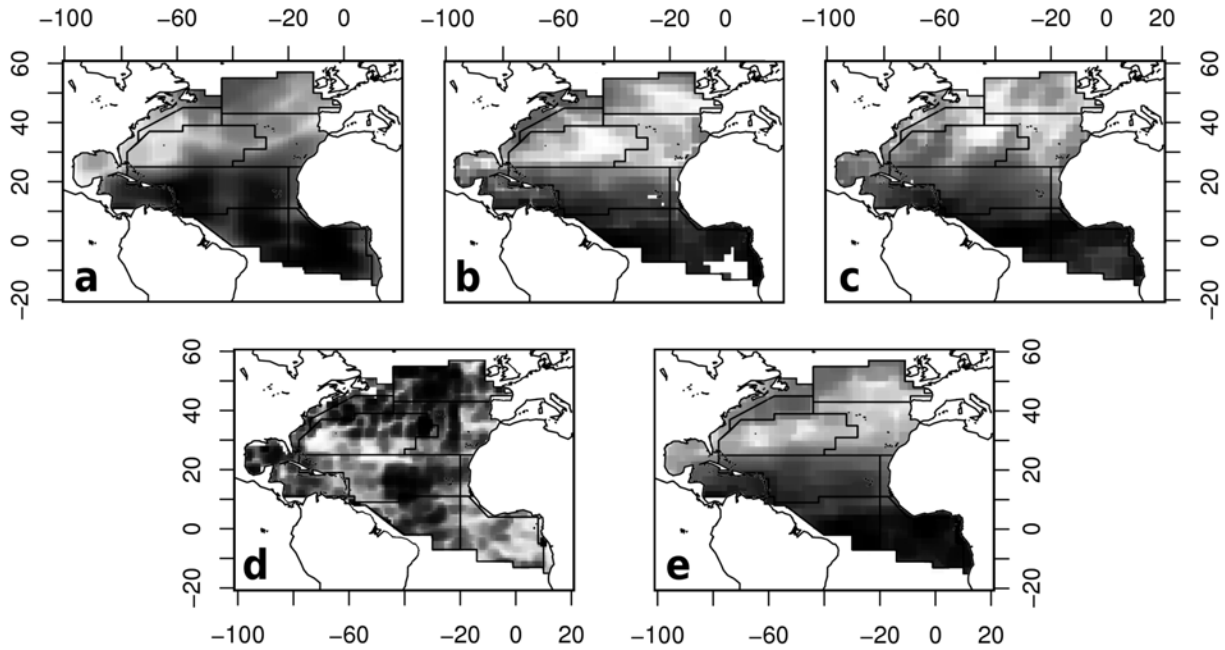
variables.

Fig. 3. Maps a, b, c and d present the scaling exponent computed for each available pixel of the four different variables (SST, UST, VST and SAL, respectively). Map e presents the ENI, obtained as the first component of a PCA performed on the scaling exponent estimated for the four environmental variables (see Section 2.4.). For all maps, and as indicated by the histogram of the scaling exponents in the top left of each map, the darker the pixel the more important the low frequencies in the time series.
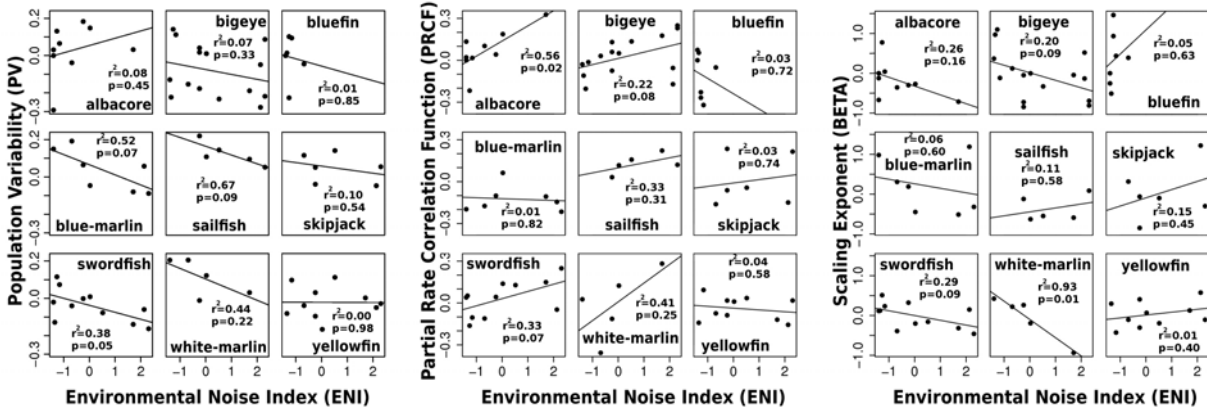
Fig. 4. The graphs present the PV of the CPUE time series plotted against the ENI for each species from the provinces they were extracted from.
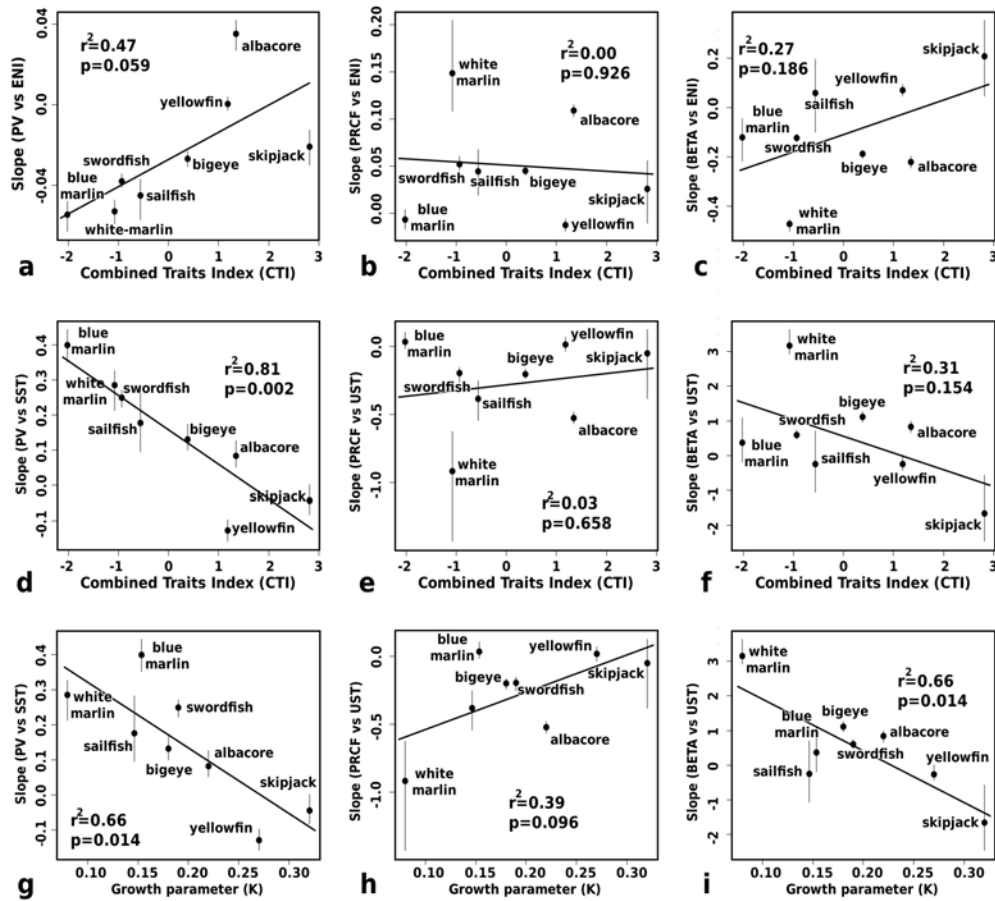
Fig. 5. Relationships between life-history traits and the effect of environmental noise on CPUE statistics for each species. The slopes of the regression between environmental noise and PV, PRCF and BETA (as in Fig. 4) for each species are plotted against their life-history traits. Panels a, b and c present the slopes obtained between ENI and PV, PRCF and BETA, respectively for the different species plotted against the CTI. Panels b, c and d present the slopes between SST and PV, UST and PRCF, UST and BETA, respectively for the different species plotted against the CTI. Finally, panels g, h and i present the slopes between SST and PV, UST and PRCF, UST and BETA for the different species plotted against the growth parameter (K).

Table 1. Growth parameters for the von Bertalanffy curve (K), size max (Lm) and size at maturity (L50) for the nine tuna and billfish species. The number in brackets indicates the reference from the literature: (1) Fromentin and Fonteneau (2001), (2) ICCAT manual (2008), (3) Freire et al. (1999), (4) Porch (2003), (5) Lessa and Duarte-Neto (2004), (6) Goodyear and Arocha (2001), and (7) Arocha and Marcano (2006).

	K	Lm (cm)	L50 (cm)
Albacore	0.22 (2)	120 (1)	90 (1)
Bigeye tuna	0.18 (2)	180 (1)	115 (1)
Bluefin tuna	0.09 (2)	295 (1)	115 (1)
Blue-marlin	0.15 (2)	300 (6)	256 (7)
Sailfish	0.15 (3)	255 (1)	130 (1)
Skipjack	0.32 (2)	75 (1)	45 (1)
Swordfish	0.19 (2)	290 (1)	175 (1)
White-marlin	0.08 (4)	260 (1)	130 (1)
Yellowfin tuna	0.27 (5)	170 (1)	105 (1)

Table 2. Acronyms for the Longhurst Provinces and average scaling exponent for the different environmental variables and the ENI.

Province	Acronym	SST	UST	VST	SAL	ENI
Carribean	CARB	-1.17	-0.21	-0.05	-1.36	0.39
Canary Coastal Province	CNRY	-1.22	-0.19	-0.07	-1.11	0.28
Eastern Tropical	ETRA	-1.68	-0.49	-0.54	-1.22	2.39
Gulf Stream	GFST	-1.07	-0.15	-0.03	-1.16	-1.09
Guinean current	GUIN	-1.30	-0.63	-0.62	-1.20	2.30
North Atlantic Drift	NADR	-1.22	-0.08	-0.01	-1.30	-1.65
North Atlantic Sub-Tropical Eastern	NASTE	-1.26	0.02	0.11	-1.34	-1.54
North Atlantic Sub-Tropical Western	NASTW	-1.07	0.02	0.12	-1.10	-1.31
North Atlantic Tropical	NATR	-1.53	-0.35	-0.52	-1.30	0.69
North West Coastal	NWCS	-1.13	-0.29	0.01	-1.24	-1.31
Western Tropical	WTRA	-1.54	-0.46	-0.52	-1.43	1.61