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Complex interplays among population dynamics, environmental forcing, and exploitation in fisheries

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Abstract:

The patterns of variations in fisheries time series are known to result from a complex combination of species and fisheries dynamics all coupled with environmental forcing (including climate, trophic interactions, etc.). Disentangling the relative effects of these factors has been a major goal of fisheries science for both conceptual and management reasons. By examining the variability of 169 tuna and billfish time series of catch and catch per unit effort (CPUE) throughout the Atlantic as well as their linkage to the North Atlantic Oscillation (NAO), we find that the importance of these factors differed according to the spatial scale. At the scale of the entire Atlantic the patterns of variations are primarily spatially structured, whereas at a more regional scale the patterns of variations were primarily related to the fishing gear. Furthermore, the NAO appeared to also structure the patterns of variations of tuna time series, especially over the North Atlantic. We conclude that the patterns of variations in fisheries time series of tuna and billfish only poorly reflect the underlying dynamics of these fish populations; they appear to be shaped by several successive embedded processes, each interacting with each other. Our results emphasize the necessity for scientific data when investigating the population dynamics of large pelagic fishes, because CPUE fluctuations are not directly attributable to change in species' abundance.

Keywords: Atlantic tuna, time series analysis, NAO, fisheries

INTRODUCTION

Fish stocks are highly variable in size at most time scales (i.e., from the short-term to the long-term (1, 2)). Understanding the underlying mechanisms of such variations have been of focal interest during the past century (3) for both conceptual and management perspectives. On the one hand we now know that fish populations are affected by a broad spectrum of environmental factors, be it biotic or abiotic. However, on the other hand it is now widely accepted that fishing activity cannot be reduced to a simple removal of individuals, as such removals profoundly modify the population demography and structure as well as alter species and trophic interactions (4-8).

Time series of commercial catch contain (as is generally the case for most ecological time series) noisy and mixed information on the respective effects of climate variability, environmental forcing, population dynamics and exploitation. Disentangling the relative effects of the many factors affecting the dynamics of populations has been considered to be the ultimate target of fisheries science. Recent work has, however, demonstrated that such effects are not simply additive, but rather do interact (9-12). Analysing the patterns of variations of different fish species, in contrasting environments and subject to a variety of fishing pressures, is, thus, expected to shed light on the relative effects of these factors and/or the way they interact.

As part of this study we have examined an original and extensive data set of 169 time series, composed with 75 catch per unit effort (CPUE) and 94 catch time series of tuna and billfish species from the Atlantic Ocean. These large pelagics top predators inhabit the open ocean and their population dynamics are affected by climatic factors (13, 4, 14). Tropical and temperate Atlantic tuna and billfish display different exploitation history, but also different geographic locations (15) as well as contrasting life history traits (16), all of which constitute an appropriate case study for comparative purposes.

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Since nonlinearity and nonstationnarity in ecological time series are the rule rather the exception (17-20) we have applied wavelet analysis, a time-frequency decomposition that is especially powerful for analysing nonstationary, aperiodic and noisy signals (21). Using this approach enabled us to describe the variability of the time series on a time frequency plane, the wavelet spectra, but also to investigate in time and frequency the local covariance and linear correlation between the fisheries time series and the North Atlantic Oscillation (NAO), obtained by bivariate wavelet analyses. Then, quantifying the similarity between time frequency patterns enabled us to classify these results using hierarchical clustering, to evaluate the impact of four key factors (i.e., species, fishing gear, geographical location, and NAO) on the variability of the Atlantic tuna and billfish fisheries time series.

Our results are two-fold. Firstly we show that neither catch nor CPUE data are simply linked to the underlying fluctuations of tuna and billfish abundance. Secondly, we show that the variability of the fisheries time series are the result of several successive embedded processes acting like filters (22) that modify the real ecological variations at different spatial and temporal scales. On this basis we conclude that research on Atlantic large pelagics requires the availability of scientific data tracking the population dynamics of the species under study as well as to understand how environmental variability modulate the ecological dynamics.

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RESULTS

Patterns of variation among the fisheries time series

We first applied the wavelet analysis on each CPUE time series. The wavelet spectra displayed the variability of the time series in time and frequency domains, enabling us to characterize the changes of frequency through time. To ensure comparable and relevant results, the time series were analyzed on the same time period and on the same range of frequencies. These patterns of variation were then compared to each other using a multivariate method defining an orthonormal basis which maximizes the mutual covariance for each pair of wavelet spectra. Comparing the decomposition of the wavelet spectra onto this orthornormal basis enabled us to quantify the dissimilarity between their time frequency patterns (23, see methods). The set of dissimilarities obtained was first analyzed by hierarchical clustering which grouped the wavelet spectra according to the similarity of their time frequency patterns.

Computed on a large number of time series (i.e., 75), the cluster tree mixed various and confounding effects and did not displayed any clear grouping by species and gears factor (SI Fig. 2). However, grouping by province were identified as the wavelet spectra were in general grouped by main geographic areas: those from Southern provinces (below 20° North) formed more homogenous groups that were, in most of the cases, separated from the Northern ones. Looking at the mean dissimilarity exhibited by main factor (province, species and gear) allowed us to identify the factor according to which the patterns of variations were the more similar. As the data-set was indeed unbalanced, classical inference methods (i.e. comparisons of distributions) could not be used. We then used bootstrap to estimate the mean dissimilarity for each factor in order to compensate for the different sample size and ensure robust results. Note that such means remove the comparisons between the different classes of each factor (e.g., between longline, purse seine and baitboat within the “gear” factor) and is therefore less exhaustive than the cluster tree. The lowest

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mean dissimilarity was found within provinces (d=0.039, ± 0.002), while higher values were found among species (d=0.043, ± 0.0015) and among gears (d=0.043, ± 0.0005). This result showed that the CPUE variations of species differed from one province to another. For instance, it indicated that the CPUE time series of ubiquitous species, such as bluefin or yellowfin tuna, did not exhibited the same fluctuations in the different provinces, whereas the patterns of variations of different species in a given province were more similar.

Figure 1 (About here)

However, the province and species effects appear to be partly confounded as suggested by the lower dissimilarities displayed by the species with small geographic repartition (e.g., sailfish) than those with large distribution (e.g., bluefin). In addition, the Northern species (albacore, bluefin and swordfish) also exhibited more different variations of CPUE than Southern ones (yellowfin, bigeye and skipjack, Fig. 1a). Comparing the Northern provinces (above 20° North) to the Southern ones so confirmed this finding as the dissimilarities were significantly lower in the Southern ones (p=1.6e-13, Fig. 1b).

Figure 2 (About here)

Analyzing the wavelet spectra within each province allowed us to remove, to some extent, the province effect. In the Canary province, located in the West coast of North Africa, the wavelet spectra of CPUE time series from a same gear were more similar than those from a same species, see the case of bigeye tuna (Fig. 2). For instance, the longline spectra of white-marlin, blue-marlin and sailfish displayed common fluctuations during the 1970's at high and low frequencies, whereas the two baitboats spectra and the swordfish longline spectrum displayed comparable fluctuations during the 1990's. The last group that included the three purse-seiners spectra and the yellowfin

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spectrum from baitboats, were mostly characterized by high-frequency fluctuations during the 1980's.

Figure 3 (about here)

The same “gear effect” was found in all provinces that displayed a sufficient number of time series required for the analysis (Fig. 3). The longliners were in general clearly separated from the other gears, even if they were more numerous and concerned species with very different life history traits. Whereas baitboat and purse seiner fleets also formed distinct groups no grouping was found according to any of the species, the same species being separated by gears. These results indicated that, at the province scale, the patterns of variation of the CPUE time series were more related to the type of fishing gear than to the species. In other words, the CPUE of different species fished with the same gear displayed more common fluctuations than the CPUE of a given species fished with different gears.

Influence of the climate

Using bivariate wavelet analyses allowed us to investigate the patterns of covariation between the NAO and the CPUE time series, by identifying time periods with common frequencies between the different signals (see methods). As previously, we compared the bivariate spectra to each other and grouped them according to the similarity of their time frequency patterns.

These results confirmed the previously found spatial pattern, as the classification mainly separated the Northern and Southern provinces (SI Fig. 3 and Fig. 4). Computing the mean dissimilarity by main factor showed that the common time frequency patterns between the NAO and the CPUE time series were further found more similar within provinces than within species or gears. This

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demonstrate that the NAO and the CPUE time series displayed linkages that involved different frequencies and time periods in the different geographical areas. This result was confirmed by the individual inspection of the bivariate spectra that revealed numerous consistent patterns of covariation between the NAO and the CPUE time series in the Northern provinces, while in the Southern ones they were often weak and poorly consistent. These results demonstrate that the NAO seems, thus, to structure the patterns of variations of the CPUE time series over the North Atlantic at a larger scale than the province.

Comparison with the catch data set

We re-did all the analyses using the catch data in order to check the previous results. Even if the wavelet spectra computed on catch time series were different from those computed on CPUE time series, we found the same qualitative results. Considering the whole Atlantic, the patterns of variations between catch time series were more similar within provinces than within species or gears, whereas at the province scale the gears had the most important effect. The analyses of the catch data set thus strongly supported the above findings and indicated that these results were not simply linked to the intrinsic properties of the CPUE time series.

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DISCUSSION

Our analysis demonstrates that the catch and CPUE time series of tuna and billfish can hardly reflect the underlying population dynamics. This is because of complex interplays between population dynamics, environmental forcing and exploitation whose effects are expressed differently according to the spatial scale considered. We highlight here that the observed variability of the fisheries time series (both CPUE and catch data) is the result of several embedded processes that shape, at different spatial and temporal scales, the observed fluctuations.

At the province scale, the variability of the time series were importantly affected by the type of fishing gear. This indicated that differences in catchability (i.e., the probability to catch a fish by a unit of effort of a given boat) and fishing strategies have a major influence on the fluctuations observed (4). At the inter-province scale, the results counter-intuitively revealed that the variability of the time series was more related to the province than to the species. Indeed, this result may be partly explained by the confounded province and species effects; the larger the spatial extent of a species, the more different the fluctuations of the fisheries time series. However, this also suggest that the different environmental profiles displayed by the Longhurst provinces (24) can consistently interact with the catchability of gears and the ecology of species, through biological processes, and thus affect the variability of the fisheries time series.

Considering the results at the oceanic scale further demonstrate that the variability of the fisheries time series were affected at a even higher scale; the fluctuations of the fisheries time series being significantly more similar in the southern than in the northern provinces. This large scale effect was also supported by the relationships found between the NAO and the fisheries time series, as stronger and more consistent links were found in the Northern provinces than in the Southern ones. Past studies already advocated for a potential impact of the NAO or sea surface temperature on local time series of bluefin tuna or albacore (25, 26, 14). In this study we have shown that the NAO may affect many fisheries time series of Atlantic tuna and billfish species, but also demonstrate that its effect is strongly spatially structured complying with the stronger impacts of the NAO on the North Atlantic than in the South (27, 28).

Our results stress the key role of the spatial scales when analyzing fisheries data (catch and CPUE 1, 8, 29). The patterns of variations in CPUE and catch time series are complex as they exhibited, at different spatial scales, different facets of the interplays between the environment, the fishing strategies and the population dynamics. Consequently, CPUE or catch time series cannot reflect accurately annual stock trends. The standardization of such series can further hardly help because these different effects are not simply additive but interactive. Our results thus confirm that aggregating CPUE over the whole oceanic basin can strongly blur most of the signature of the underlying processes that shape the fluctuations (30). According to our results, inspecting the trends of such aggregated CPUE indices (or catch) cannot be used alone to document any potential change in biomass or depletion of large pelagic fish stocks (30). This view thus supports, though with different arguments, previous analyses (31-35) that also expressed concerns about inferring important change in biomass on the basis of CPUE trends alone. Furthermore, as fisheries-independent data are scarce for large pelagic fish, catch and CPUE still remain the chief source of data for stock assessments (see e.g. 36)**.** Hence, identifying origins of fluctuations in fisheries data are still a key issue in the fisheries community (biases in CPUE are indeed known to strongly affect biomass and fish mortality estimates from classical stock assessment models, see e.g., 37), but also in the whole scientific community, as CPUE are used to depict fish abundance and diversity in ecological studies (e.g., 38). Integrated stock assessment models now enable to use data from disparate sources and to partially account for temporal variations in catchability (e.g., 35), but understanding the complex interactions between fish dynamics, catchability, space and environment

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remain to be addressed.

Figure 4 (about here)

On the one hand, the biological processes of a given population induce a dynamics that might display both short- and long-term oscillations due to biotic interactions (39, 40). On the other hand, a population is not isolated and is necessarily affected by the ecosystem within which it is embedded, the ecosystem being itself affected by climatic variations (1, 5). These interactions do not always affect population abundance directly, as the biology and the life-cycle may act as a filter of the environmental noise (29, 22). Our study stresses that such complex dynamics can hardly be observed through catch or CPUE time series, because they are altered by, at least, two additional filters, the geographic location and the gear (Fig. 4). Each geographic area displays particular environmental properties and is more or less affected by large-scale climatic oscillations, such as the NAO. Furthermore, tropical areas are known to be dominated by more long-term fluctuations (i.e. displaying more reddened spectra) than temperate ones, which might also affect differently the patterns of variability of a given population (41-43). The second filter results from the exploitation process and mostly from the use of different gears that induce different fishing strategies in both space and targeted species. These gears also involve different fishing fleets whose dynamics can be subjected to long-term changes in species targeting, observation errors and undocumented changes in effort. This constitutes another source of modulation which may in turn be affected by the climate, through changes in catchability and fishermen's behaviour (4). The patterns of variations identified within an observed time series are thus inherited by several successive filters and finally by the observation process itself that can blur the perception of the underlying population dynamics. Therefore neither CPUE nor catch can be considered to reliably reflect the fluctuations of

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abundance of large pelagics in the Atlantic.

Understanding the interactions between the environmental variability and the biology of large pelagic species is a key question for fisheries research and management. Our results show that research on this topic requires additional information and would strongly benefit from scientific data, such as large-scale electronic tagging or genetic experiments (e.g., 44). This "fishing-free" data would provide accurate knowledge on the timing and location of key biological processes, such as spawning and migrations, necessary to understand the response of Atlantic large pelagics populations to environmental variability.

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MATERIAL AND METHODS

Tuna and billfish time series

Tuna catches are, in general, seldom proportional to abundance because they are affected by effort, gear catchability and fishing strategy. Hence, Catch-Per-Unit-Effort (CPUE) or outputs of stock assessment models are typically used to study the patterns of variations when direct estimates of abundance are lacking (8). However, these two sources of data are also problematic for large pelagics vessels since CPUE estimates as outputs from stock assessment models are generally strongly biased due to large observation errors (not taken into account in models) and frequent, but not quantified, changes in fishing strategies (38, 35). For these reasons, we performed the analyses not on a single data source, but on both CPUE and catch datasets. This allowed us to confront the results from both sources of data and then to check for consistency/differences of the outputs. We extracted time series of CPUE and catch from various institutional datasets (mostly ICCAT, see www.iccat.int) with critical advices from experts of these fisheries. The first dataset included 333 time series but was validated with 169 yearly time series (75 of CPUE and 94 of catch, see supporting information (SI)), as we discarded time series that were either too short, plagued with missing values or because the time series were poorly informative. The most important source of catch data (i.e., 70% of the time series) came from Japanese longlines because they were amongst the oldest ones operating in the Atlantic and because their catches concern all the species throughout the ocean. Other time series mostly come from European baitboat and purse seiner fleets (SI Fig. 1).

For consistency, time series have been produced within a common and neutral spatial grid. We chose the Longhurst provinces which are based on a classification of the biogeochemical properties of world oceans (24). These provinces have already been used for mapping tuna fisheries data as they allow to spatially disaggregate by areas displaying homogeneous environmental properties

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(15). Time series from longliners are available for each province and each species, unlike baitboat and purse-seine (see SI). Similarly, due to differences in species spatial distributions some provinces and gears did not display all species. This led to an unbalanced dataset that has constrained the methodological approach.

Nine tropical and temperate tuna and billfish species were finally retained (SI Table 1). Skipjack, yellowfin and bigeye constitute the bulk of the catches of tropical tuna (15) whereas the billfishes (i.e., white marlin, blue marlin and sailfish) are generally bycatch of these tropical fisheries, and are as a result of interest since they are affected differently by changes in fishing strategy and techniques (45). Albacore and swordfish are considered as sub-tropical species, but they are also common in temperate waters whereas bluefin tuna is the only strict temperate tuna (16).

If populations experience (and often respond to) their environment locally, large-scale climate indices seem to be better predictors of ecological processes than local environmental variables because local climate often fails to capture complex associations between weather and ecological process (46). For this reason and because the North Atlantic Oscillation (NAO) governs the pattern and strength of wind, temperature and precipitation over the whole North Atlantic, Northeast American and western European coasts, we chose to investigate potential relationships between Atlantic tuna and climate, using the winter NAO index (27).

The Wavelet analysis

Analyzing the frequency composition of time series is classically achieved by using the Fourier decomposition of time series. However, it requires the second order stationarity of the time series and it is further not able to characterize changes in frequency through time, as it is often the case in ecological or environmental time series (19-20). The wavelets methodology is thus highly suited for

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such signals as it enables to describe the variability of a time series in both time and frequency domains and to cope with aperiodic components, noise and transient dynamics (21, 47, 48).

The wavelet transform is based on the convolution product between the time series and mathematical functions that are dilated/translated onto the signal. We used the Morlet wavelet, a continuous and complex wavelet adapted to wavelike signals, that allows to extract time-dependant amplitude and whose scales are related to frequencies in a simple way (49, 50). The relative importance of frequencies for each time step may be represented in the time/frequency plane to form the wavelet power spectrum on a 2D plot (see SI). The wavelet analysis may be extended to bivariate cases, in order to analyse patterns of covariation between two signals. We compared the fisheries time series and the NAO using the wavelet cross-spectrum and the wavelet coherency that identify the transient covariance and the transient linear correlation between the two signals, respectively (see SI).

Analysing large datasets of Wavelet spectra

We have computed 169 wavelet spectra that describe the time-frequency pattern of each CPUE or catch time series. To compare all these patterns of variations, we calculated the dissimilarities between all the wavelet spectra, using a method based on the Maximum Correlation Analysis (23). Doing so, we generated two dissimilarity matrices (one for the CPUE and the catch time series, respectively) on which the cluster analysis is finally performed. We applied the same methodological approach to compare all the cross-spectra and cross coherency obtained between each tuna time series and the NAO. The relative importance of each factor (i.e. province or space, gear and species) was then analyzed through the cluster tree (see SI).

All the computations were done using R version 2.4 (51, http://www.R-project.org) on the basis of

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the wavelet libraries developed by B. Cazelles and M. Chavez.

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FIGURES

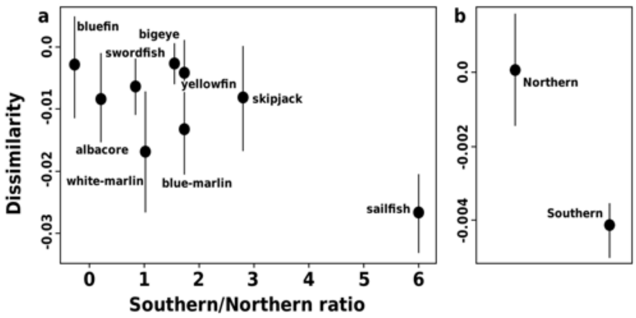

Figure 1: Bootstrap estimates of the mean dissimilarity a) between the wavelet spectra of each species, versus their spatial repartition expressed through the southern/northern ratio b) between the wavelet spectra from southern and northern areas. The southern/northern ratio is computed for each species as the number of time series from southern areas divided by the number of time series from northern areas.

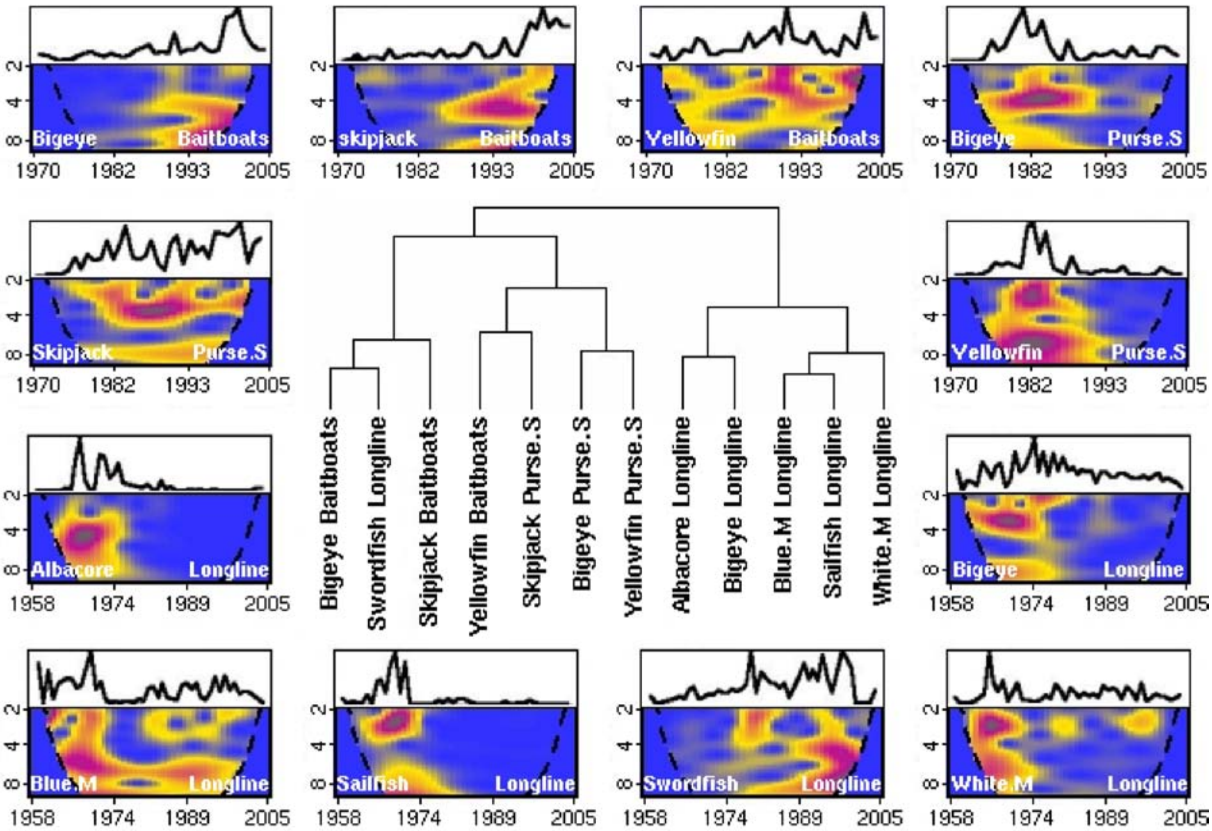

Figure 2: Cluster tree of the wavelet spectra for the catch per unit effort time series in the Eastern Canary Coastal (CNRY) province, on the west african coast. The wavelet spectra decompose the variance of time series over time (x-axis) and frequencies (y-axis), enabling one to follow the time evolution of the relative importance of frequencies in the signal. The colors gradient, from dark blue to dark red, codes for low to high power values. The wavelet spectra were then compared and a dissimilarity matrix was produced (see methods). The cluster tree was obtained using the disimilarity matrix on which flexible clustering was applied. The CPUE time series analysed are plotted in black line on the top of the corresponding wavelet spectrum.

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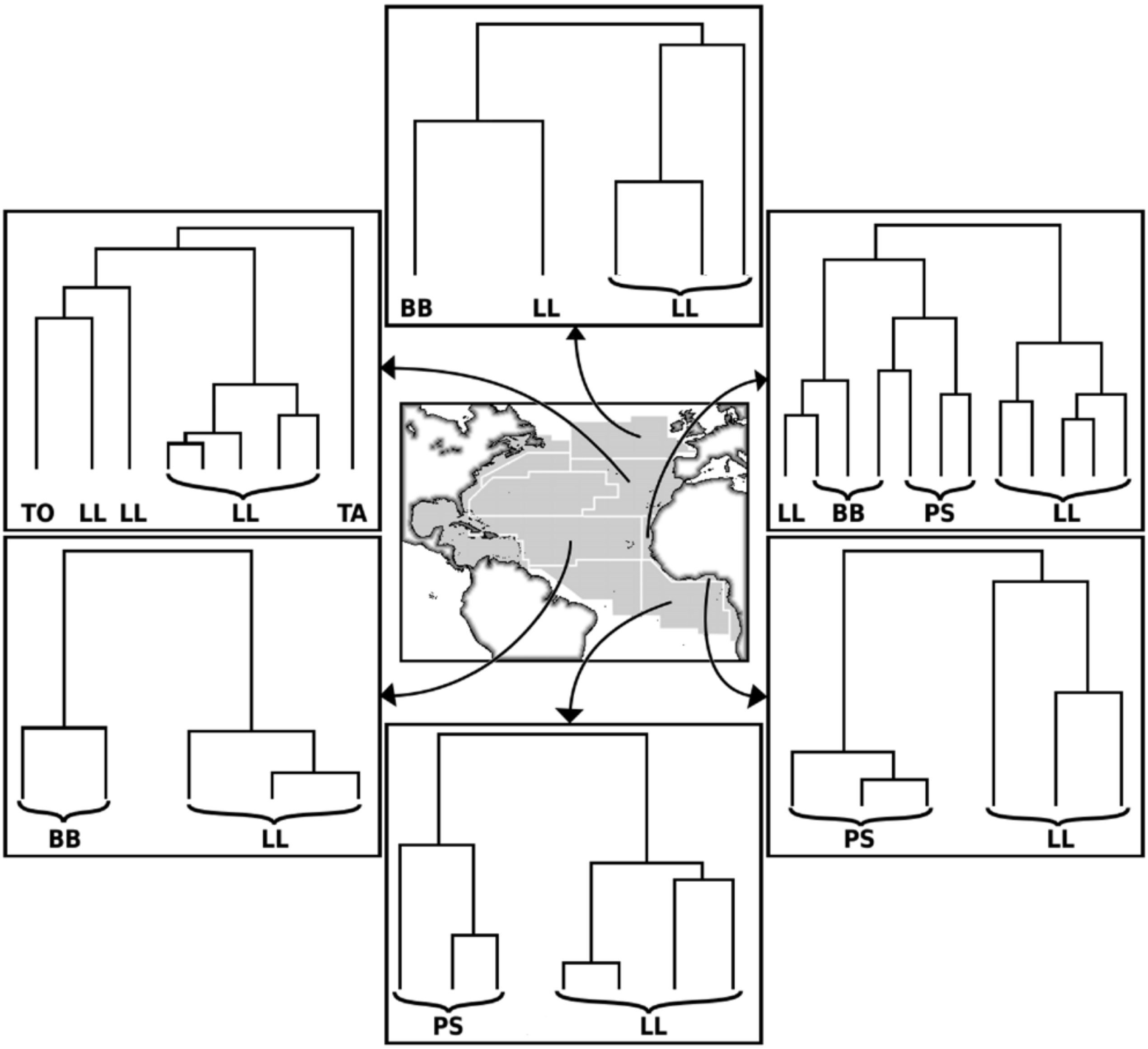

Figure 3: Clusters trees of wavelet spectra in the provinces that displayed several gears. The cluster trees were obtained using the dissimilarity matrix constructed with the wavelet spectra of the CPUE time series, on which flexible clustering was applied. LL stands for longline, BB stands for baitboats, PS stands for purse-seine, TA stands for Trap and TO stands for Troll.

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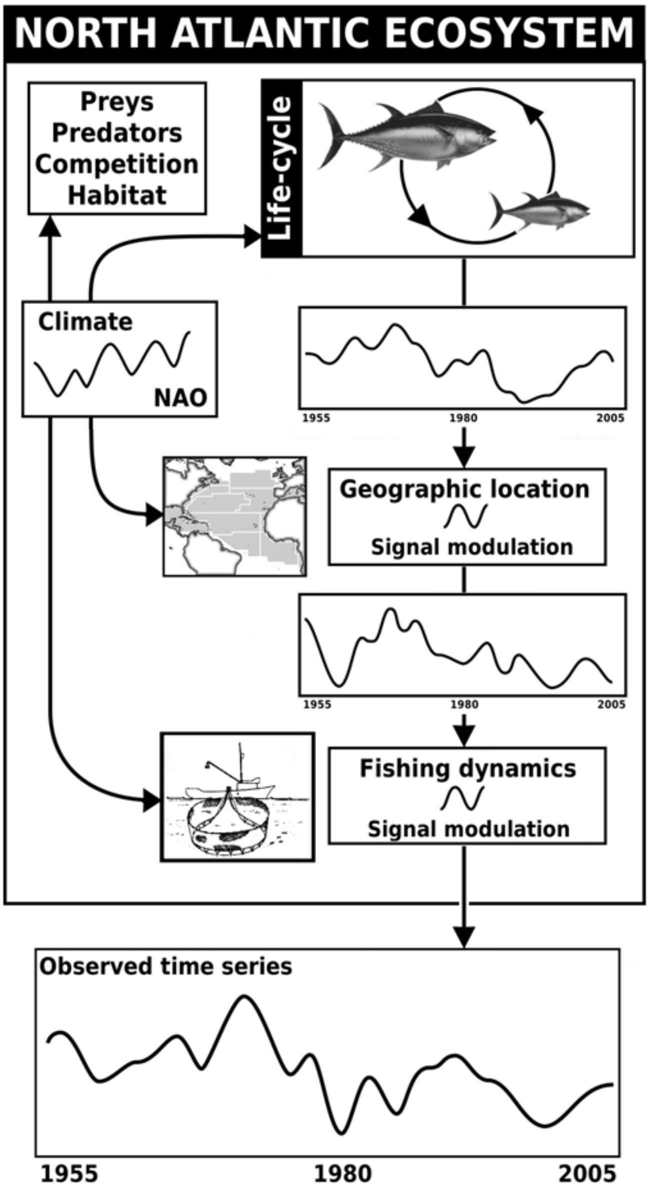

Figure 4: Representation of the successive modulations of signal that shape the fisheries time-series. The dynamics induced at the population level is first influenced by the ecosystem and climate. The signal is then modulated depending on the geographic location and on the local properties, also influenced by the climate. Finally, the different fishing gears and dynamics also constitute a source of modulation.

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