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# Assessment of Community Health Via New Statistical Tools and Functional and Structural Indices

Katyana Vert-Pré

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# Assessment of Community Health Via New Statistical Tools and Functional and Structural Indices



Katyana A. Vert-Pre

PhD Dissertation

Departement UMR BOREA Diversity and Interactions in Coastal systems

2019



MUSÉUM  
NATIONAL D'HISTOIRE NATURELLE



PHD Dissertation

# Assessment of Community Health Via New Statistical Tools and Functional and Structural Indices.

Ph.d Program

Museum National d'Histoire Naturelle de Paris

Presented by

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A dissertation submitted to

UMR BOREA, Department of

Diversity and Interactions in Coastal systems

for the degree of Doctor of Philosophy

Year 2019



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*To the remarkable women in my family:*

*A delicate balance of warmth, grace, laughter and affection. You redirect my path, incite my dreams, and  
praise my every success*

*To Peyton,*

*though very young, your love for science and life was truly inspiring*





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# Introduction

## 1. Historical background

During the past decade, policy makers have been moving from single species management towards ecosystem management. Single species management focuses on characteristics occurring at the species scale. For example, demographic parameters, density-dependent effects, stock-recruitment relationships, genetic diversity and reference points (Link, 2002). Compared to traditional resource management, ecosystem management can incorporate ecological, economic, and social patterns and can respond to challenges hard to solve with traditional methods (Godfray et al., 2010; Foley et al., 2011; Tschardt et al., 2012). These three components can then be subset as three ecosystem panels. In our study, we will focus on the ecological panel. Therefore, when we refer to ecosystem we define it as “an ecological community situated within its environment, considered as a unit” (adapted from Tansley, 1935; Link, 2002). Ecosystems are analyzed by focusing on species interactions, allocation of biomass, changes in ecosystem function, biodiversity, non-fishing ecosystem services, rare species and non-target species (Link, 2002).

Given the strong increase in anthropogenic pressures and significant changes in the environment, scientists need a way to assess the state of the ecosystem. This is particularly expected in the European Union where member states have agreed through the Marine Strategy Framework Directive (MSFD) to reach the good ecological status of marine ecosystems by 2021. This requires developing robust evaluations of the environmental status by assessing the impact of anthropogenic and environmental pressures on species interactions, ecosystem functions,

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biodiversity, community structure and populations. This implies focusing on all species including rare and non-targeted species that are usually harder to analyze due to the scarcity of data.

Ecosystem indices have been proven to be efficient tools both to summarize the state of an ecosystem given all these aspects, and to lead to successful management decisions (Fath and Cabezas, 2004). Along with management methods, these indices have been moving from simple indices to impact matrix, in incremental steps.

The first type of indices was defined as simple indices. In the ecology field, these indices can be used to measure biodiversity (Whittaker, 1972). They measure “...the variety and heterogeneity of organisms or traits at all levels of the hierarchy of life, from molecules to ecosystems...” (Morris et al., 2014). For example, the Richness, the Shannon’ diversity, the Simpson’ diversity, the Berger-Parker dominance indices (Shannon, 1948; Simpson, 1949; Hill, 1973; McCune and Grace, 2002) have been used in the past and are still widely used today (Magurran, 2004). In the environmental field, environmental quality indices (EQI) were used to develop the U.S Environmental Protection Agency’s Clean Air Act (1972) and Clean Water Act (1976). These were discussed by Ott (1978) as a mean to represent environmental data and results in a simplistic manner, while keeping accuracy in the information provided. In 1972, the Clean Air Act imposed a new minimum level regulation on six pollutants: carbon monoxide, nitrogen oxides, sulfur oxides, hydrocarbons, photochemical oxidants and particulate matter. The EQI summarized the frequency and severity in which counties violated the Air Act. It helped scientists and stakeholders make an informed decision.

However, simple indices are limited to representing unidimensional traits, which does not capture the mixed effects of traits present in the ecosystems. Moreover, their use is limited in space and time. Thus, as use of simple indices extended, they started being combined to form multi-criteria

indices. For example, EQI extended to soil ecology and are still widely used in this field. However, they moved from a simple approach to a multidimensional approach. Amacher et al. (2007) designed a new Soil Quality Index (SQI) to assess forest soil health. This SQI combined 19 physical and chemical properties of forest soils into a single number. Scientists built indices from each physical and chemical soil properties and sum them up into one value. This value is then compared to the sum of the maxima of each index expressed as a rate. Followed over time SQI gives a trend on overall soil quality. Because the index is based on the sum of indices, it requires a large number of indices to produce an accurate value. A way to balance the amount of data vs index accuracy is to use weighted measures (Amacher et al., 2007). Like the SQI, in other ecological field, several ecological indices were built to assess the state and trends in the environment, like nutrient levels, hydrologic flow, stream invertebrate diversity, ecosystem integrity. Types (Dale and Beyeler, 2001), comparison and methodologies of indices were widely documented in special issues of Marine Pollution Bulletin on the European water framework directive (WFD) (55(1/6), 2007) and in a review by Diaz et al. (2004).

In natural resource disciplines, the need for developing ecosystem indices was first instigated to translate and communicate successful management strategies in regard to environmental and anthropogenic pressure (Borja et al., 2008). They should provide accurate and reliable information to keep ecosystem at a healthy state. When building ecosystem indices, the challenge comes from the complexity of marine ecosystems. They usually have high biodiversity and are driven by diverse external and internal factors with confounding effects. Each factor impacts the ecosystem health at a different intensity. Thus, aggregating many factors into a single variable giving a relative value reference to a base line is challenging (Borja et al., 2008), and despite their widespread use,

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scientists and decision makers keep some doubts about their accuracy in detecting trends in an ecosystem and assessing health of an ecosystem (Gotelli et al., 2010). In the ecosystem framework, decision makers need upgraded, more reliable indices (Fath and Cabezas, 2004).

Biodiversity indices are increasingly used to assess ecosystem health (Worm et al., 2006; Duffy et al., 2007; Pinto et al., 2014). Recent studies showed that anthropogenic impact on ecosystems have led to a loss of biodiversity, disrupting multitrophic-level interactions (Costanza et al., 1998; Schneiders et al., 2012) and leading to trophic cascade (Frank et al., 2005). International legislation strikes the importance of protecting biodiversity by creating the convention of biological diversity (CBD; UNEP, 1992). In more recent years, the European Union also started to work toward the same goal. They stated in the Marine Strategy Framework Directive (MSFD, 2008; European Commission, 2008) that biodiversity is one of the cornerstones of good environmental management (Worm et al., 2007; Pinto et al., 2014). Biodiversity is a multi-dimensional matrix including data from genes and species, functional groups, habitats and ecosystems (Laurila-Pant et al., 2015). All these dimensions participate in the balance of ecosystems (Schneiders et al., 2012).

To assess the consequences of these dimensions on ecosystems, scientists have been using Ecosystem-based management (EBM) as required by the CBD and MSFD (Pikitch et al., 2004, McCauley et al., 2015). This new direction for management targets ecosystems rather than species. The main objective is to sustain a healthy ecosystem. As described in Pikitch et al. (2004), these management methods should (1) prevent degradation of ecosystems using quality indicators and system status; (2) limit changes in species communities and ecosystem functions to avoid reaching a point at which resilience is not possible; (3) set lasting socioeconomic benefits while keeping the ecosystem healthy; (4) provide insight of ecosystem processes necessary to monitor anthropogenic

pressures. In the marine environment, the focus of EBM has been mainly on the fishing industry. Scientists aimed to set reference points, and control rules like the control rules used in single species management (Rice, 2000; Murawski, 2000; Link et al., 2002). Therefore, the focus under the biodiversity umbrella was often on exploited species. For example, on the direct impact of a fishing gear on species richness, on trophic levels or their stock-recruit relationship. Moreover, the most commonly used EBM (e.g. Ecopath with Ecosim) requires high amount of data (Heymans et al., 2014; Colleter et al., 2015), ultimately leading to a strong bias towards using fishery-dependent data.

Focusing mainly on fishery-oriented questions often leads to a lack of interest in rare species. However, rare species have a pivotal role in ecosystems and are often restricted to small geographic distributions (Gaston, 1994). Many studies have proven that rare species are extremely vulnerable to fishing pressure, habitat loss and environmental changes (Dulvy et al., 2003; Lavergne et al., 2005; Jelks et al., 2008; Sekercioglu et al., 2008). Moreover, they constitute an important link in maintaining stability in the biogeochemical and dynamic properties of the ecosystem (Naeem et al., 2012; Mouillot et al. 2013a). To each species in the ecosystem corresponds a function, and functional redundancy has been proven to be an essential component to ecosystem stability.

Loosing rare species might lead to the loss of functionality, which can result in the loss of ecosystem processes such as organic matter degradation, bioturbation, bioerosion, and productivity (Mouillot et al. 2013b). For example, Mouillot et al. (2013) found that in coral reef ecosystems, 98% of fish species that potentially support highly vulnerable functions are regionally rare species.

The rare species issue is linked to sparse data, which is a challenge when wanting to analyze species assemblages with rare and abundant species using covariance patterns. Indeed, it is commonly



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thought that detecting changes in covariance patterns over space and time requires high quality data (Warton and Shepherd, 2010). However, new methods in spatial and temporal multivariate analysis offer means for predicting assemblages in sparse data conditions and without a priori specifying the driving variables. For example, the latent variable framework, including joint spatial distribution models, have given flexibility in that matter (Olden and Jackson, 2002; Thorson et al., 2016). These methods allow us to define statistical assemblages, which have rarely been done in the marine environment.

Solving the issue of identifying communities statistically would open the way to answering multiple ecological and management questions. This study helps define statistically a new study unit, that we will refer to as communities. Previous studies consider the ecosystem through a species-to-species interactions' magnifying glass. However, recent research in other fields shifted to consider the ecosystem as communities interacting to balance ecosystem health. These communities, as they composed of species with various functions, can be defined as functional groups. Studying the interactions within and between the groups, will help measure the true resistance of an ecosystem to external environmental and anthropogenic pressure.

To proceed with this analysis, we focused on The Eastern English Channel (EEC). It is part of the "Greater North Sea" sub-region in the Marine Strategy Framework Directive (Olenin *et al.*, 2010). This area is of interest as it has the world's busiest sea area with intense commercial marine activities, recreational and fishing activities, and it is also of great conservation concern (Glegg and Fletcher, 2015; Le Goff *et al.*, 2017). The Eastern part of the English Channel is the narrowest as it goes from 160km wide on the western side to 30km on the eastern side over a 500km span. It also presents a shallow water shelf with an east to west down slope up to 0.5 degrees (Gibbard and

Lautridou, 2003). The shelf is sculpted in valleys, hills and fosses due to the heavy flow river discharges from the Seine, Somme, Bethune, Solent and Arun (Smith, 1985). Marine life is strongly influenced by the East to West current, strong tidal currents and high tidal range along with the nutrients brought by the 500 cubic meters per second freshwater discharge from the Seine (Salomon and Breton, 1993; Passy *et al.*, 2016) together with the other catchments of England and France. The anthropogenic and environmental stressors in this area are numerous and well monitored by surveys, giving the opportunity for a comprehensive and well-defined ecosystem study.

## **2. Scientific objectives**

The general objective of this dissertation is to improve the knowledge on organization of communities within a marine ecosystem. This will be done studying the case of the EEC, using fishery independent data of a wide variety of fish and cephalopods. In more detail, the main goal is to determine spatial and spatio-temporal fish community patterns using a combination of statistical methods, the functional groups they define and how these groups evolve in time (chap 1 and 2). Some interest will be also given to how that knowledge can be used both to assess quality and to manage fishes under high anthropogenic pressures in a changing environment (chap 3 and 4).

To explore the main objective, we designed the following research topic:

1. Identify the most appropriate spatial scale to define statistical relationships between species of the ecosystem, given the sparsity and spatial distribution of survey data.

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2. Develop appropriate tools to select statistical communities structuring a marine ecosystem.
3. Build statistically accurate functional indices for marine ecosystem while studying the functional temporal composition and trends of communities within a marine ecosystem.
4. Identify surrogate species within marine environment that will help forecast rare and endangered species abundance.

These topics lead to the more practical aim of providing European scientists and stake holders with new tools adequate to deal with spatial management. Moreover, they lead the way to understanding marine community resilience when under strong anthropogenic pressure and in a changing environment.

### **3. Working hypothesis**

This process began with a working hypothesis, a direct statement of the research idea that will ultimately lead to the disclosure of new scientific material (Pierce, 1908; Dewey, 1938). Given the current knowledge in this field and the observed evidence, we elaborated the following working hypothesis:

*The assessment of communities' health for improved spatial management requires the development of new tools and community functional and structural indices?*

### **4. Dissertation structure**

The variety in ecological questions answered in this dissertation and the associated variety of methods led to presenting each topic separately. Thus, each chapter is organized as an individual

scientific paper with individual introduction, material and methods, results and discussion.

Therefore, there might be information redundancy in some sections.

*Chapter 1: Autoregressive Spatial Temporal Clustering Model: An innovative method to assess statistically Spatio-Temporal Patterns in Marine Species Communities*

Chapter 1 develops a statistical method to determine the different marine communities and their respective species composition. To this end, we selected the most resilient species of the Eastern Channel and tested whether spatial and spatio-temporal community patterns could be detected, and subsequently explained by environmental variability. The goal was to identify and combine the strength of methods that could provide strong statistical answers to this question that, in the past, was mostly answered with expert knowledge.

*Chapter 2: The impact of scale on identifying Spatio-Temporal Patterns in Marine Species Communities*

Chapter 2 intends to assess the impact of spatial scale on spatio-temporal communities defined statistically by ASTEC. In marine ecology, spatial and temporal fish community structure is important to depict ecosystem's responses to anthropogenic and environmental factors. Although spatial distribution patterns and fish time series of abundance have been studied in the past, little research has addressed the impact of spatial scale on mapping spatio-temporal patterns. This chapter evidences the supplemental results for chapter 1 that validates statistically and ecologically the choice of the scale at which the main analysis was performed.

*Chapter 3: Spatio-Temporal Trends of Functional Indices for Marine Species Communities in a Changing Climate*

## *Introduction*

Chapter 3 intends to build spatially explicit functional indices of marine ecosystem status. To do so, the trends and intensity of functional indices of fishes and cephalopods were compared between marine spatial and spatio-temporal communities. Moreover, we assessed and discussed the impact of omitting spatial structure when calculating functional indices.

### *Chapter 4: Neighbors helping Neighbors: Managing Endangered Marine Species with Surrogate Species*

Chapter 4 offers a needed answer for the management of rare or endangered marine species. Surrogate species are identified statistically within marine communities. Then the estimated index of these species allows to forecast rare and endangered species abundance.

For each chapter, analysis was performed using data on fish and cephalopod community from EEC ecosystem as a case study. Marine species count data was extracted from the Channel Ground Fishery Survey dating from 1988 to 2014.

# Chapter 1. Spatio-Temporal Patterns in Marine Fish Communities Across Scales: using an Autoregressive Spatio-temporal Clustering Model: A study of fish and cephalopods of the Eastern English Channel

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Short title      Spatio-Temporal Patterns in Marine Fish Communities Across Scales

## **Abstract**

In marine ecology, spatial and temporal fish community structure is important to understand ecosystem's responses to anthropogenic and environmental factors. Although spatial distribution patterns and fish time series of abundance have been studied in the past, little research has addressed the impact of spatial scale on mapping spatio-temporal patterns. To achieve this goal, the first step is to develop a method describing spatio-temporal communities statistically. At three spatial resolutions, from 1043 km<sup>2</sup> to 522 km<sup>2</sup>, we compared the output of a new framework, the Autoregressive Spatio-temporal Clustering analysis (ASTECC) and we finally retained the most parsimonious scale: 522 km<sup>2</sup>. ASTECC combines a zero-inflated Poisson model with latent predictors alongside a hierarchical clustering analysis using multiscale bootstrap resampling. It estimates the spatial and spatio-temporal communities formed by 16 species in the Eastern English Channel using 20 years of data from the Channel Ground Fishery Survey. Community structure was strongly dependent upon the spatial scale of analysis and the smallest scale provided the most parsimonious model. Moreover, integrating temporality in spatial studies defined a stable composition and richness community structure. Combining a spatial and spatio-temporal approaches highlighted cluster composition shifts over time. It shows that small scale data should be used for studies on spatial connectivity and meta-community when integrating temporality. Moreover, the scale of the study did not matter anymore in a spatio-temporal case. A combined spatial and spatio-temporal approach defines community dynamics, and should help management and conservation efforts facing climate change and anthropogenic pressures.

French title

Patrons d'organisation spatio-temporelle de communautés de poissons et céphalopodes à différentes échelles géographiques : apports d'un Modèle de Clustering Spatio-Temporel Autorégressif. Exemple d'application à la Manche Orientale

French Abstract

En écologie marine, l'analyse des variations spatiales et temporelles des communautés est essentielle pour comprendre les réponses de l'écosystème à l'impact des facteurs anthropiques et environnementaux. Les patrons de distributions spatiales et les séries temporelles d'abondance des poissons ont été étudiés par le passé, cependant peu de recherches ont été consacrées aux effets de l'échelle spatiale sur la structure des patrons spatio-temporels. Pour atteindre ces objectifs, il est essentiel de développer une méthode statistique d'analyse capable d'identifier les patrons spatio-temporels d'organisation de ces communautés. Nous avons comparé, à trois échelles spatiales, de 1043 km<sup>2</sup> à 522 km<sup>2</sup>, les sorties de modèles de clustering spatio-temporel autorégressif (ASTEAC). ASTEAC combine un modèle de Poisson zéro-inflation avec variables latentes suivi d'un modèle de clustering hiérarchique avec bootstrap multi échelle. La méthode identifie les communautés spatiales et spatio-temporelles de 16 espèces de la Manche orientale à partir des données de campagne d'échantillonnage des espèces démersales de la manche (CGFS) sur une période de 20 ans. La répartition des espèces en différentes communautés dépend fortement de l'échelle spatiale de l'étude et l'on a montré la plus petite échelle utilisée (522 km<sup>2</sup>) était la plus parcimonieuse. De plus, l'intégration de temporalité dans les études spatiales a permis de définir une composition spécifique et une diversité spécifiques stables des communautés. En outre, l'association



## Chapter 1

d'approches spatiales et spatio-temporelles a révélé des changements de proportion des espèces des communautés. ASTEC fournit une quantification précise de la structure des communautés spatiales et spatio-temporelles. Ce modèle suggère que des données à petite échelle devraient s'utiliser pour les études des méta-populations. De plus, l'effet de l'échelle pourrait devenir négligeable quand on intègre des variations temporelles à l'étude des communautés. Joindre une approche spatiale à une approche spatio-temporelle permet de définir la dynamique des communautés et contribue à l'amélioration de la prise de décision en matière de gestion et de conservation face au changement climatique et aux pressions anthropiques.

### Keywords

Marine communities, spatial scale, spatial-temporal model, species cluster distribution

## 1. Introduction

Understanding mechanistic processes related to ecosystem dynamics is of paramount importance in ecology. Analyzing spatial and temporal distributions of species is a key step to determine the community structure in an ecosystem. In turn, an appropriate comprehension of community structure, spatial distribution and temporal shifts helps assessing ecosystem resilience and providing management tools (Elton, 1927; Hooten and Wikle 2010; Rassweiler, Costello, Hilborn, and Siegel, 2014). Several researchers have focused on abundance-occurrence relationships, identifying biogeographic distribution of species assemblages or predicting outcomes from species interactions (Keddy, 1992; Olden and Jackson, 2002; Peet and White, 1998; Scheller *et al.*, 1999; Oberdorff *et al.*, 2001; Rodriguez and Lewis, 1997; Magnuson *et al.*, 1998). In marine ecosystems, the large

number of fish species (i.e. approx. 1000 species in metropolitan French waters, Bearez et al. 2017), their mobility and detectability hinders the possibility to correctly, address the structure of assemblages and spatial and spatio-temporal patterns. Indeed, a high number of species with low occurrences limits the power of statistical analysis and modeling of spatio-temporal community patterns.

It is commonly thought that detecting changes in covariance patterns over space and time requires high quality data (Warton and Shepherd, 2010). However, most data sets present imperfect detection due to inadequate survey protocols and low abundance species leading to high amounts of zeros (Guillera-Arroita *et al.*, 2010; Guillera-Arroita, 2017). It has been shown by Guillera-Arroita *et al.*, (2014) that ignoring imperfect detection in surveys can lead to the wrong conclusion about the spatial distribution of species. The “true zeros”, which represent an absent species from the area at the time are confounded with the “excess zeros” featuring the species present but not caught during the survey. Accounting for the “excess zeros” is a relevant issue in spatial modeling. The zero-inflation Poisson is a good solution to overcome these issues (Zuur *et al.*, 2009). The zero-inflation attempts to account for and correct the bias created by “excess zeros” present in the data while the Poisson-lognormal section of the predictor deals with the over-dispersion assumed in the data (Aitchison and Ho, 1989; Williams and Ebel, 2012). The Zero-inflated Poisson-lognormal is a strong model to analyze the joint distribution and densities of species; however, it lacks a convenient way to identify and visualize statistical significance of the identified spatial pattern. This kind of approach has given flexibility to encompass the quality of datasets including a high number of species of low occurrences (Olden and Jackson, 2002; Thorson *et al.*, 2016).

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However, there is a need to develop a method that will not only detect and predict communities in space and time but will also identify the most fundamental drivers that control spatio-temporal shifts of community patterns. Indeed, most studies consider a high proportion of species within the ecosystem which includes focusing on the most variable species that are the most sensitive to ecosystem changes or schooling behaviors. For example, Vaz *et al.*, (2007) provides distribution maps of fish communities, including all species, according to bathymetric and mean bottom temperature gradients of the Eastern Channel.

Most community studies fail to analyze effects of spatial scales and timeliness on the model outputs. Long-term survey spatial analyses implicitly consider that species forming communities use the same habitat, but they do not account for temporal matches. Spatio-temporal analyses seek for species that are present in the same habitat at the same time. Thus, three definitions of communities are implicitly used. Communities can be defined as: 1) a group of species pertaining to the same habitat (Roughgarden and Diamond, 1986), 2) a group of species present in the same habitat at the same time (Begon *et al.*, 1990; Mittelbach and McGill, 2019), 3) a group of species interacting directly or indirectly within a similar habitat over time (Fauth *et al.*, 1996; Morin, 2011; Stroud *et al.*, 2015). To simplify terminology here, our communities are the statistical units defined by the model developed in this paper and can be interpreted as any of these three definitions. These definitions could lead to very different interpretations of habitat use and community structure.

The Eastern Channel is an interesting area to study the structure and patterns of fish and cephalopod communities and the effects of environmental pressures and climate change on the variability of patterns. Indeed, i) a bottom trawl survey covering the whole area, has been conducted

since 1988, ii) the Eastern Channel is a huge transition zone between the western Channel (under the influence of the North East Atlantic) and the North Sea where biogeographic gradients occur (Foveau et al. 2017).

In the current study we introduce a robust method to detect community patterns and their resilience at the scale of a biogeographical transition zone, the Eastern English Channel (EEC). To this end, we firstly selected the most resilient fraction of the community by excluding the most abundant and the most variable species. Secondly, we developed and fitted a two-part autoregressive spatio-temporal cluster model (ASTECC): including firstly, a zero-inflated Poisson model implemented in ‘vast’ version 1.5.0 (Thorson and Barnett, 2017) to predict species probability of co-occurrence; and secondly, an agglomerative hierarchical bootstrap cluster analysis in ‘pvclust’ version 2.0.0 (Suzuki and Shimodaira, 2015) which identifies species communities statistically, thirdly we compared the outputs of the models at three different spatial scales and retained the best fitted scale, and finally we suggest distribution maps of the communities derived from spatial and spatio-temporal analysis.

## **2. Materials and Methods**

### **2.1. Study area**

The West of the EEC bathymetric gradient has the deepest waters between 33 to 80 meters with mean temperature ranging from 14.7 and 16 degrees Celsius. In the East of the EEC, waters are shallower with temperature between 15.4 and 17 degrees Celsius. The EEC includes numerous estuaries, muddy and sandy sediment are found close to the coast. They are associated with river Somme, Seine, Canche, Authie, and Solent (Foveau *et al.*, 2017).

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The EEC, part of the "Greater North Sea" sub-region in the Marine Strategy Framework Directive (Olenin *et al.*, 2010), is of interest as it has the world's busiest sea area with intense commercial marine activities, recreational and fishing activities, and is also of great conservation concern (Glegg and Fletcher, 2015; Le Goff *et al.*, 2017). The Eastern part of the English Channel is the narrowest as it goes from 160km wide on the western side to 30km on the eastern side, over a 500km span. It also features a shallow water shelf with an east to west down slope up to a 0.5 degree (Gibbard and Lautridou, 2003). The shelf is sculpted in valleys, hills and fosses due to the heavy flow river discharges from the Seine, Somme, Bethune, Solent and Arun (Smith, 1985). Marine life is strongly influenced by the East to West current, strong tidal currents and high tidal range along with the nutrients brought by the 500 cubic meters per second fresh water discharge from the Seine (Salomon and Breton, 1993; Passy *et al.*, 2016) together with the other catchments of England and France. The anthropogenic and environmental stressors in this area are numerous and well monitored by surveys, giving the opportunity for a comprehensive and well-defined ecosystem study to quantify and qualify the joint spatial-temporal patterns in community structure.

### 2.2. Data

Spatial survey data with numbers, fishing traits, and area swept in km square were extracted from the yearly standardized Channel Groundfish Survey (CGFS) for 108 stocks with time series from 1988 to 2014. The survey is conducted between the 15<sup>th</sup> of September and the 15<sup>th</sup> of November on the Gwen Drez vessel with a 10 meter Very High Vertical Opening (VHVO) bottom trawl with a 10mm mesh size at the cod-end to catch juveniles. Sampling follows a stratified random sampling

design with standard 30-minute hauls conducted at a speed of four nautical miles per hour (ICES, 2017).

We started the time series at year 1995 (year at which the survey became standardized) and eliminated 70 species with gap years and 22 species that prevented the model from converging due to extreme high variance. In these 22 species, we rejected three species (*Trisopterus minutus*, *Trisopterus luscus*, *Trachurus trachurus*) that constitute 62% of the numbers of the catches. That would highly skew the results of any statistical analysis. Therefore, we focused on the 16 species that represent 36% of the total sampled abundance. Finally, out of 108 species a total of 16 species were selected for the analysis. These species represent some of the most resilient and evenly distributed species of the fish and cephalopod community of the EEC.

### 2.3. ASTEC

To map the spatial (s) and temporal (t) distribution of species (c) in the EEC we developed and implemented a two-step autoregressive spatio-temporal cluster analysis (ASTEC). This method visually and statistically emphasized temporal and spatial species co-occurrence. These methods have been used separately for other ecological issues. However, once combined they provide a robust statistical manner to detect community structures and their spatio-temporal patterns.

In the first step of ASTEC, the ‘vast’ zero-inflated Poisson count-data model used two linear predictors, to deal with the extra zeros and with the count prediction. It assessed joint similarities in spatial distribution caused by unobserved covariates, temporal variations and correlated

distributions of multiple species. These models are described in Welsh *et al.*, (1996); Faddy, (1997, 1998) for species abundance.

The expected values of the data were related to the linear predictors through link functions. Thus, we approximated spatio-temporal variations in the zero-inflation model  $r_1(i)$  applying a logit-link logistic function to the first linear predictor for observation  $i$ ,  $p_1(i)$ :

$$r_1(i) = \text{logit}^{-1}(p_1(i))$$

We then approximated the mean intensity function  $r_2(i)$  as an exponential function of the second linear predictor,  $p_2(i)$ , offset linearly by  $a_i$  which is the area-swept for observation  $i$ :

$$r_2(i) = a_i \times \log^{-1}(p_2(i))$$

Thus, the probability of the count data ( $b_i$ ) is specified as:

$$Pr(b_i = B) = \begin{cases} (1 - r_1(i)) + g\{0|r_2(i)\} & \text{if } B = 0 \\ r_1(x_i, c_i, t_i) \times g\{B|r_2(i)\} & \text{if } B > 0 \end{cases}$$

where  $(1 - r_1(i))$  is the “zero-inflation probability”, while  $r_2(i)$  is the expected value for the Poisson distribution  $g\{\}$ .

The zero-inflation in these approximations attempts to correct for the bias created by excess zeros present in the data. Indeed, our data presented high amounts of zeros separated in two categories. The first category being the “true zeros”, which stands for an absent species from the area at the time and, the second one being the “excess zeros” where, for example, the species was present but

was not caught during the survey. The first linear predictor for observation  $i$ ,  $p_1(i)$ , models this zero-inflation as:

$$p_1(i) = \beta_1(c)$$

where  $\beta_1(c)$  is a constant intercept for each species  $c$  across years. As our main interest is to define species co-occurrence given their distribution and abundance, we set the number of factors for the first predictor to 0, which turned off the estimation for the spatial and spatial-temporal covariance matrix and saved computational time.

The variance observed in our data is assumed to be higher than the variance of the theoretical model. Thus, the Poisson-lognormal section of the predictor dealt with the over-dispersion as suggested by Williams and Ebel (2012). Considering these terms, the second linear predictor  $p_2(i)$  models the count-data intensity function:

$$p_2(i) = \beta_2(c, t) + \sum_{f=1}^3 L_{\omega_2}(c_i, f) \omega_2(s_i, f) + \sum_{f=1}^2 L_{\varepsilon_2}(c_i, f) \varepsilon_2(s_i, f, t_i)$$

where  $\beta_2(c, t)$  is the fixed effect intercept for species  $c$  and year  $t$  assuming the abundance estimates are independent for each year which is necessary to estimate an abundance index that can be used for management (Thorson, in press). The  $\omega_2(s_i, f)$  coefficients represents spatial variation at location  $s_i$  for factor  $f$  and  $L_{\omega_2}(c_i, f)$  is the loadings matrix that generates spatial covariation among species,  $\varepsilon_2(s_i, f, t_i)$  is spatio-temporal variation and  $L_{\varepsilon_2}(c_i, f)$  is the loadings matrix that generated spatio-temporal covariation for this predictor. After running a sensitivity analysis on the number of factors to use for the second predictor, we settled on three latent spatial



covariates ( $n_{\omega 2} = 3$ ) and two latent spatio-temporal covariates ( $n_{\epsilon 2} = 2$ ). The fixed effects and random effects given by this parametrization are described in Table 3. This configuration lead to the best convergence for the models.

## 2.4. Spatial and Spatio-temporal correlation matrix

Previous research suggested that joint distribution models are statistically efficient to estimate covariance as they allow to compare various types of species and summarize the effect of external factors on species distribution (Ovaskainen and Soininen, 2011; Thorson *et al.*, 2015a). As described in Thorson *et al.* (2015a) the loadings matrices are generated such that  $\mathbf{L}^T \mathbf{L}$  is the covariance among categories for a given spatial or spatio-temporal process. The covariance is a common measure of the relationship between two random variables; however, the values of the covariance matrix cannot be compared across pairs of species, because the variable scale between abundance of species can make the patterns hard to decipher. Thus, covariance pairs were scaled per their standard deviation, creating correlation matrices (Cudeck, 1989; Borgognone *et al.*, 2001) with values comprised between -1 and 1. The correlation matrices are the stepping-stone for ASTEC to define how species are distributed in space and time.

The spatial matrix expresses similarities in presence-absence in the area of study and the spatio-temporal matrix pairs species with similarities in spatial presence-absence combined with similarities in trends of abundance. Last, to understand shifts of species in space and time we combined the results of the spatial correlation matrix with the absolute values of the spatio-temporal correlation matrix. This reveals all the species that were present at the same time in an area and to whose abundance is shaped by environmental pressure either in sync or in opposite.

## 2.5. Spatial domain specification

'Vast' (Thorson and Barnett, 2017) uses a stochastic partial differential equation (SPDE) approximation of the probability density function for spatial and spatio-temporal variation (Illian *et al.*, 2012).

The SPDE generates a triangulated mesh that has a vertex of a triangle at each knot of the spatial domain. The location of knots is distributed as a function of the observed data spatial frequency and defines the average spatial scale at which the analysis was performed. As correlations usually decline slowly when moving along depth contour but faster when moving perpendicular to the depth contour, we assumed a Matérn function following geometric anisotropy (Thorson *et al.*, 2015b).

We then consider three spatial scale, using triangular mesh from 1043km<sup>2</sup>, 782km<sup>2</sup> and 522km<sup>2</sup> by increasing the number of knots from 30 to 40 and 60 knots. After running multiple simulations, we selected the largest and the smallest scale allowing the model to converge, then we also selected the average scale between these two.

## 2.6. Parameter estimation

First, Template Model Builder using package 'TMB' (Kristensen *et al.*, 2015) estimates the value of random effects maximizing the joint likelihood conditional on the fixed effects (Tab. 3). Second, the value of fixed effects maximizing the Laplace approximation to the marginal likelihood were identified with a nonlinear minimizer. All the hessian matrices were positive definite and the

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maximum gradients were well below 0.001, providing no evidence that the model had not converged.

### 2.7. Hierarchical clustering

The hierarchical clustering step of ASTEC aims to reveal communities by visualizing them as a tree structure. This not only facilitates interpretation, compared to the ordinated correlation matrix output from VAST, but also helps define species cluster rather than giving only two species pair correlation. The multiscale bootstrap resampling (Shimodaira, 2004) allows then calculation of standard errors, probabilities and statistical significance for the chosen clusters.

This agglomerative approach does not require the number of clusters to be specified a priori. Instead each co-occurrence starts in its own cluster then is paired and moved up the hierarchy given how either similar or dissimilar they are in their spatial or spatio-temporal distribution. To determine proximity, the dissimilarity or distance of distribution between two species  $x$  and  $y$  for spatial and spatio-temporal variations is calculated as:

$$d(x, y) = 1 - correlation(x, y)$$

Given this definition, the more similar two vectors are, the shorter their distance.

For absolute spatio-temporal variations, the distance will approach 0 as the correlation goes to 1 or

-1:

$$d(x, y) = 1 - \|correlation(x, y)\|$$

Then, the most similar species is repeatedly fused per the average linkage ( $\bar{L}$ ) criterion until all species forms a group. This criterion determines the distance between clusters of species ( $A, B$ ), helping the decision on whether a species pertains to cluster A or B:

$$\bar{L} = \frac{1}{|A||B|} \sum_{x \in A} \sum_{y \in B} d(x, y)$$

The average linkage method provides a more accurate evaluation of the distance between clusters and other methods of linkage, avoiding the production of chain-shape clusters as the single linkage does, and has a higher tolerance for outliers than the complete linkage (Liu *et al.*, 2012; Yim and Ramdeen, 2015). To define the best tree from a set of competing trees (Shimodaira, 2002) we used a multiscale bootstrap analysis. We ran 60,000 bootstraps of the previous process and gave a score to each tree that is a function of tree parameters (e.g. number of edges). Then, we tested the null hypothesis (i.e. that the selected tree has the largest score compared to that of a tree with infinite number of edges) assuming a level of significance  $\alpha = 0.1$ . This approximated the unbiased p-values for each cluster as described in Shimodaira (2004).

## 2.8. Selection of the most parsimonious spatial scale

We compared three model increasing the average resolution of the triangular mesh from 1043km<sup>2</sup>, 782km<sup>2</sup> and 522km<sup>2</sup> by increasing the number of knots from 30 to 40 and 60 knots. Then we used AIC model selection to identify the most parsimonious VAST model between scales. The entire set of analysis and packages used for ASTEC was coded in R version 3.4.2 (R Core Team, 2017). This analysis was repeated when separately considering spatial patterns, spatio-temporal patterns and absolute spatio-temporal patterns (e.g. a combination of spatial and spatio-temporal patterns).

## 2.9. Interpretation of results

ASTECC defines clusters that we will refer to in our results as communities. Communities are defined by Stroud *et al.*, (2015) as “the collection of species found in a particular space” (Morin, 2011); however, not necessarily at the same time; or, “all the species of organisms found in a defined area over ecological time”, regardless of type of interactions between species” (Dodds, 2009). To make ecological inferences, first we mapped the sum densities among the spatial, spatio-temporal or absolute spatio-temporal clusters defined by ASTECC. To confirm that the communities identified were relevant we cross referenced our results with the results from previous study on the EEC. We used maps of environmental gradients (e.g. mean bottom temperature), bathymetry, sub-marine topography, and sediment characteristics.

## 3. Results

The model fitting the data from the CGFS survey (Fig. 1) converged at every scale. For scale 522km<sup>2</sup>, 782km<sup>2</sup> and 1043km<sup>2</sup> the AICs are 115036, 115218 and 115283 respectively, suggesting the most parsimonious model is at scale 522km<sup>2</sup> (Tab. 2). The results of the fit for the other two models are displayed in the supplemental materials (Fig. S1-S7).

Consequently, this section introduces the results for the 522 km<sup>2</sup> spatial scale and compares spatial, spatio-temporal and absolute spatio-temporal scenarios. Community patterns were analyzed for 16 species among 108 species listed in the data set (Fig. 1a) using a hierarchical agglomerative cluster analysis on the spatial correlation matrices (Fig. 2) and spatial-temporal correlation matrix (Fig. 3). The spatial and spatial-temporal correlation trees give a precise description of the

communities by pairing species based on the intensity and sign of correlations (Fig. 4 and Fig. 5).

ASTECC identified two spatial and two spatio-temporal communities. The absolute spatio-temporal scenario revealed that 14 pairs of species were aphyasic temporally but belonged to the same spatial unit. The key code for the species name and the communities' description is described in table 1 and table S1, respectively.

ASTECC identified two spatial communities (S522) and two spatio-temporal (ST522) communities. S522c1 with two sub-communities: *Raja clavata* (Linnaeus, 1758), *Chelidonichthys lucernus* (Linnaeus, 1758), *Loligo sp.* (Lamarck, 1798) (S522c1.1) and *Scophthalmus maximus* (Linnaeus, 1758), *Merlangius merlangus* (Linnaeus, 1758), *Scomber scombrus* (Linnaeus, 1758) (S522c1.2). The S522c2 community was constituted of two sub-communities: *Galeorhinus galeus* (Linnaeus, 1758), *Scophthalmus rhombus* (Linnaeus, 1758), *Agonus cataphractus* (Linnaeus, 1758), *Zeus faber* (Linnaeus, 1758), *Trigloporus lastoviza* (Bonnaterre, 1788), *Alosa sp.* (Linnaeus, 1758), *Callionymus sp.* (Linnaeus, 1758) (S522c2.1) and *Sardina pilchardus* (Walbaum, 1792), *Raja undulata* (Lacepède, 1802), *Scyliorhinus stellaris* (Linnaeus, 1758) (S522c2.2). In the S522c1 community, the pairwise spatial correlations were the highest for *Chelidonichthys lucernus* and *Loligo sp.* with 93%, *Raja clavata* and *Chelidonichthys lucernus* with 93%, and *Raja clavata* and *Loligo sp.* with 83%. In the S522c2 community, pairwise correlations ranged from 95% between *Alosa sp.* (Linnaeus, 1758) and *Callionymus sp.*, 92% between *Raja undulata* and *Scyliorhinus stellaris*, to 88% between *Agonus cataphractus* and *Zeus faber*. While some correlations were strong (e.g. *Agonus cataphractus* and *Alosa sp.* at 84%, *Agonus cataphractus* and *Callionymus sp.* at 83%), species interactions were weaker for other species (e.g. *Scyliorhinus stellaris* and *Sardina pilchardus*, *Merlangius merlangus* and *Loligo sp.* showing strength at 30% and 67% respectively).

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The community patterns defined using spatio-temporal variations varied widely from the spatial scenario. The statistical community ST522c2, integrate *Trigloporus lastoviza*, *Galeorhinus galeus*, *Scyliorhinus stellaris*, *Raja clavata* and *Raja undulata*. The statistical community ST522c1, included two sub-communities: *Agonus cataphractus*, *Chelidonichthys lucernus*, *Merlangius merlangus*, *Callionymus sp.*, *Scophthalmus rhombus*, *Alosa sp.*, *Scophthalmus maximus*, and *Scomber scombrus*, *Zeus faber*, *Loligo sp.*, *Sardina pilchardus*. In the ST522c2, community, most pairwise correlations were stronger when considering temporal variations (e.g. *Alosa sp.* and *Callionymus sp.* show a 99% spatio-temporal correlation instead of a 95% spatial correlations). However, rare correlations were weaker (e.g. *Chelidonichthys lucernus* and *Loligo sp.* displayed a 19% instead of 93%). In the ST522c1 community, *Alosa sp.* and *Scophthalmus maximus* with 100% correlation was the highest pairwise correlation followed by *Alosa sp.* and *Callionymus sp.* with 99%. The stronger negative correlation was *Agonus cataphractus* and *Sardina pilchardus* at negative 40%.

To assess species association and avoidance, the hierarchical cluster analysis was run with absolute values of spatio-temporal correlations and the results were compared to those of the spatial clusters. Indeed, when using the absolute value of spatio-temporal correlation, we statistically associate species with strong correlations regardless of the sign of the correlation (Fig. 6). This defines a new type of community that clusters species that have abundances influenced by the environment in sync or always in opposite fashion. Meaning that when strongly positive the abundance of both species shows similar trends and if strongly negative, they show opposite trends. The most interesting results will be found by crossing positive spatial variations with negative spatio-temporal variations and vice-versa. Revealing species that are always in the same habitat with opposite trends in abundance and species that are never in the same habitat but have

abundance following similar trends. Thirty-two pair-species with positive spatial interactions had negative spatial-temporal variations and fourteen species with negative spatial interactions had positive spatial-temporal interactions. Hence, the absolute spatial-temporal communities were: The AST522c2 statistical community included *Raja clavata*, *Scophthalmus rhombus*, *Zeus faber*, *Sardina pilchardus*, *Raja undulata* and the AST522c1 statistical community included the remaining species. The fourteen species with negative spatial but positive spatial-temporal correlation might represent species located in different spatial niches being influenced by the same large scale factors.

The spatial, spatial-temporal and absolute spatial-temporal distribution of the communities show different organizations. They are respectively featured on maps in Figure 7, 8 and 9. The first spatial community is mainly concentrated in the far side eastern part of the EEC. The second spatial community is represented in higher density closer to the coast at river mouths (Fig. 7). The spatio-temporal communities are strongly separated and are following a West to East gradient. ST522c1 is on the western side with stronger densities to the western center side of the channel and the ST522c2 is more present on the Eastern side of the Channel with a stronger concentration towards the strait of Dover (Fig 8.). The absolute spatio-temporal shows that species from both communities are structured in the same way with high densities in the south-eastern part of the channel and following a strong gradient from east to west (Fig. 9). Figure 10 and 11 show a highly compartmented distribution of *Alosa sp.* and *S. rhombus* respectively.

## **4. Discussion**

The English Channel has been highly studied due to its unique confined topography and the strong environmental and anthropogenic stressors present in the region (Billen *et al.*, 2001).



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Spatial distribution models were applied to CGFS data previously (Martin *et al.*, 2012; Girardin *et al.*, 2016; Bourdaud *et al.*, 2017). However, the main goal of this study was to define a method, combining recent available spatial tools, that can identify communities and their abundance in a statistical framework. The first step of our method was to select species based on statistical rules excluding those with patchy distributions and high variance in abundance. This ended with a selection of 16 of the most evenly distributed and temporarily resilient fraction of the fish and cephalopod community. The first outcome of this study was to show that significant community patterns were evidenced when using only 16/108 species. We are confident here that by studying the structure of the most resilient fraction of the ecosystem we can evaluate how resilient the ecosystem is.

Secondly, our results revealed that the model that fits the CGFS data the best is the 522km<sup>2</sup>, i.e. the smallest scale we studied, rather than 782km<sup>2</sup> and 1043km<sup>2</sup>. Our results also clearly illustrate that, within this CGFS dataset, community patterns vary according to scales when performing a spatial analysis while they remain stable among scales when using a spatio-temporal analysis. The results of the difference in spatial scales are mostly in the supplemental material (Fig. S1-S7).

Moreover, we show how essential it is to consider temporality in spatial studies as omitting it can lead to erroneous conclusions if the wrong spatial scale is used.

Community spatial and spatio-temporal patterns were highly variable given the resolution at which the model was set, but also given the nature of variations considered for the study (i.e. spatial, spatio-temporal or absolute spatio-temporal). Patterns in ecosystems are most often organized according to biogeographic gradients and habitats properties. Indeed, biogeographic patterns are set by environmental gradients like temperature (Mandrak, 1995) and hydrodynamic conditions,

but are also dependent upon the bathymetry and sub-marine topography (Rex *et al.*, 2005; Trancart *et al.*, 2014). Species distribution can also be dependent upon the characteristics of essential habitats (i.e. spawning, nursery, growth, shelter, ...) and the distance between them. This is particularly the case for migratory species as for example Shads (*Alosa sp.*), Horse Mackerels (*Scomber scombrus*) and Sea Bass (*Dicentrarchus labrax*) that will migrate between zones to fulfill the different events of their biological cycle, sometimes covering considerable distances.

#### 4.1. Spatial patterns: Realized Habitat distribution

In this kind of analysis, the model clusters species use the same habitats, regardless of temporal matching. In other words, communities group species that are found in the same habitats but not necessarily at the same time. This results in a variation of the species clusters (i.e. the communities) according to the chosen spatial resolution at which the analysis is performed.

In the Eastern Channel, community patterns vary from large to small scale (Fig. S1-S7, Fig. 2, Fig 4). At all scales, 2 communities are revealed, but they have significantly different compositions. The small 522km<sup>2</sup> scale community patterns reveal two spatial statistical communities (Fig. 2, Fig. 4). At the largest scale of 1043 km<sup>2</sup> two distinct communities are revealed, while more than 1/3 of the species are not assigned to either communities. Moreover, an increase in negative correlations results in more compartmented ecological niches. These niches are the result of heterogeneity in abiotic and biotic factors defining community specific habitat structure (Chesson, 2000).

This study shows that ASTEC can be used to analyze the distribution of species within communities. For example, *Alosa sp.* and *S. Rhombus* distribution map (Fig. 10 and Fig. 11) are

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mainly concentrated in habitats with specific properties covering a small surface of the EEC: estuaries with turbid shallow waters, and high nutrient concentrations. For these species, our results suggest that strong anthropogenic disturbance or habitat destruction in these areas would lead to significant abundance loss for these species (Gibson, 1994; McConnaughey and Smith, 2000). The spatial scenario helps assess ecological realized niches and can be used as a community conservation or habitat conservation tool.

### 4.2. Spatio-temporal analysis reveal biogeographical patterns

Additionally, to spatial pairing, the spatio-temporal scenario pairs species given how they respond to the temporal environmental changes. i.e. spatio-temporal analysis allows us to identify species that will similarly be affected by climate change. This is essential for setting efficient management strategies in the long term. Spatio-temporal analyses are used to cluster species to which the abundance responds to external pressure similarly and that are often found in the same habitat. Interestingly, the community patterns did not change significantly according to spatial resolution of the analysis: two sub communities were observed for the three spatial resolutions which were tested in the Eastern Channel. This emphasizes that modeling spatio-temporal variations reveal biogeographical patterns.

The EEC is separated in two fundamental niches, from East to West (Fig. 8). The first statistical community consists of two sub-communities: *T. lastoviza*, *G. galeus*, *S. stellaris* and *R. clavata*, *R. undulata* (Fig. 3, Fig. 5). This community is localized in the west of the Seine river with abundance peaks in the Bay of Veys, the entrance of the Seine river and the center of the channel. The second statistical community includes two sub-communities: *A. cataphractus*, *C. lucernus*, *M.*

*merlangus*, *Callionymus sp.*, *S. rhombus*, *Alosa sp.*, *S. maximus*, and *S. scombrus*, *Z. faber*, *Loligo sp.*, *S. pilchardus*. They are localized in the East of the EEC with the highest abundance at the shallower estuaries and areas with muddy sediments. Vaz *et al.* (2007) multivariate and spatial analysis provided bathymetric maps that helped us confirm the nature of the habitat for these communities. This allowed us to speculate that the very abundant *Solea* and *Pleuronectes platessa* often found in such habitat (that were not selected in our species list due to their fragmented distribution) would be mostly grouped in the ST522c2 statistical community with flatfish. The species within spatial-temporal communities present stronger correlations than spatial communities as they are strengthened by similar fluctuations in abundance. These fluctuations are forced by biogeographic factors that shaped two areas. These areas coincide with areas of highest disturbance in sediments due to currents, waves and storms. Disturbance does not only affect the abundance of species through limiting or increasing food availability and modifying habitat quality (Grime, 1977), but is also defined as temporal persistence of habitat structure (Foveau *et al.*, 2017). ASTEC reveals that there are significant differences in structure within and between communities when considering temporality. Spatial study focuses on the habitat and can be useful in implementing spatial management tools at a small scale (e.g. marine protected areas). However important, it becomes unreliable in studying the effect of climate change or large-scale anthropogenic pressures or even when studying the impact of a web of marine protected areas. This is due to the lack of temporal dynamics (e.g. species replacement, functional redundancy) in a spatial study. Spatial study assumes temporal uniformity which has been proven untrue. Time plays an important role in how species respond to climate change through processes like population plasticity; thus species redundancy (Valladares *et al.*, 2014) need to be included in

climate change studies. The effect of these processes can be read in the structure of the communities via studying both spatial and spatio-temporal variations. Moreover, using combined spatial and temporal variations to study spatial ecology resolves the issue of choosing an appropriate spatial scale described in Levin (1992).

#### 4.3. Absolute Spatio-temporal: Distribution shifts

To understand shifts of species in space and time we combined the results of the spatial correlation matrix with the absolute values of the spatio-temporal correlation matrix. Spatio-temporal matrix shows the co-variance of species distribution in sync (if strongly positive) or in perfect opposite trends (if strongly negative). The spatial correlation matrixes enable to distinguish between positive and negative correlations, in other words co-occurrence and avoidance between species. When negative spatio-temporal correlations exist between species that are found in the same habitats, it means that they are temporally mutually exclusive. These cases are interesting to examine, because they might reveal species replacement in time, i.e. according to oceanographic regime shifts such as temperature changes.

At the smallest scale, which most parsimoniously fits the CGFS data with (Tab. 2), 32 pair-species interactions occur in the same areas but with opposite trends in abundance. This leads to the conclusion that these species are shifting over time in a community given environmental conditions. These interactions are referred to in this paper as absolute spatio-temporal interactions. Hence in the AST522c2 community, when the environment regime is favorable for species like *S. pilchardus* and *S. scombrus* (Vert-pre *et al.*, 2013) it is unfavorable for *R. clavata* and *R. undulata* (Fig. 6). Moreover, the overall abundance trend from 1995 to 2014 are decreasing for *S.*

*pilchardus* and *S. scombrus* while increasing for *R. clavata* and *R. undulata* (Fig. S13 – Fig. S16). The defined communities explain how the ecosystem would reorganize spatially over time presumably following a more heterogeneous and resilient structure (Fig. 9) (Ives and Carpenter; 2007).

This suggests ASTEC can capture the relative impact of global environmental change on community patterns. These results become crucial when studying resilience of an ecosystem to climate change, environmental shifts or strong anthropogenic pressures. They also provide valuable information when it comes to disruption of community structure due to species invasion. ASTEC is less computing and data demanding than a full ecosystem model for prospecting the occurrence of replacement within communities and how the shift affects spatial-temporal patterns. Thus, it can be a good alternative to inform managers in data poor or data moderate environment. Moreover, this study suggests that spatial models are to be used with caution when defining spatial community patterns. In ecology, the tendency among scientists has been to focus on spatial models when studying patterns. However, these results show that spatial models lack some crucial information when it comes to understanding ecosystem responses to environmental changes. We also recommend using ASTEC to define spatial-temporal communities and emphasize species shifts between communities. This model is a fitting new tool for assessing how community structure within a given ecosystem would respond to species invasion or other external pressure. This model is explorative and did not include some of the most abundant species of the EEC ecosystem. However, the model represented the most resilient species with the largest spatial representation in the EEC. ASTEC enables us to take a step towards assessing functional structure of communities and indicating the resilience of an ecosystem facing environmental shifts and climate change.

## Tables

Table 1: Code and name for the sixteen studied species.

Code	Species name
AGONCAT	<i>Agonus cataphractus</i>
ALOS	<i>Alosa sp.</i>
CALM	<i>Callionymus sp.</i>
CHELLUC	<i>Chelidonichthys lucernus</i>
GALOGAL	<i>Galeorhinus galeus</i>
LOLI	<i>Loligo sp.</i>
MERNMER	<i>Merlangius merlangus</i>
RAJACLA	<i>Raja clavata</i>
RAJAUND	<i>Raja undulata</i>
SARDPIL	<i>Sardina pilchardus</i>
SCOMSCO	<i>Scomber scombrus</i>
SCOPMAX	<i>Scophthalmus maximus</i>
SCOPRHO	<i>Scophthalmus rhombus</i>
SCYOSTE	<i>Scyliorhinus stellaris</i>
TRGPLAS	<i>Trigloporus lastoviza</i>

<b>ZEUSFAB</b>	<i>Zeus faber</i>
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Table 2: Maximum gradient, Akaike criteria and number of coefficients for the VAST model at 522km<sup>2</sup>, 782km<sup>2</sup> and 1043km<sup>2</sup> scales.

Scale in km <sup>2</sup>	Maximum gradient	AIC	Number of Coefficients		
			Total	Fixed	Random
522	7.701651e-06	115036	58346	431	57915
782	2.432513e-05	115218	57486	431	57055
1043	2.390698e-05	115283	57056	431	56625

Table 3: Random and fixed effect for the VAST model at 522km<sup>2</sup>, 782km<sup>2</sup> and 1043km<sup>2</sup> scales.

Scale in km <sup>2</sup>	522	782	1043	
<b>n_x</b>	60	40	30	
<b>beta1_ct</b>	16	16	16	Fixed
<b>beta2_ct</b>	320	320	320	Fixed
<b>L_epsilon2_z</b>	31	31	31	Fixed
<b>L_omega2_z</b>	45	45	45	Fixed
<b>ln_H_input</b>	2	2	2	Fixed
<b>logkappa2</b>	1	1	1	Fixed
<b>L2_z</b>	16	16	16	Fixed
<b>eta2_vf</b>	54647	54647	54647	Random
<b>Epsiloninput2_sft</b>	3040	2240	1840	Random
<b>Omegainput2_sf</b>	228	168	138	Random



## Figures

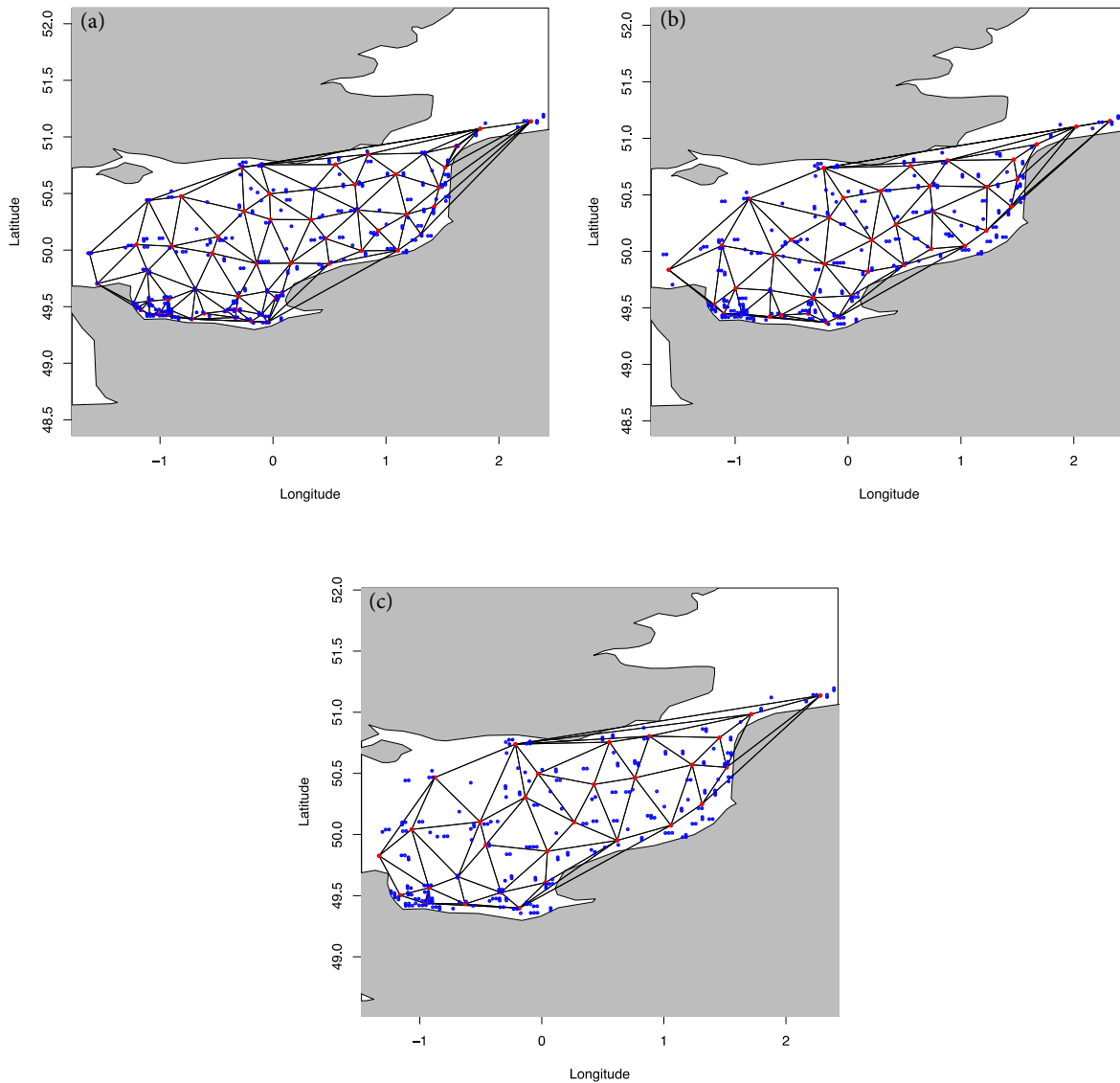


Figure 1: Eastern English Channel spatial grid using a triangular mesh at a  $522\text{km}^2$  (a),  $782\text{km}^2$  (b) and  $1043\text{km}^2$  (c) average scale with the geographic coordinates in WGS84 of all the English

Channel groundfish hauls survey from 1995 to 2014 (blue). The red points are the vertices used to define the mesh.

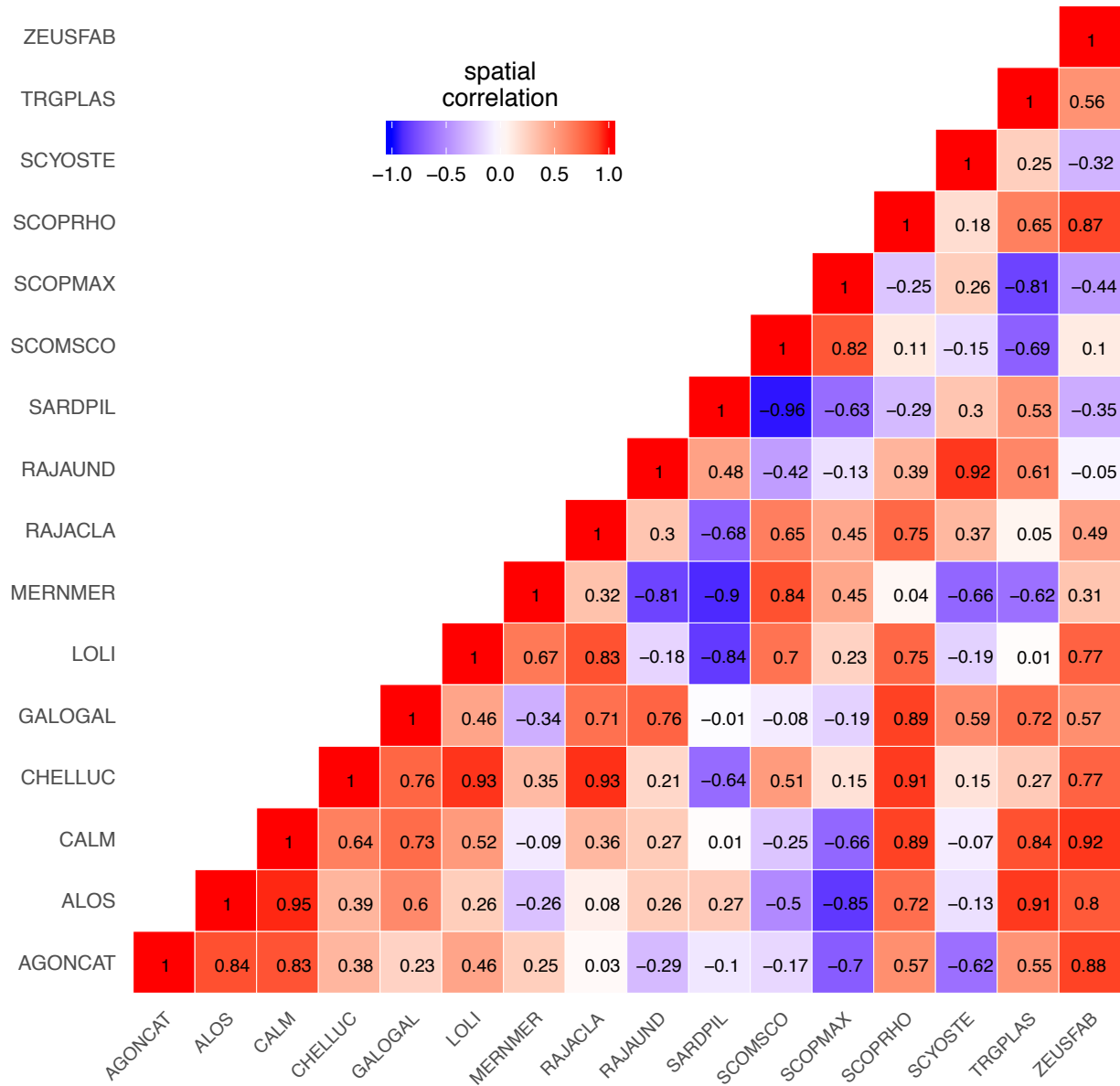


Figure 2: Spatial correlation matrix at a 522km<sup>2</sup> scale displaying correlation from strongly negative (dark blue) to strongly positive (dark red).

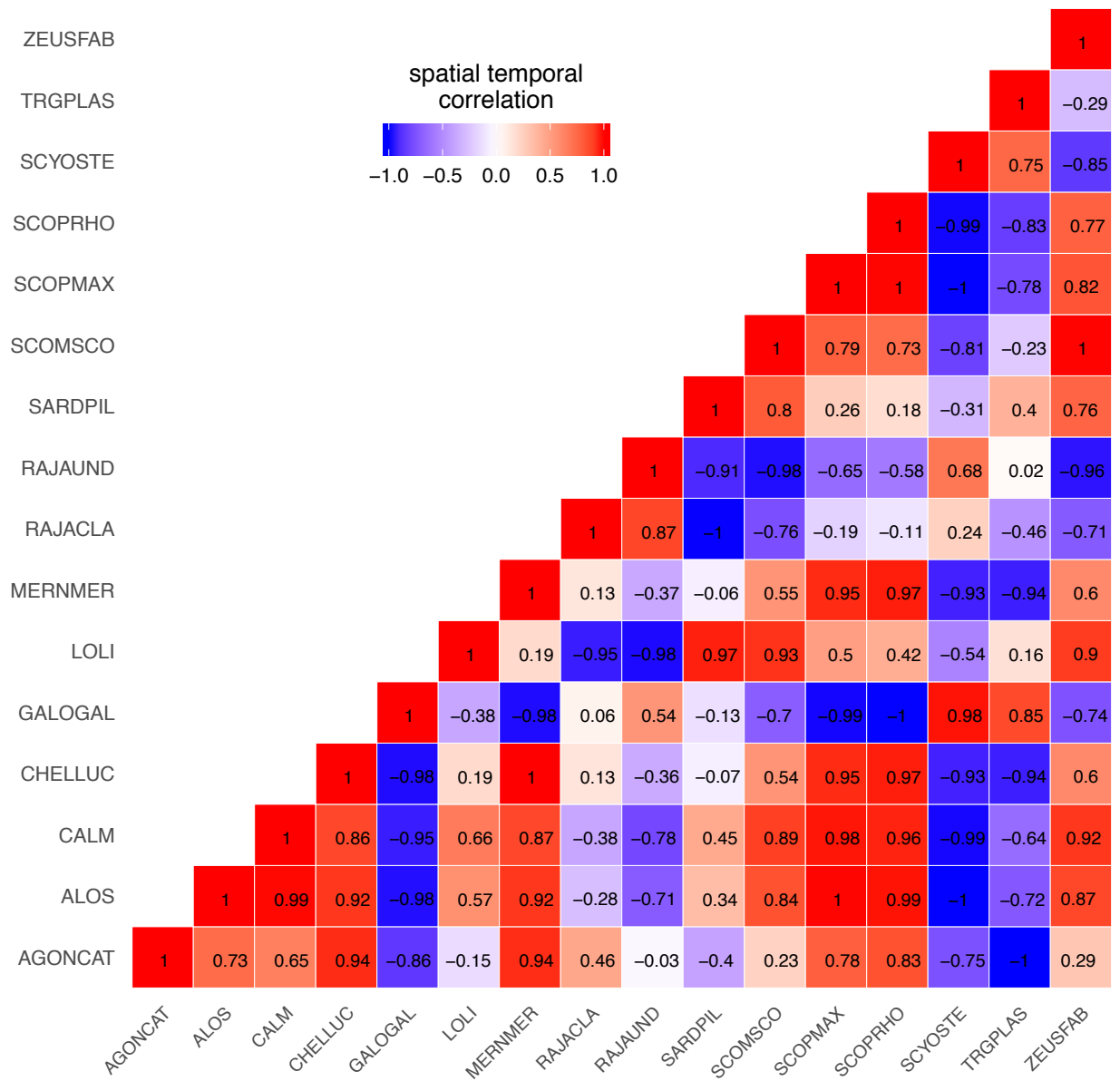


Figure 3: Spatial-temporal correlation matrix at a 522km<sup>2</sup> scale displaying correlation from strongly negative (dark blue) to strongly positive (dark red).

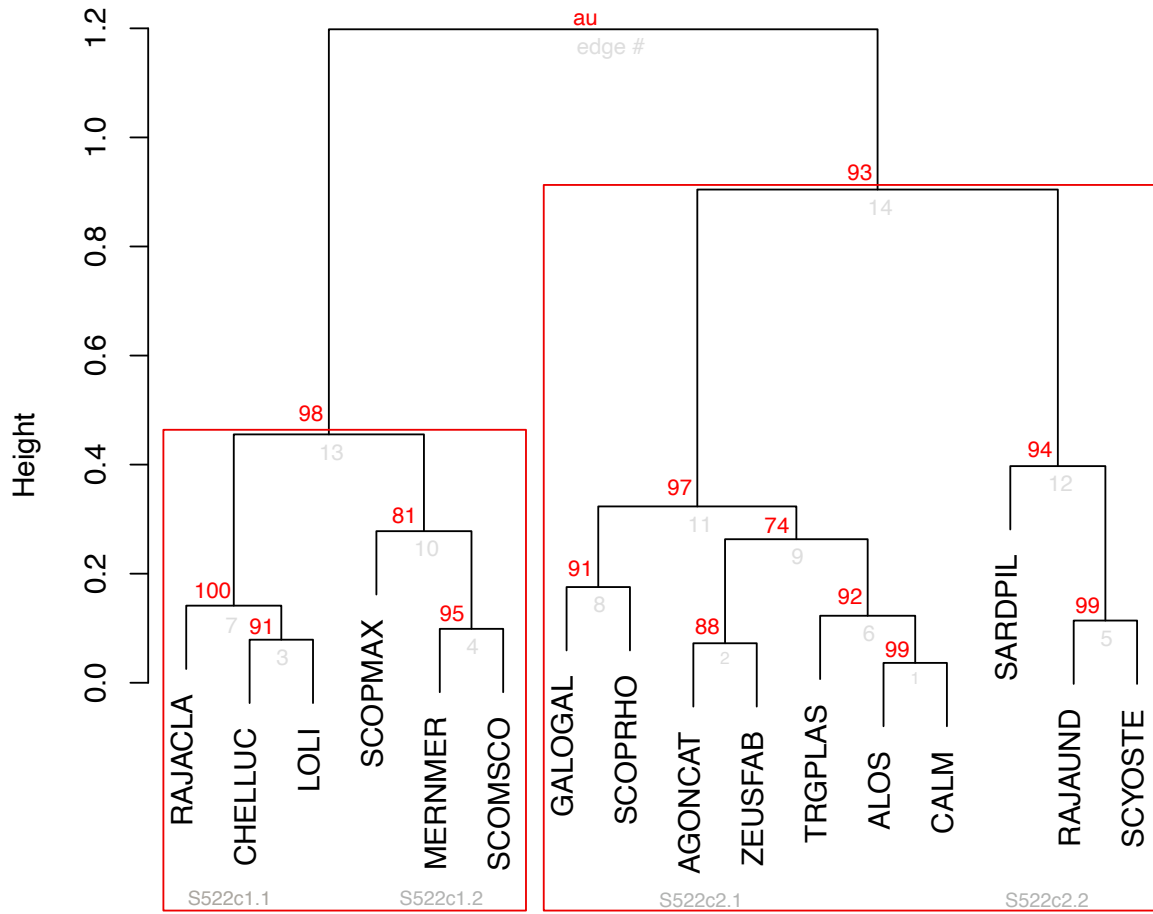


Figure 4: Spatial hierarchical clustering at a 522km<sup>2</sup> scale. The rectangle outlines the communities that were statistically significant by ASTEC given the approximately unbiased p-values expressed in percentage (red). The light grey numbers represent the edge number of the tree.

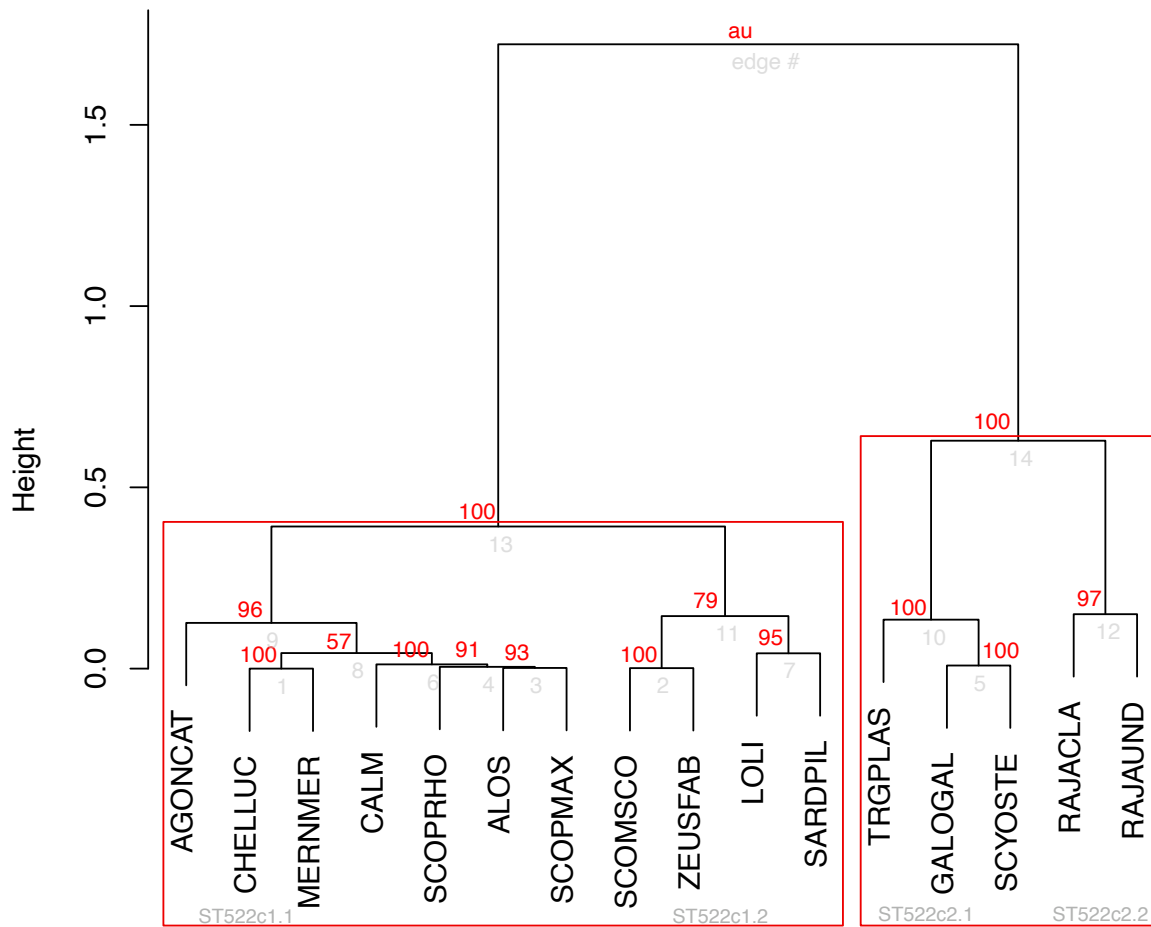


Figure 5: Spatial-temporal hierarchical clustering at a 522km<sup>2</sup> scale. The rectangle outlines the communities that were found statistically significant by ASTEC given the approximately unbiased p-values in percentage (red). The light grey numbers represent the edge number of the tree.

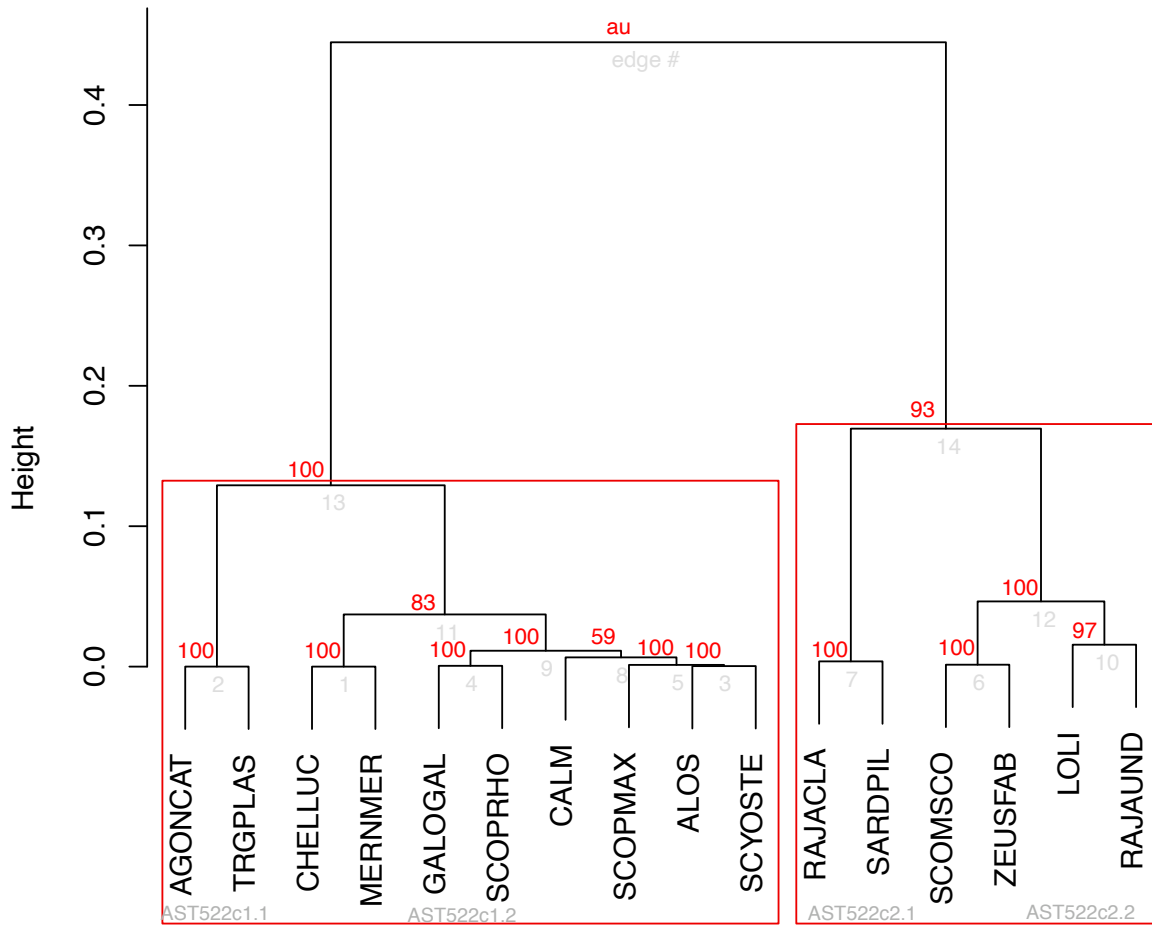


Figure 6: Absolute values of spatial-temporal hierarchical clustering at a 522km<sup>2</sup> scale. The rectangle outlines the communities that were found statistically significant by ASTEC given the approximately unbiased p-values in percentage (red). The light grey numbers represent the edge number of the tree.

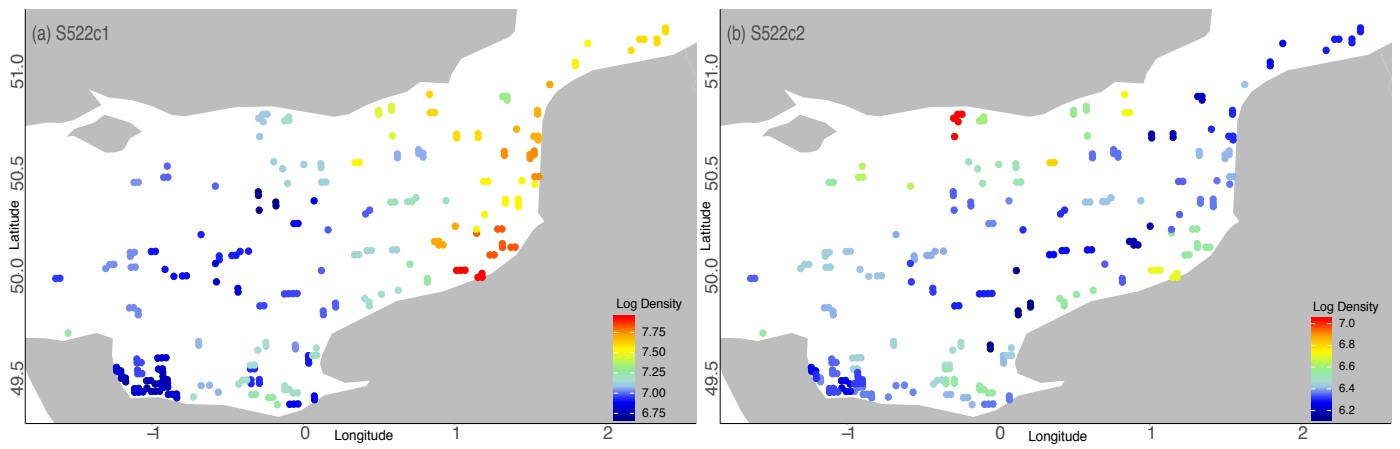


Figure 7: Eastern English Channel spatial community from low (blue) to high (red) median densities of numbers/ km<sup>2</sup> in log scale are mapped, S522c1 (a), S522c2 (b).

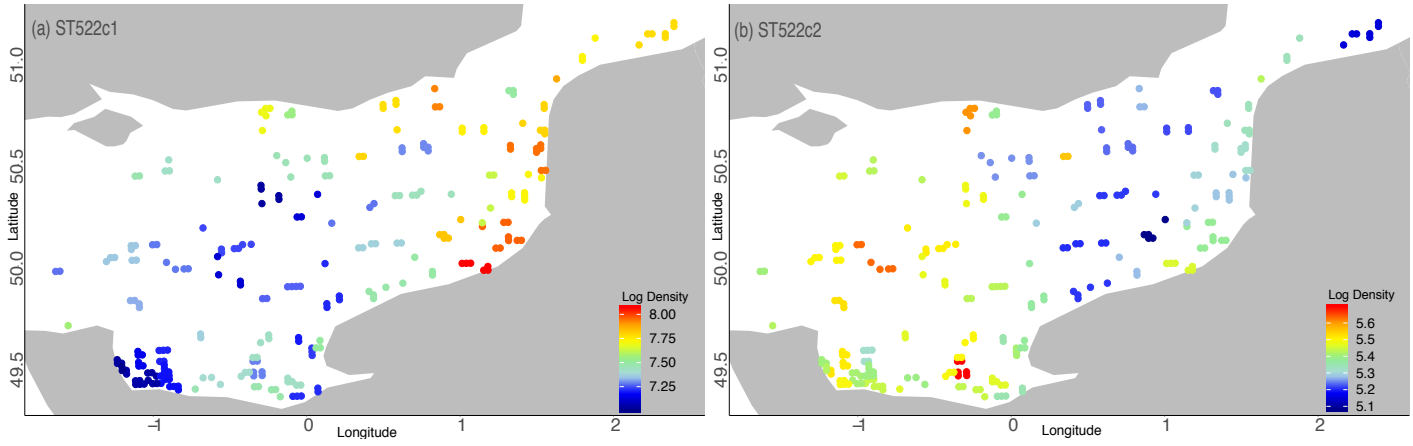


Figure 8: Eastern English Channel spatio-temporal community from low (blue) to high (red) median densities of numbers/ km<sup>2</sup> in log scale for communities ST522c1 (a), ST522c2 (b).



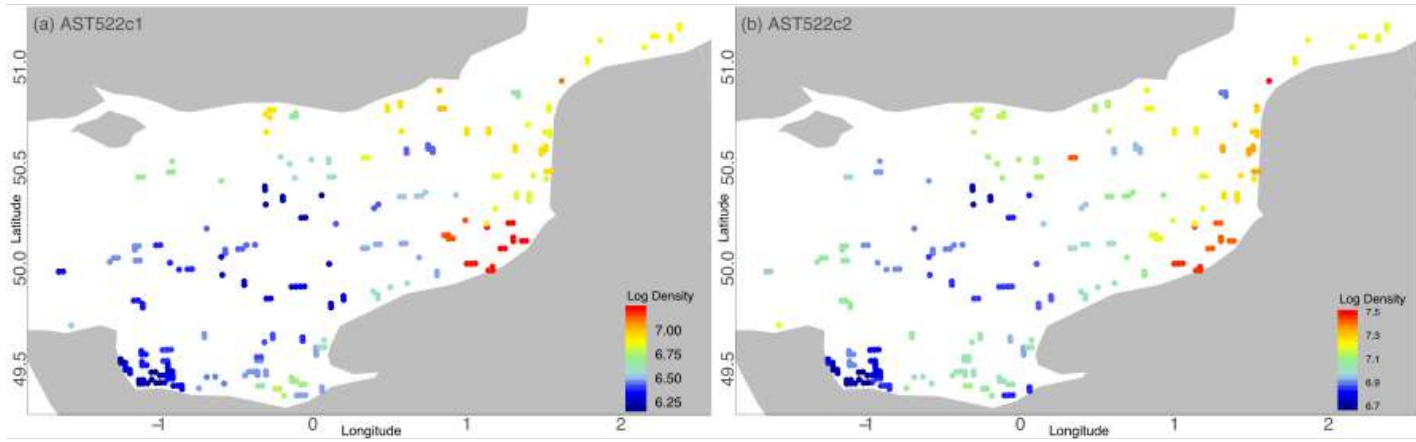


Figure 9: Eastern English Channel absolute spatio-temporal community from low (blue) to high (red) median densities of numbers/ km<sup>2</sup> in log scale for communities, AST522c1 (a), AST522c2 (b).

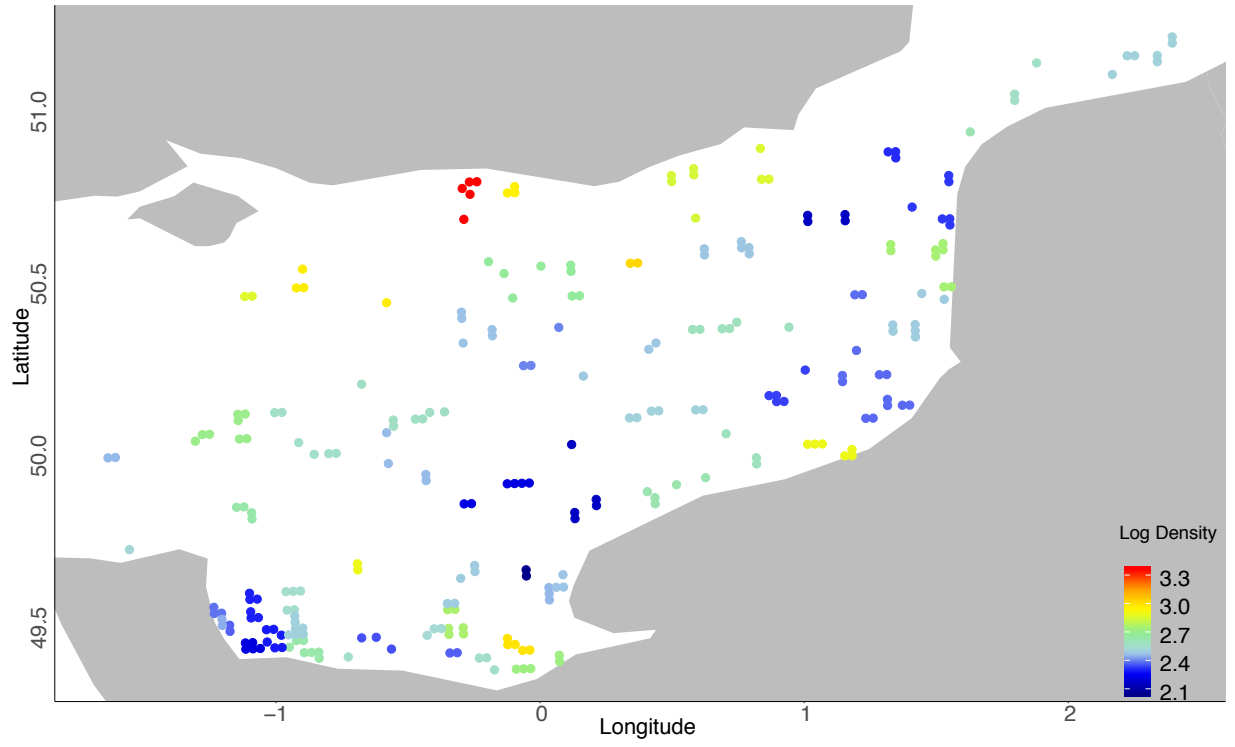


Figure 10: *Alosa* sp. from low(blue) to high(red) median densities of numbers/ km<sup>2</sup> in log scale for 522km<sup>2</sup>, for the Eastern English Channel.

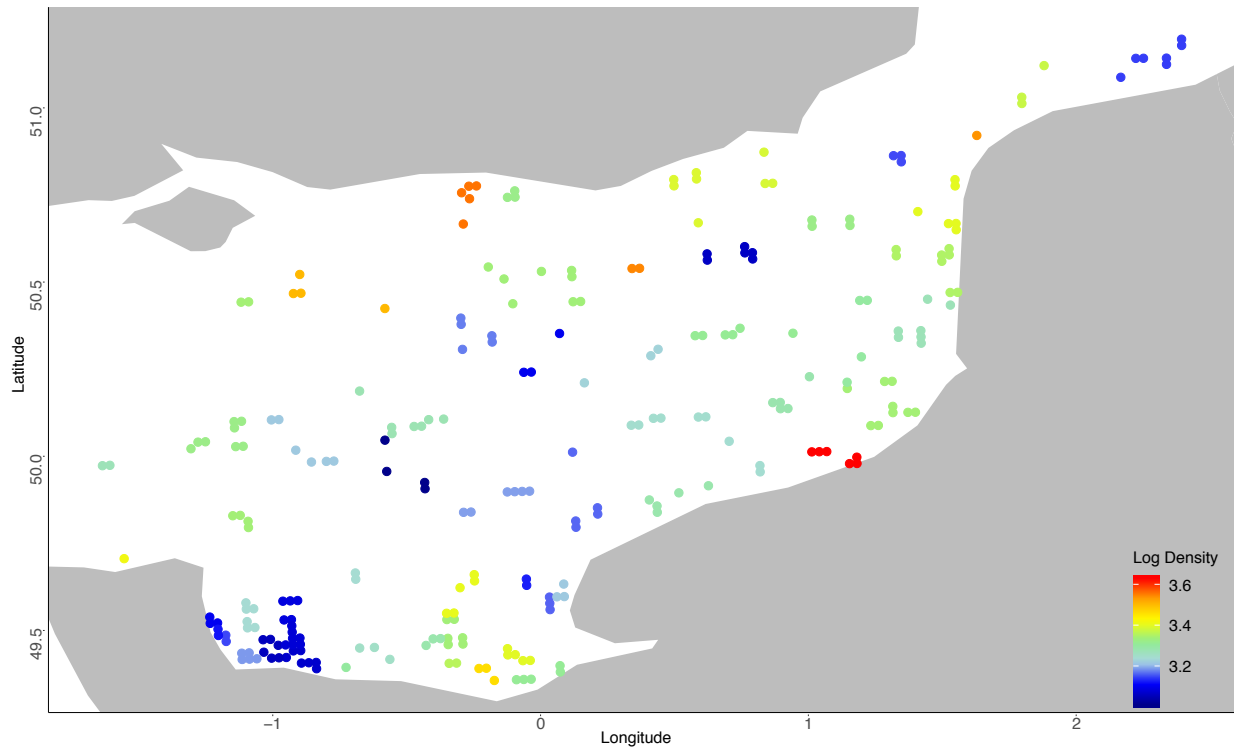


Figure 11: *S. rhombus*. from low (blue) to high (red) median densities of numbers/ km<sup>2</sup> in log scale for 522km<sup>2</sup> for the Eastern English Channel.

# Chapter 2. Supplemental materials of Spatio-Temporal Patterns in Marine Fish Communities Across Scales: using an Autoregressive Spatial Temporal Clustering Model: A study of fish and cephalopods of the Eastern English Channel

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Short title      Spatio-Temporal Patterns in Marine Fish Communities Across Scales

## **1. Supplemental Introduction**

Many studies of the patterns of ecological processes use a non-appropriate scale for the intent (Cooper *et al.*, 1998). Levin (1992) stated that ecosystem patterns occurring at a smaller scale are revealing of a structure in processes from a larger scale. However, in evolution ecology and population biology, processes and patterns that play out on different scales are related to one another and have critical effects on the predictions and scientific conclusions drawn about ecosystem, community and population structure, distribution and patterns (Power, 1990, 1992). Major scientific studies have warned about potential errors when inferring small-scale process from patterns arising at large scales (Winemiller and Polis, 1996; Hetherington and Woodward, 2003) because pattern determination is typically scale-dependent. Suzuki *et al.*, (2005) showed that aggregated patterns of plants are often scale-dependent. Hutchinson (1953) found that species patch distribution varied with the scale of observation. A common assumption is that these patches, often referred to as clusters of species, are organized with spatial redundancy. The spatio-temporal redundancy of patterns has major influence on assessing the resilience of communities or ecosystems (Ives and Carpenter, 2007). Defining repetitive patterns is also beneficial for increasing accuracy in predictions of ecosystem processes, species distribution and abundance (MacArthur, 1972). Thus, species assemblages, distribution and distribution patterns very likely depend upon the scale at which the analyses are performed. In this supplement, we used ASTEC model described in the main paper to analyze the effect of scaling on assemblage structure, distribution and distribution patterns.

## 2. Supplemental Methods

To this end, we changed the number of knots from 30 to 40 and 60 knots. In turn this changed the average resolution from 1043 square kilometers to 782 and 522 square kilometers. Then, we used AIC model selection to identify the most parsimonious model between scales. The entire set of analysis and packages used for ASTEC was coded in R version 3.4.2 (R Core Team, 2017). This analysis was repeated when separately considering spatial patterns, spatio-temporal patterns and absolute spatio-temporal patterns (e.g. a combination of spatial and spatio-temporal patterns).

## 3. Supplemental Results

### 3.1. Spatial patterns

In Figure S3b, five species, forming a non-statistical community, did not belong to any cluster at the 1043km<sup>2</sup> scale. This community comprised three shallow and deeper water elasmobranchs (*Scyliorhinus stellaris* (Linnaeus, 1758), *Raja undulata* (Lacepède, 1802) and *Galeorhinus galeus* (Linnaeus, 1758)) and *Sardina pilchardus* (Walbaum, 1792) and *Trigloporus lastoviza* (Bonnaterre, 1788). These two latter species had correlations ranging from 60 to 70% with the elasmobranchs. Spatial correlation between *Scyliorhinus stellaris* and *Raja undulata* were the strongest with 78% (Fig. S1b). The weakest correlations were -0.03% between *Sardina pilchardus* and *Galeorhinus galeus*, 20% for the *Scyliorhinus stellaris* and *Galeorhinus galeus* pair and 31% for *Scyliorhinus stellaris* and *Trigloporus lastoviza*.

Spatial correlations in the two statistical communities were on average stronger than in the non-statistical community. The community S1043sc1, displayed correlation ranging from 34% between

### *Supplemental of spatio-temporal patterns in communities*

*Scophthalmus maximus* (Linnaeus, 1758) and *Merlangius merlangus* (Linnaeus, 1758) to a high of 91% between *Raja clavata* (Linnaeus, 1758) and *Scophthalmus maximus*. This community had a total of six species including *Chelidonichthys lucernus* (Linnaeus, 1758), *Loligo* sp. (Lamarck, 1798), *Merlangius merlangus* and *Scomber scombrus* (Linnaeus, 1758) (Fig. 4). The second community, S1043sc2 correlations ranged from a low 57% between *Agonus cataphractus* (Linnaeus, 1758) and *Callionymus* sp. (Linnaeus, 1758) to a high 99% between *Scophthalmus rhombus* (Linnaeus, 1758) and *Callionymus* sp.

At finer 782km<sup>2</sup> and 522km<sup>2</sup> scales, the species that were non-assigned to a community at the 1043km<sup>2</sup> scale were merged to S782c2 and S522c2 statistical community respectively. *Scophthalmus rhombus* pertained to the S782c2 statistical community at 782km<sup>2</sup> and to the S522c1 statistical community at 522km<sup>2</sup> scale. At the 522km<sup>2</sup> scale, the S522c1 spatial statistical community presented two sub-communities: *Raja clavata*, *Chelidonichthys lucernus*, *Loligo* sp. (S522c1.1) and *Scophthalmus maximus*, *Merlangius merlangus*, *Scomber scombrus* (S522c1.2). The S522c2 statistical community constituted of two sub-communities: *Galeorhinus galeus*, *Scophthalmus rhombus*, *Agonus cataphractus*, *Zeus faber* (Linnaeus, 1758), *Trigloporus lastoviza*, *Alosa* sp., *Callionymus* sp. (S522sc2.1) and *Sardina pilchardus*, *Raja undulata*, *Scyliorhinus stellaris* (S522sc2.2). In the S522c1 community, the pairwise spatial correlations were the highest for *Chelidonichthys lucernus* and *Loligo* sp. with 93%, *Raja clavata* and *Chelidonichthys lucernus* with 93%, and *Raja clavata* and *Loligo* sp. with 83%. In the S522c2 community, for pairwise association the spatial correlation ranged from *Alosa* sp. (Linnaeus, 1758) and *Callionymus* sp. with 95%, *Raja undulata* and *Scyliorhinus stellaris* with 92%, to *Agonus cataphractus* and *Zeus faber* with 88%.

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At 782km<sup>2</sup>, in the S782c1 community the pairwise spatial correlations ranged from *Scomber scombrus* and *Scophthalmus rhombus* with -53%, to *Raja clavata* and *Chelidonichthys lucernus* with 91%, *Chelidonichthys lucernus* and *Loligo sp.* or *Chelidonichthys lucernus* and *Scophthalmus rhombus* both with 92%. From a larger to smaller scale, rare correlations got gradually stronger (e.g. *Agonus cataphractus* and *Alosa sp.* strengthened from 61% at 1043km<sup>2</sup> to 79% at 26 km<sup>2</sup> to 84% at 522km<sup>2</sup>, or *Agonus cataphractus* and *Callionymus sp.* strengthened from 57% to 59% and 83%). However, most correlations remained more or less stable whatever the scale (e.g. *Galeorhinus galeus* and *Trigloporus lastoviza*, *Sardina pilchardus* and *Trigloporus lastoviza*, *Agonus cataphractus* and *Zeus faber* stayed on average 70%, 60%, and 90% respectively). Many spatial correlations decreased with the scale (e.g. *Scyliorhinus stellaris* and *Sardina pilchardus*, *Merlangius merlangus* and *Loligo sp.* decreased from 66% to 44% and 30% and from 88% to 78% and 67%). The 782km<sup>2</sup> appeared to be a transitional scale as it presented numerous negative interactions between species, e.g. *Sardina pilchardus* and *Zeus faber*, *Alosa sp.* and *Raja undulata* with -40% and -39%.

The large-scale, 1043km<sup>2</sup> patterns are organized in three distinct communities ranging from East to West (Fig. 7a-b-c) composed of two statistically significant and one non-statistically significant communities (Fig. S3). These communities align with a bathymetric and mean bottom temperature gradient mapped in Vaz *et al.*, (2007). The farthest West non-statistical community is composed mainly of either shallow or deeper water elasmobranchs. These species were found between 33 to 80 meters and at mean bottom temperatures varying between 14.7 and 16 degrees Celsius (Vaz *et al.* 2007). Its distribution ranged from the North (England) to the South (France) bank (Fig. 7c); with spatial interactions, up to 78% between *Scyliorhinus stellaris* and *Raja undulata* (Fig. 4).

However, in the same community, two species, *Sardina pilchardus* and *Trigloporus lastoviza* present



strong interactions - up to 70% with some species of elasmobranches - whereas a weak 31% with others. Moreover, these two species show weak spatial interactions between each other. This is concurrent with the fact that, at 1043km<sup>2</sup>, these two species usually do not share the same realized niche as defined by Hutchinson (1957), MacArthur (1958) and Chesson (1991). These findings are confirmed by the two sub-communities' patterns, pertaining to this large fundamental niche, part of two distinct realized niches. The first niche hosts species with temperature preference between 14.7 and 15.3 degrees Celsius. The second community hosts species with temperature preference between 15.4 to 16 degrees Celsius. In a similar distribution following bathymetry and mean sea bottom temperature gradients, the second community represents species with a depth range between 10 and 44 meters and temperature preference between 15.4 and 17 degrees Celsius with species more abundant closer to the coast (Fig. 7b). They are found more abundantly around estuaries and muddy or sandy sediment (i.e. associated to the river Somme, Seine, Canche, Authie, and Solent) (Foveau *et al.*, 2017). They use the inshore of the Eastern English Channel (EEC) as spawning grounds like, *Agonus cataphractus*, *Callionymus sp.*, *Zeus faber* (Dunn, 2001) or the anadromous shad *Alosa sp.* that spawns in rivers (Bagliniere *et al.*, 2003) (Fig. 10c). The strongest correlation is 99% between *Scophthalmus rhombus* and *Callionymus sp.* (Fig. 2). These benthic species are found on soft bottoms all year long. The small range *Callionymus sp.* is sedentary and the *S. rhombus* is thought to spawn in shallow waters. The first community represents species with preferred shallow waters and warmer temperature between 16.7 to 17.0 degrees Celsius. The area corresponds to a large fundamental niche with two smaller realized niches. This explains the unusual grouping of bottom dwellers as *C. lucernus*, *R. clavata* and *S. maximus*, a demersal species *M. merlangus* and pelagic species as the squid *Loligo sp.* and the mackerel *S. scombrus*. At 1043km<sup>2</sup>, the

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three communities are organized in three fundamental niches following biogeographic gradients, here bathymetric and bottom temperature. Similar findings were presented by Rogers *et al.*, (1998), and Ellis *et al.*, (2000).

### 3.2. Spatio-temporal patterns

The community patterns defined using spatio-temporal variations varied widely from the spatial scenario. However, contrary to spatial community, the two statistical spatial-temporal communities remained stable in species richness and composition across spatial scale (Fig. S4). The statistical community ST522c2, ST782c2, or ST1043c2 constituted of *Trigloporus lastoviza*, *Galeorhinus galeus*, *Scyliorhinus stellaris*, *Raja clavata* and *Raja undulata*. The statistical community ST522c1, ST782c1, or ST1043c1 included two sub-communities: *Agonus cataphractus*, *Chelidonichthys lucernus*, *Merlangius merlangus*, *Callionymus sp.*, *Scophthalmus rhombus*, *Alosa sp.*, *Scophthalmus maximus*, and *Scomber scombrus*, *Zeus faber*, *Loligo sp.*, *Sardina pilchardus*. In the ST522c2, ST782c2, or ST1043c2 community, most pairwise correlations were stronger when considering temporal variations, which explained the stability of this community across spatial scale (e.g. *Alosa sp.* and *Callionymus sp.* showed a 99% spatial temporal correlation instead of a 95% spatial correlations). However, some correlation can be weaker (e.g. *Chelidonichthys lucernus* and *Loligo sp.* featured a 19% instead of 93%).

In the ST522c1, ST782c1, and ST1043c1 communities, *Alosa sp.* and *Scophthalmus maximus* with 100% correlation was the highest pairwise correlation followed by *Alosa sp.* and *Callionymus sp.* with 99% to 100%. The stronger negative correlations on all scales were *Agonus cataphractus* and

*Sardina pilchardus* at 40%. Sub-communities showed strong correlations averaging 80 to 90% among them with very little correlation strength variation across scale.

Supplemental Figures

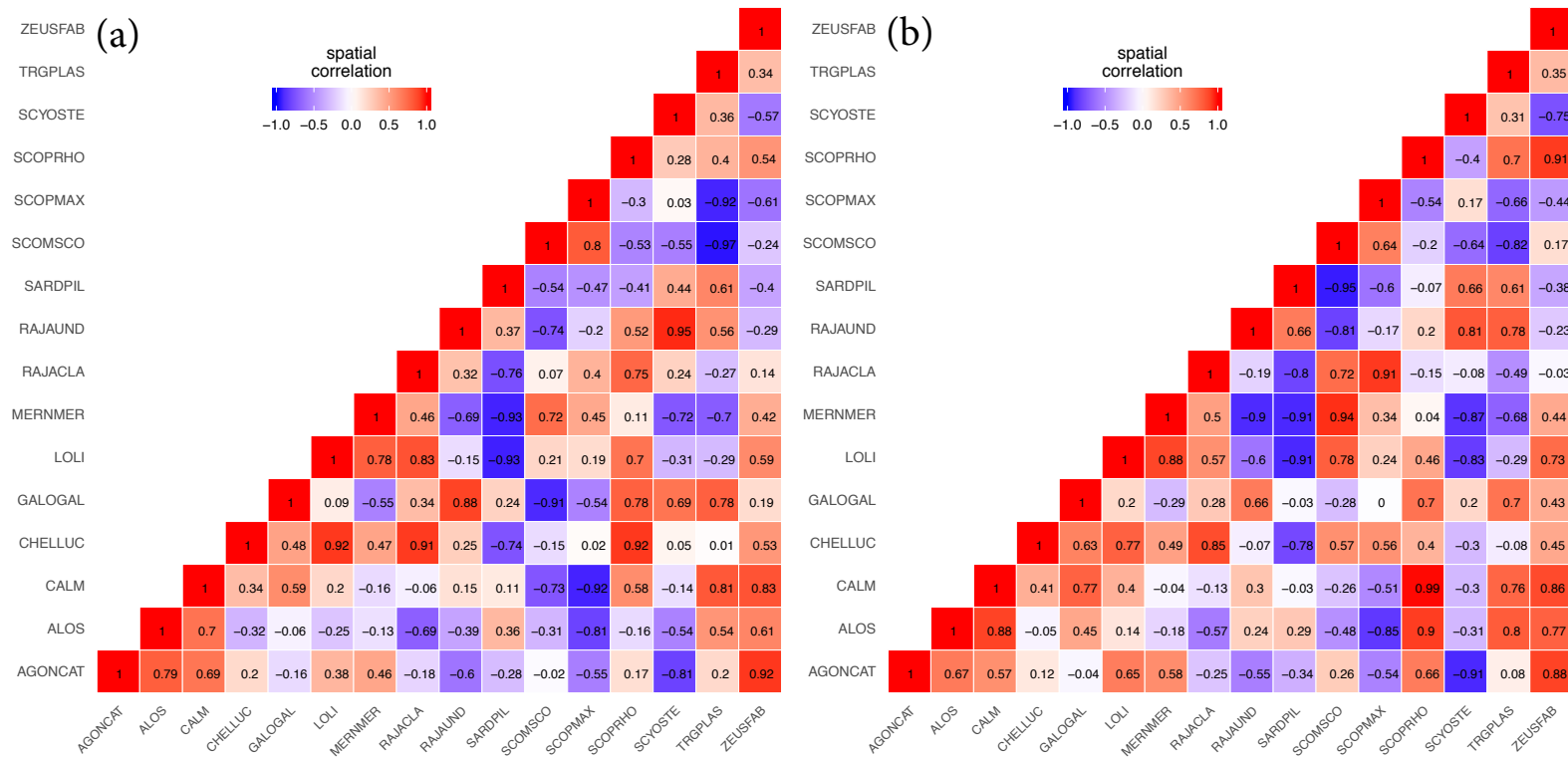


Figure S1: Spatial correlation matrix at a 782km<sup>2</sup> (a) and 1043km<sup>2</sup> (b) scale displaying correlation from strongly negative (dark blue) to strongly positive (dark red).

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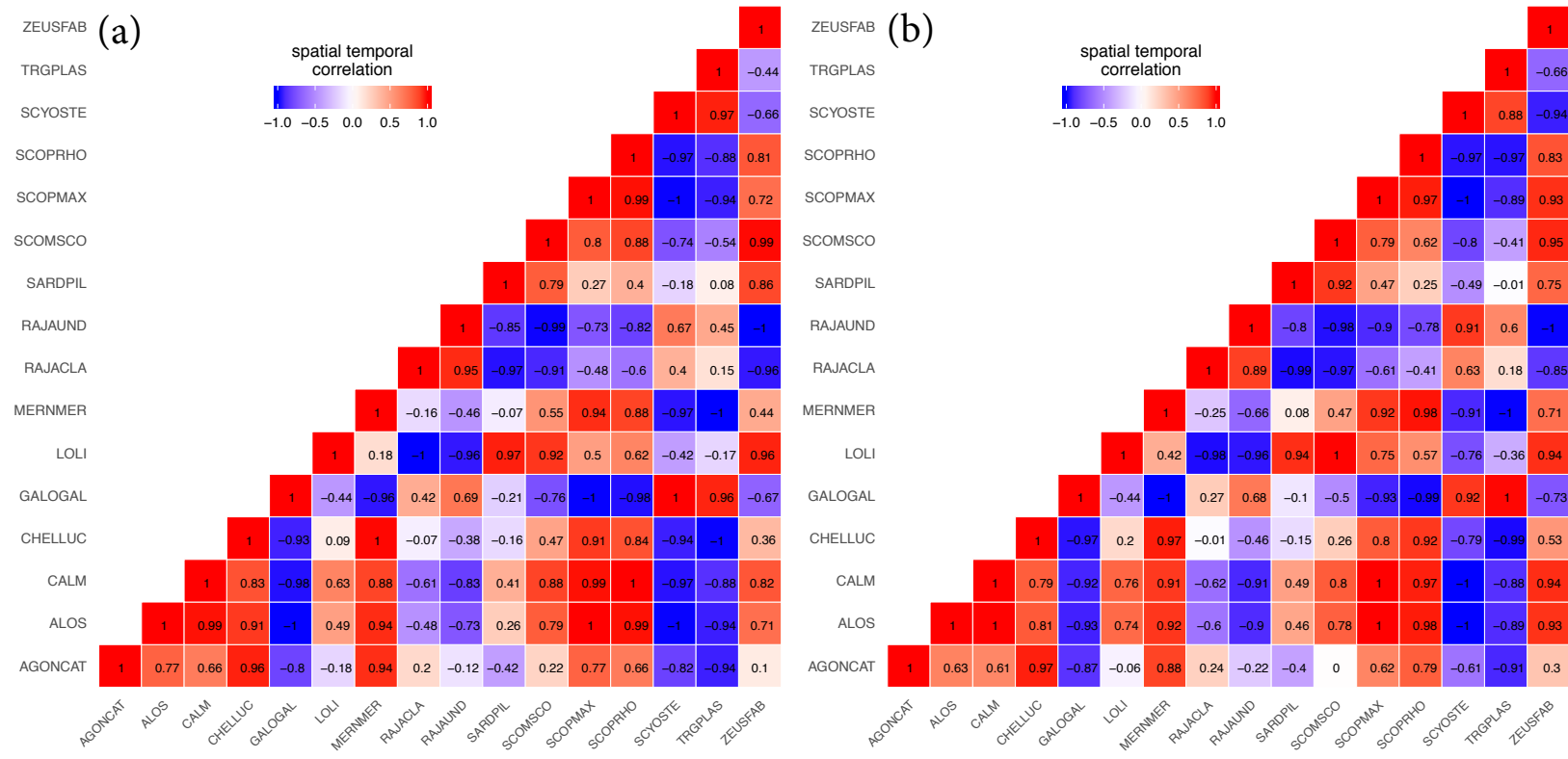


Figure S2: Spatial-temporal correlation matrix at a 782km<sup>2</sup> (a) and 1043km<sup>2</sup> (b) scale displaying correlation from strongly negative (dark blue) to strongly positive (dark red).

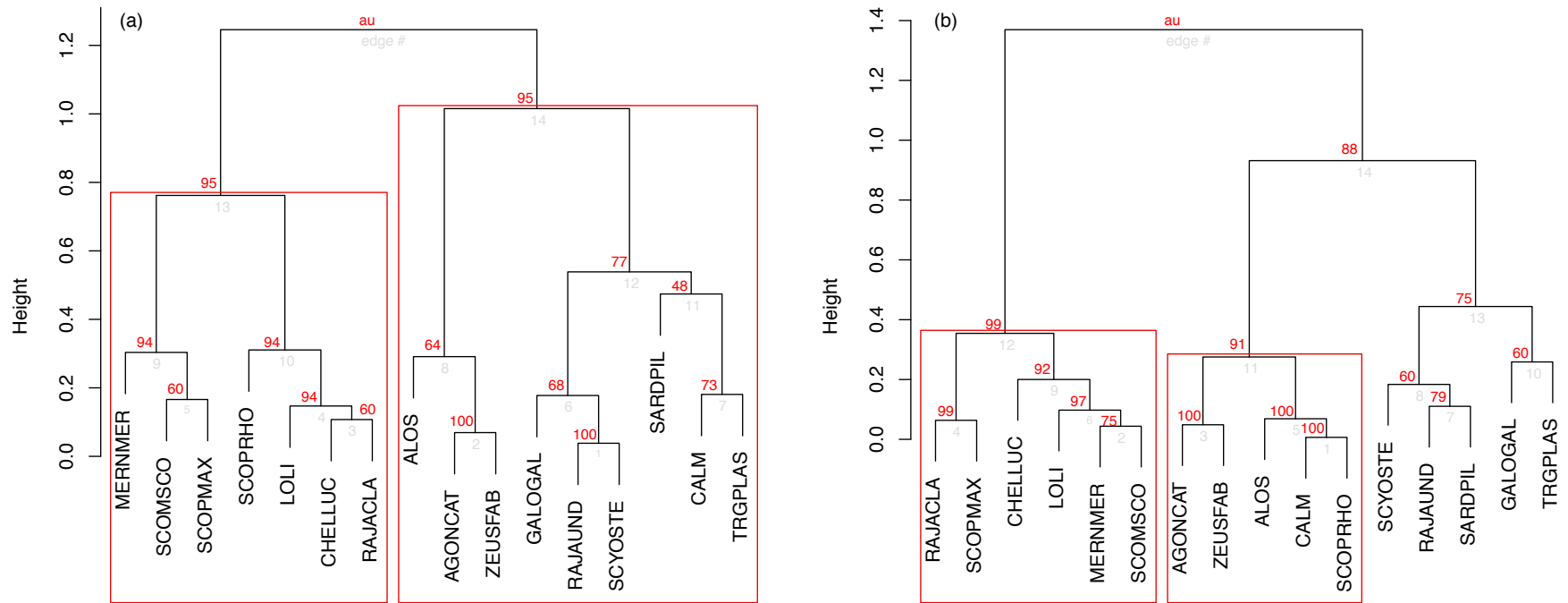


Figure S3: Spatial hierarchical clustering at a 782km<sup>2</sup> (a) and 1043km<sup>2</sup> (b) scale. The rectangle outlines the communities that were found statistically significant by ASTEC given the approximately unbiased p-values expressed as proportion (red).

Supplemental of spatio-temporal patterns in communities

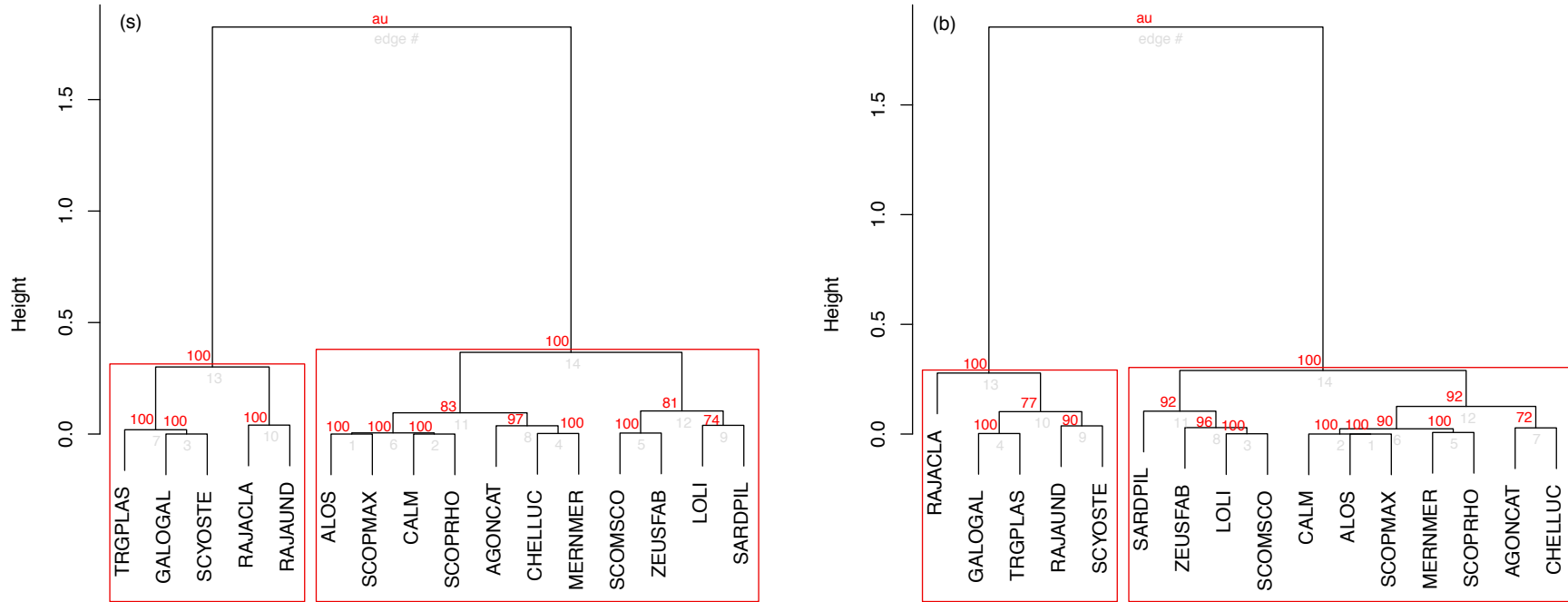


Figure S4: Spatial-temporal hierarchical clustering at a 782km<sup>2</sup> (a) and 1043km<sup>2</sup> (b) scale. The rectangle outlines the communities that were found statistically significant by ASTEC given the approximately unbiased p-values expressed as proportion (red).

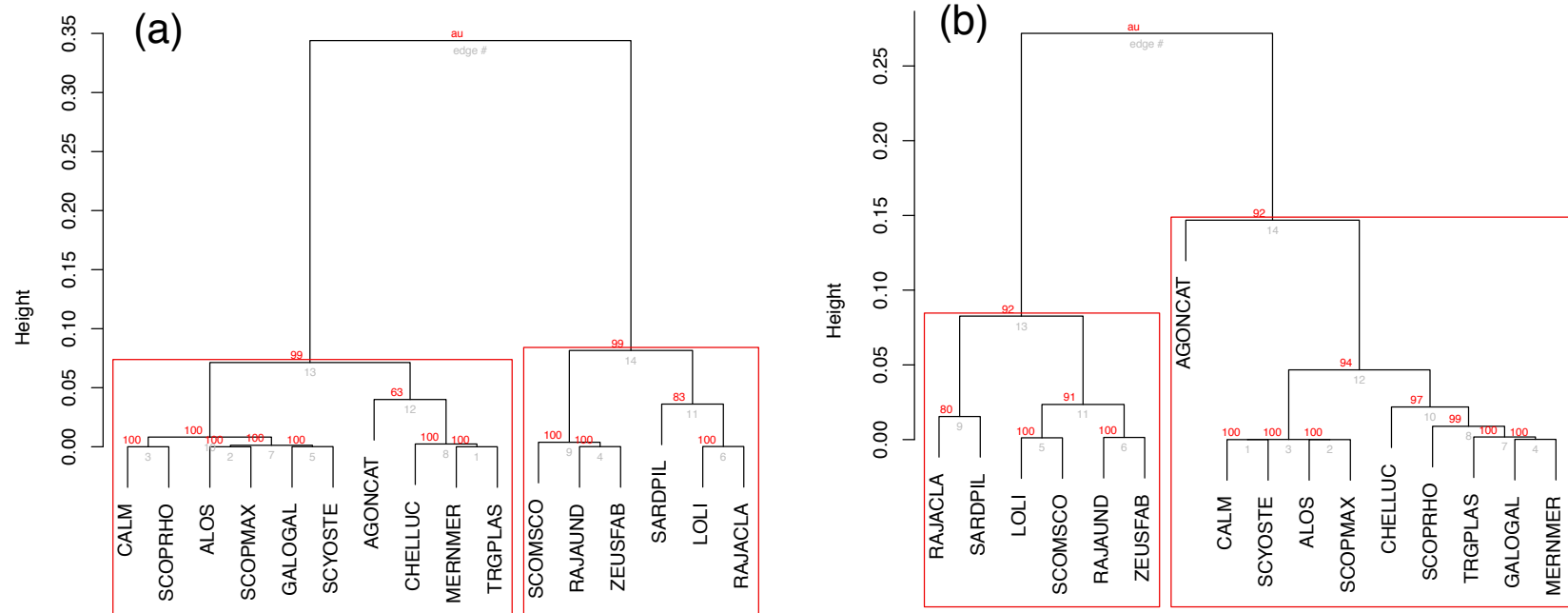


Figure S5: Absolute values of spatial-temporal hierarchical clustering at a 782km<sup>2</sup> (a) and 1043km<sup>2</sup> (b) scale. The rectangle outlines the communities that were found statistically significant by ASTEC given the approximately unbiased p-values expressed as proportion (red).



*Supplemental of spatio-temporal patterns in communities*

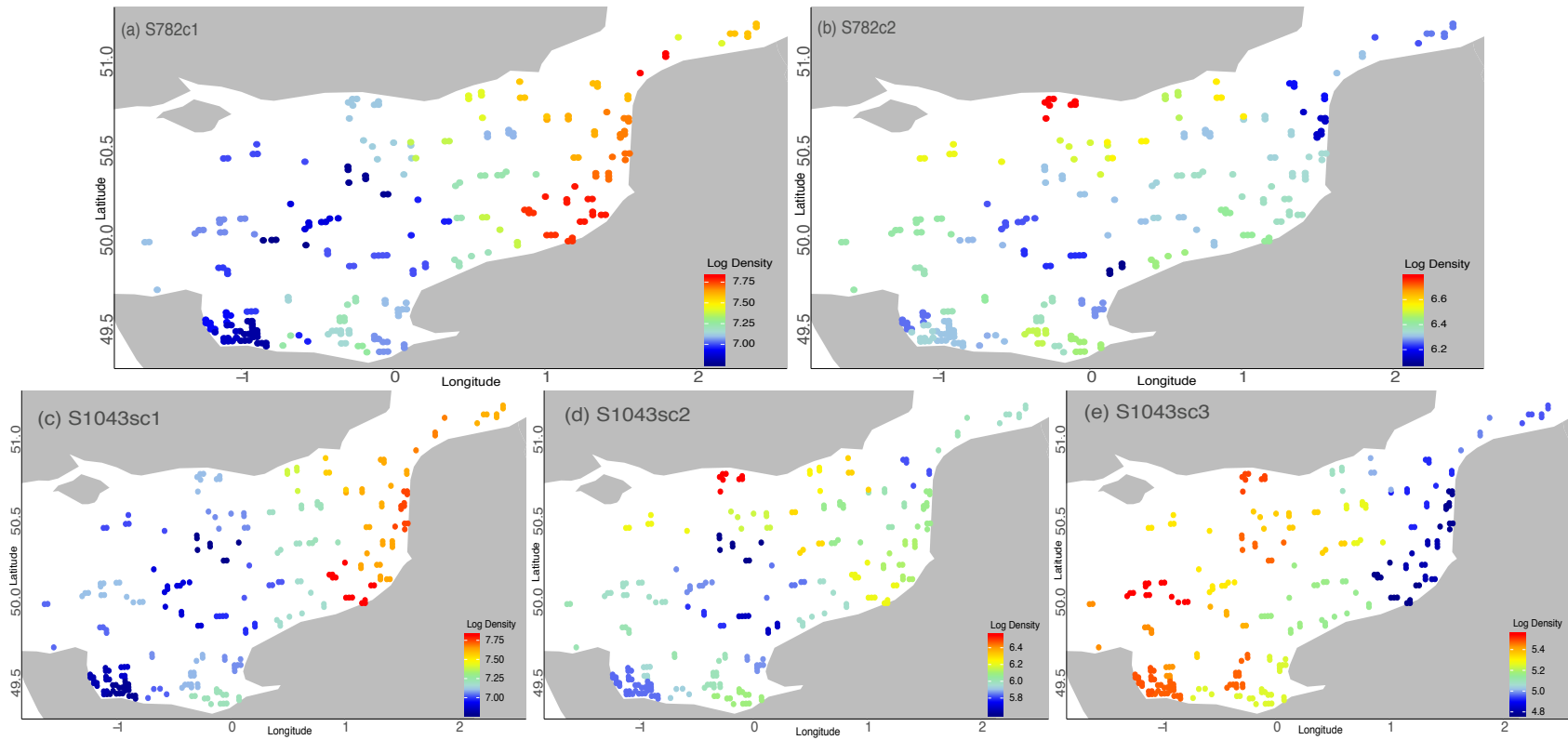


Figure S6: Eastern English Channel spatial community from low (blue) to high (red) median densities of numbers/ km<sup>2</sup> in log scale are mapped, S782c1 (a), S782c2 (b), S1043sc1 (c), S1043sc2 (d), S1043sc3 (e).

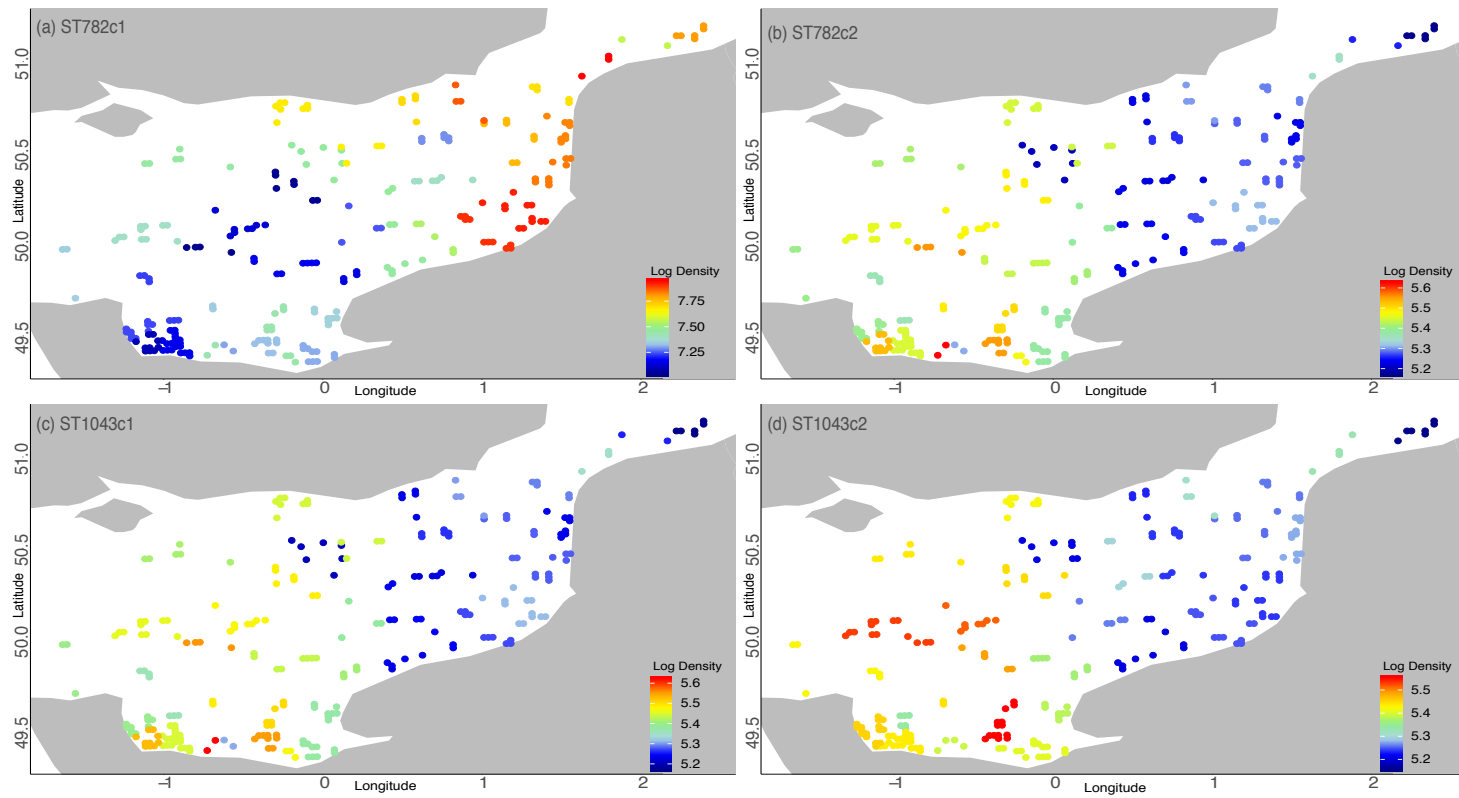


Figure S7: Eastern English Channel spatio-temporal community from low (blue) to high (red) median densities of numbers/ km<sup>2</sup> in log scale for communities ST782c1 (a), ST782c2 (b), ST1043c1 (c), ST1043c2 (d).

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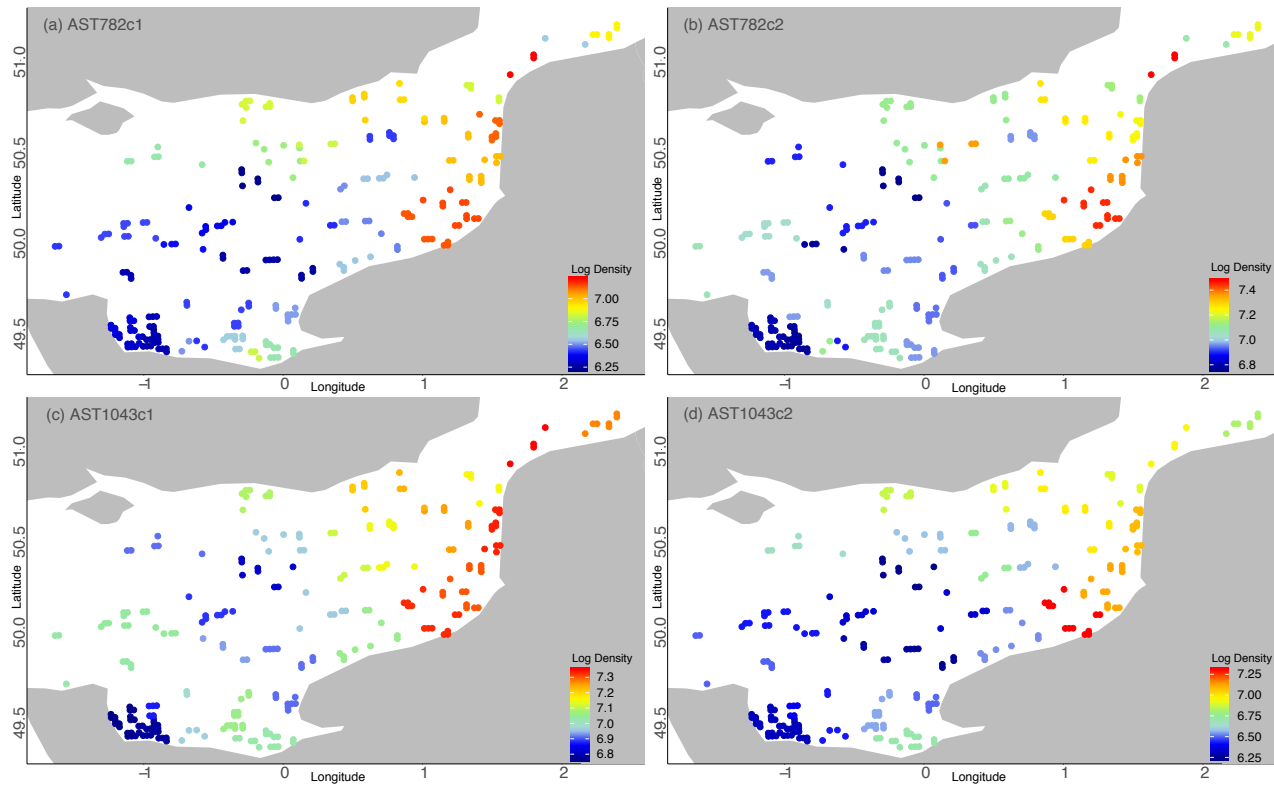


Figure S8: Eastern English Channel absolute spatio-temporal community from low (blue) to high (red) median densities of numbers/ $\text{km}^2$  in log scale for communities AST782c1 (a), AST782c2 (b), AST1043c1 (c), AST1043c2 (d).

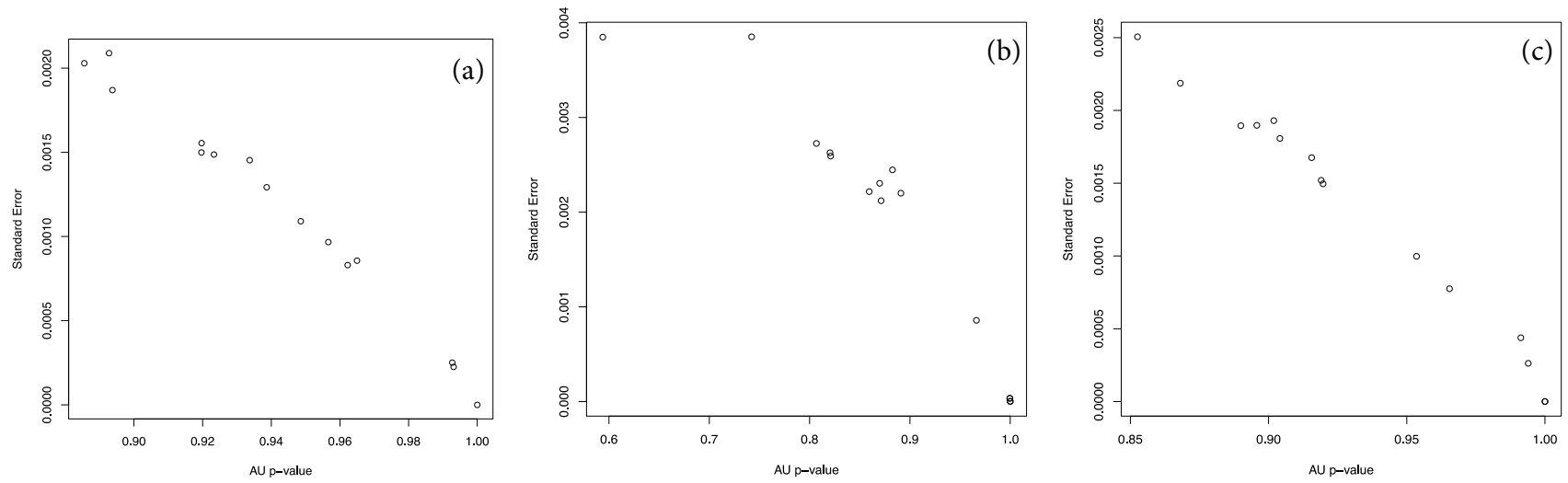


Figure S9: P-value versus standard error for the hierarchical clustering defined with absolute values of spatial correlation at a 522km<sup>2</sup> (a), 782km<sup>2</sup> (b) and 1043km<sup>2</sup> (c) scale.

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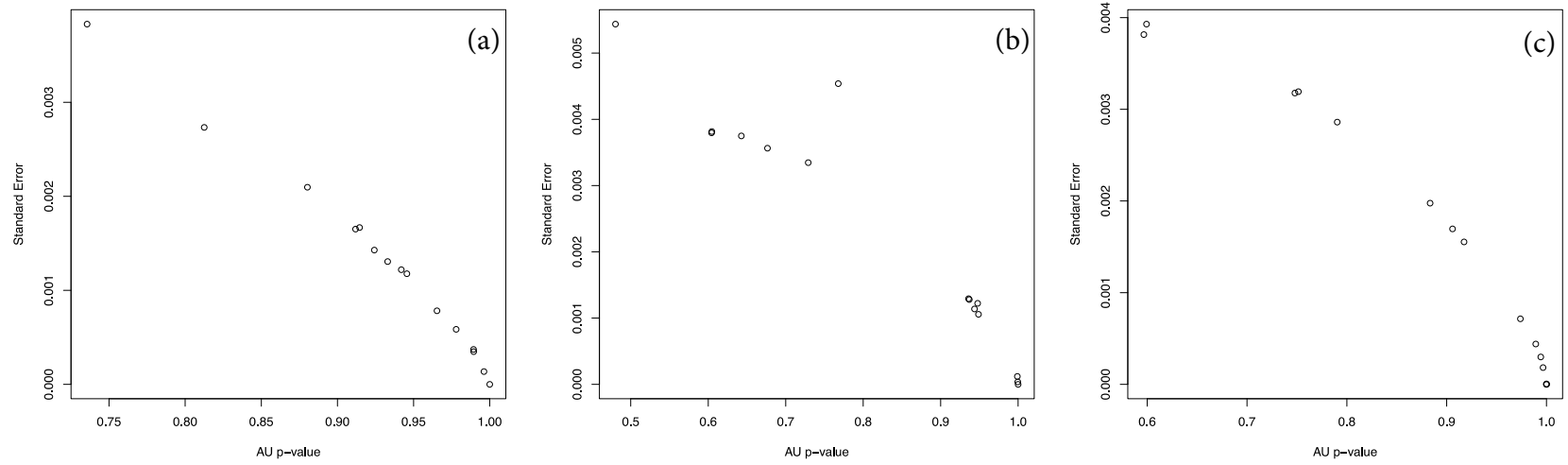


Figure S10: P-value versus standard error for the hierarchical clustering defined with spatial correlation at a 522km<sup>2</sup> (a), 782km<sup>2</sup> (b) and 1043km<sup>2</sup> (c) scale.

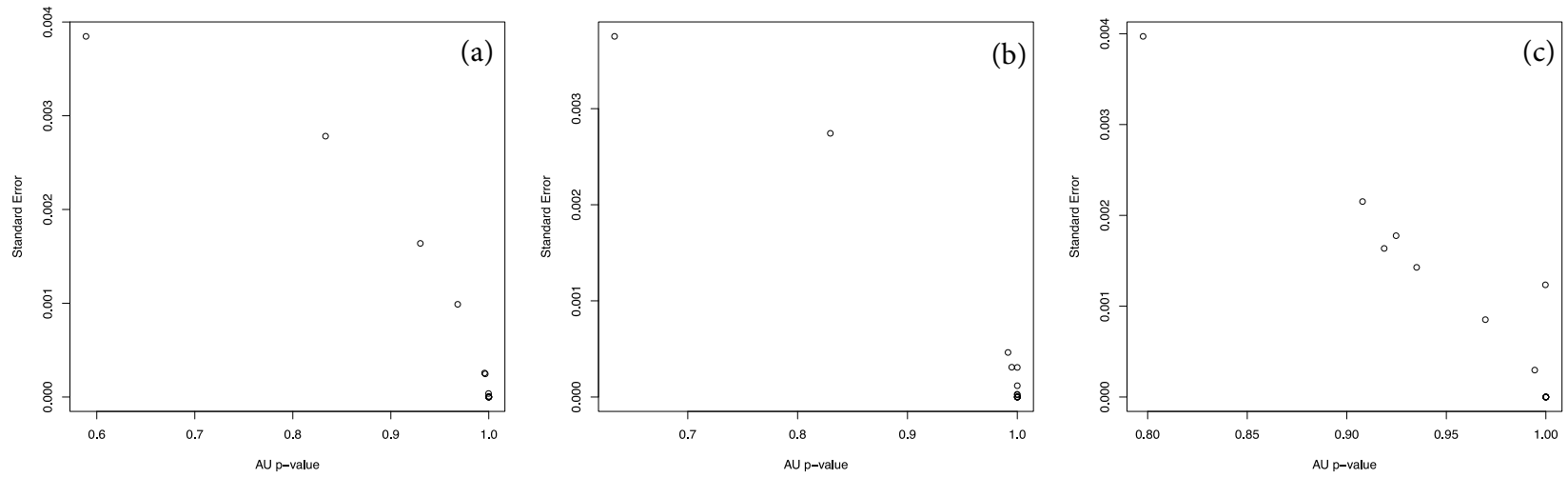


Figure S11: P-value versus standard error for the hierarchical clustering defined with absolute values of spatial-temporal correlation at a 522km<sup>2</sup> (a), 782km<sup>2</sup> (b) and 1043km<sup>2</sup> (c) scale.

*Supplemental of spatio-temporal patterns in communities*

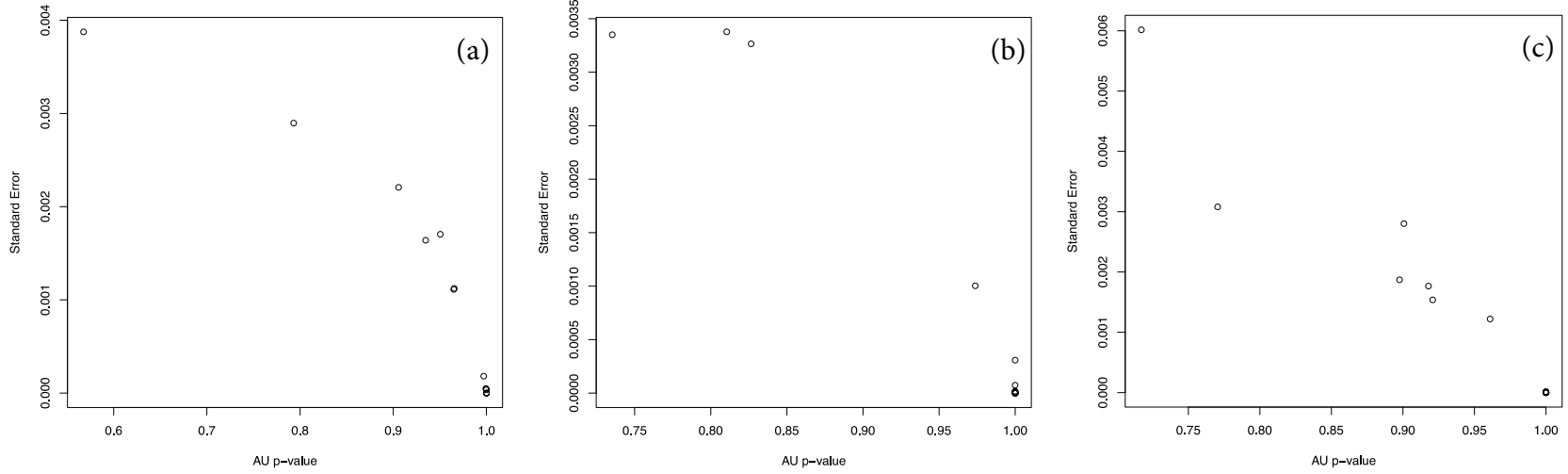


Figure S12: P-value versus standard error for the hierarchical clustering defined with spatial-temporal correlation at a 522km<sup>2</sup> (a), 782km<sup>2</sup> (b) and 1043km<sup>2</sup> (c) scale.

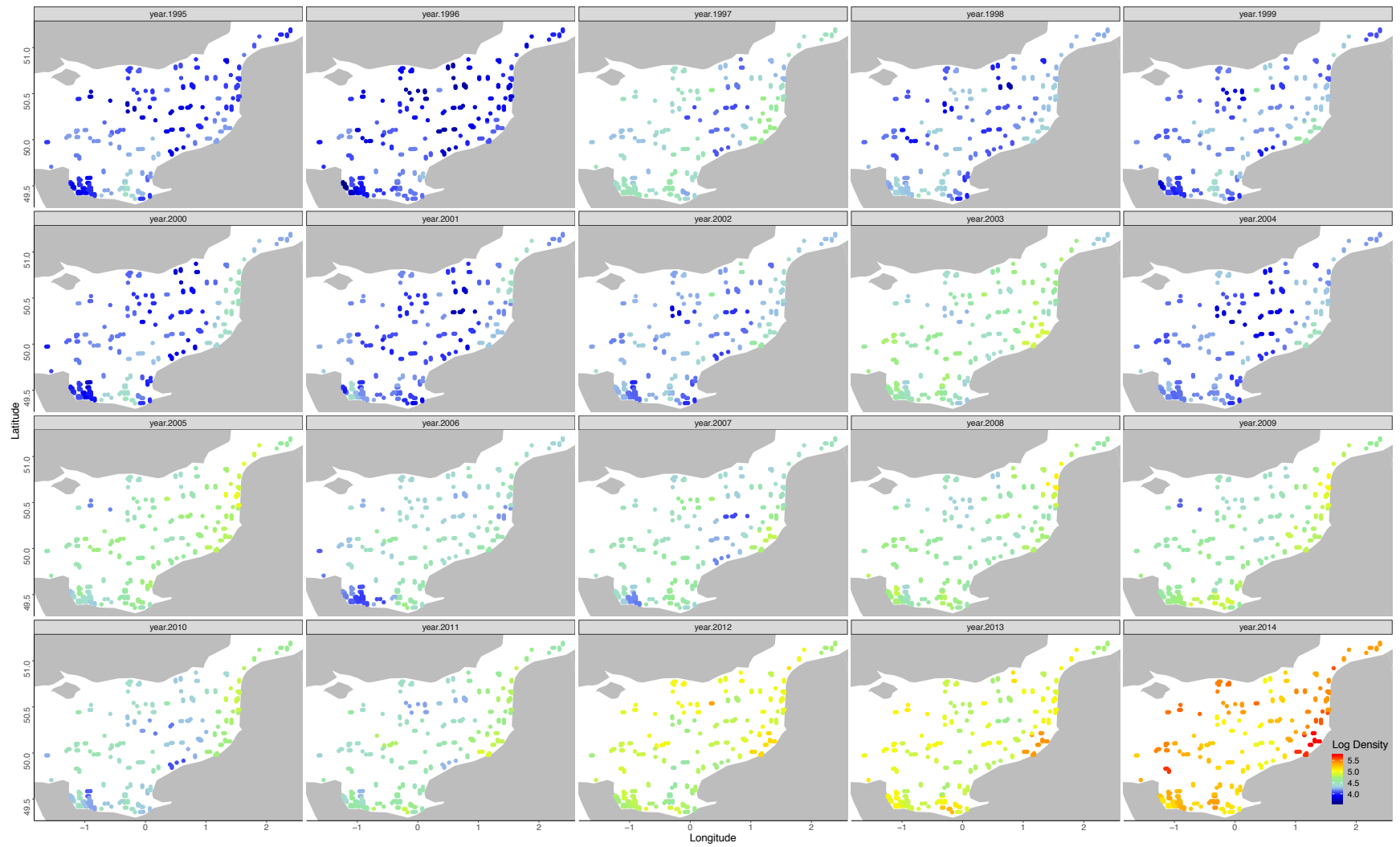


Figure S13: *R. clavata* from low (blue) to high (red) median densities in count per kilometer square in log scale from 1995 to 2014.



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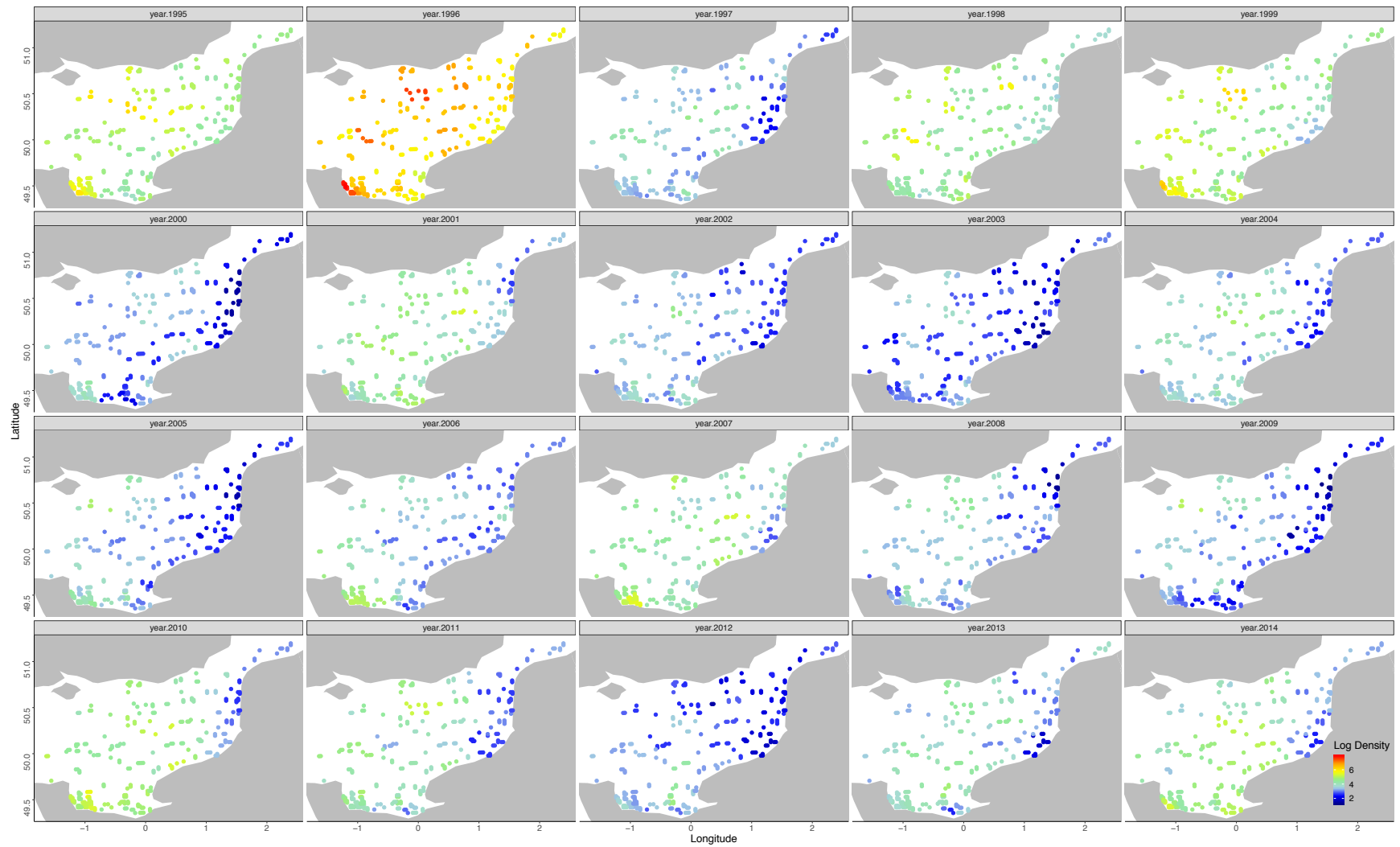


Figure S14: *S. pilchardus* from low (blue) to high (red) median densities in count per kilometer square in log scale from 1995 to 2014.

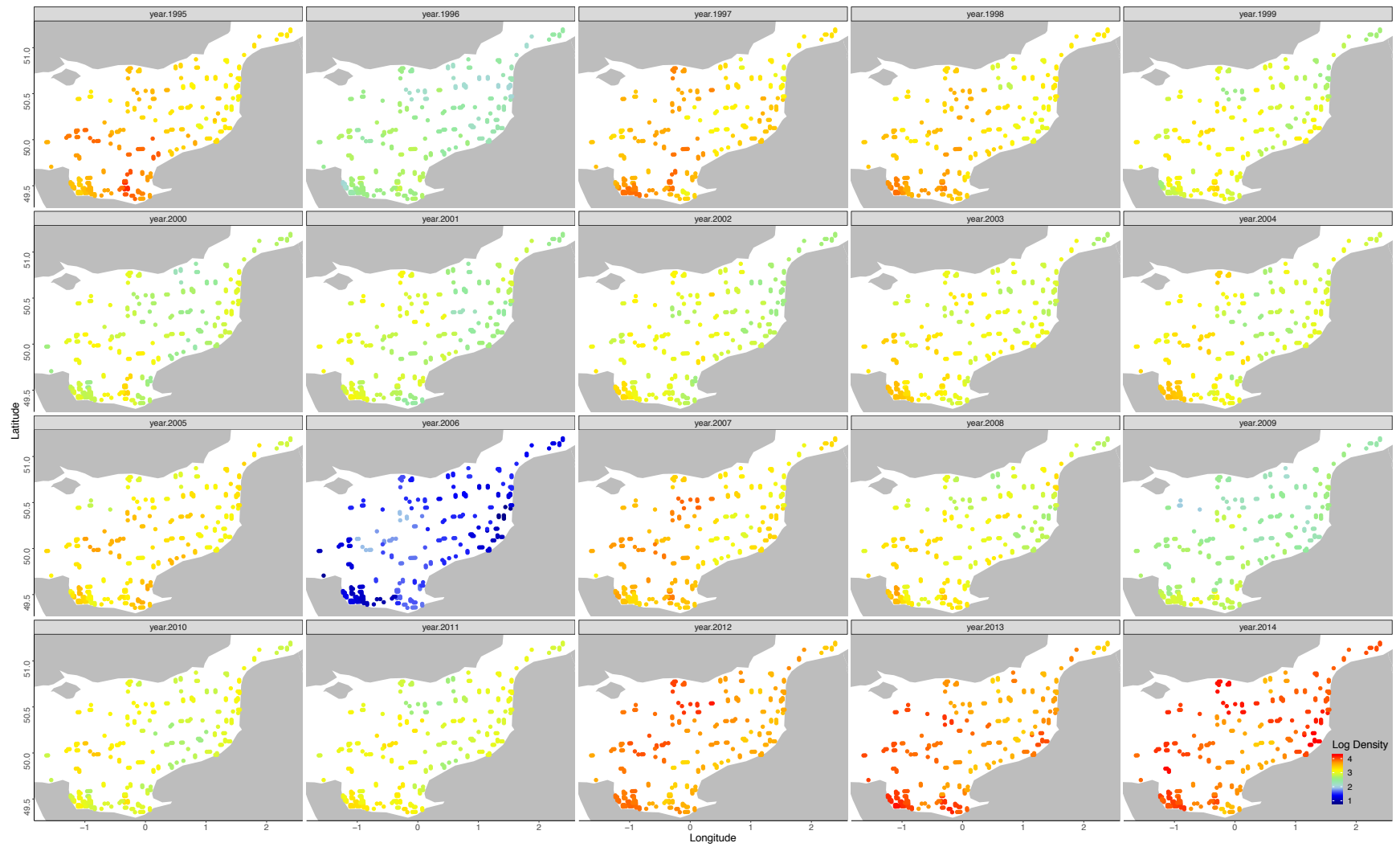


Figure S15: *R. undulata* from low (blue) to high (red) median densities in count per kilometer square in log scale from 1995 to 2014.

*Supplemental of spatio-temporal patterns in communities*

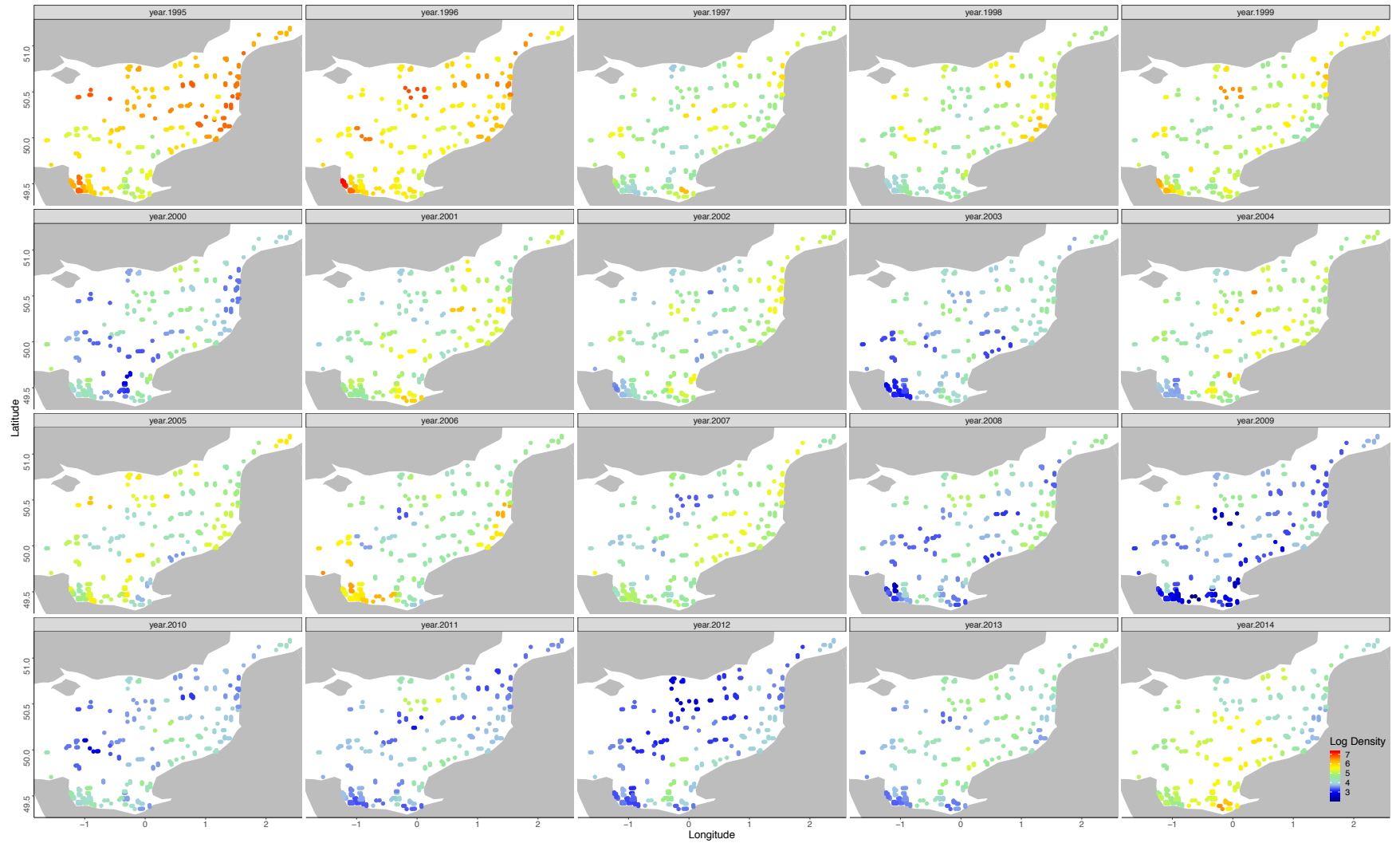


Figure S16: *S. scombrus* from low (blue) to high (red) median densities in count per kilometer square in log scale from 1995 to 2014.

## Supplemental Tables

Table S1: Key code for the spatial, spatio-temporal and absolute spatio-temporal communities and sub-communities defined by ASTEC at a 522km<sup>2</sup>, 782km<sup>2</sup> and 1043km<sup>2</sup> scale.

Model	Scale	Species Code	Group Code
Spatial	522km <sup>2</sup>	RAJACLA, CHELLUC, LOLI, SCOPMAX, MERNMER, SCOMSCO	S522c1
		RAJACLA, CHELLUC, LOLI	S522sc1.1
		SCOPMAX, MERNMER, SCOMSCO	S522sc1.2
		GALOGAL, SCOPRHO, AGONCAT, ZEUSFAB, TRGPLAS, ALOS, CALM, SARDPIL, RAJAUND, SCYOSTE	S522c2
		GALOGAL, SCOPRHO, AGONCAT, ZEUSFAB, TRGPLAS, ALOS, CALM	S522sc2.1
		SARDPIL, RAJAUND, SCYOSTE	S522sc2.2
	782 km <sup>2</sup>	MERNMER, SCOMSCO, SCOPMAX, SCOPRHO, LOLI, CHELLUC, RAJACLA	S782c1
		MERNMER, SCOMSCO, SCOPMAX	S782sc1.1
		SCOPRHO, LOLI, CHELLUC, RAJACLA	S782sc1.2
		ALOS, AGONCAT, ZEUSFAB, GALOGAL, RAJAUND, SCYOSTE, SARDPIL, CALM, TRGPLAS	S782c2
		ALOS, AGONCAT, ZEUSFAB	S782sc2.1
		GALOGAL, RAJAUND, SCYOSTE, SARDPIL, CALM, TRGPLAS	S782sc2.2
		RAJACLA, SCOPMAX, CHELLUC, LOLI, MERNMER, SCOMSCO	S1043sc1

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	1043	RAJACLA, SCOPMAX	S1043sc1.1
	km <sup>2</sup>	CHELLUC, LOLI, MERNMER, SCOMSCO	S1043sc1.2
		AGONCAT, ZEUSFAB, ALOS, CALM, SCOPRHO	S1043sc2
		AGONCAT, ZEUSFAB	S1043sc2.1
		ALOS, CALM, SCOPRHO	S1043sc2.2
		SCYOSTE, RAJAUND, SARDPIL, GALOGAL, TRGPLAS	S1043sc3
		SCYOSTE, RAJAUND, SARDPIL	S1043sc3.1
		GALOGAL, TRGPLAS	S1043sc3.2
Spatio-temporal	522km <sup>2</sup>	AGONCAT, CHELLUC, MERNMER, CALM, SCOPRHO, ALOS, SCOPMAX, SCOMSCO, ZEUSFAB, LOLI, SARDPIL	ST522c1
		AGONCAT, CHELLUC, MERNMER, CALM, SCOPRHO, ALOS, SCOPMAX	ST522c1.1
		SCOMSCO, ZEUSFAB, LOLI, SARDPIL	ST522c1.2
		TRGPLAS, GALOGAL, SCYOSTE, RAJACLA, RAJAUND	ST522c2
		TRGPLAS, GALOGAL, SCYOSTE	ST522c2.1
		RAJACLA, RAJAUND	ST522c2.2
	782	km <sup>2</sup>	ALOS, SCOPMAX, CALM, SCOPRHO, AGONCAT, CHELLUC, MERNMER, SCOMSCO, ZEUSFAB, LOLI, SARDPIL
ALOS, SCOPMAX, CALM, SCOPRHO, AGONCAT, CHELLUC, MERNMER			ST782c1.1
SCOMSCO, ZEUSFAB, LOLI, SARDPIL			ST782c1.2

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		TRGPLAS, GALOGAL, SCYOSTE, RAJACLA, RAJAUND	ST782c2
		TRGPLAS, GALOGAL, SCYOSTE	ST782c2.1
		RAJACLA, RAJAUND	ST782c2.2
	<b>1043 km<sup>2</sup></b>	SARDPIL, ZEUSFAB, LOLI, SCOMSCO, CALM, ALOS, SCOPMAX, MERNMER, SCOPRHO, AGONCAT, CHELLUC	ST1043c1
		CALM, ALOS, SCOPMAX, MERNMER, SCOPRHO, AGONCAT, CHELLUC	ST1043c1.1
		SARDPIL, ZEUSFAB, LOLI, SCOMSCO	ST1043c1.2
		RAJACLA, GALOGAL, TRGPLAS, RAJAUND, SCYOSTE	ST1043c2
		RAJACLA	ST1043c2.1
		GALOGAL, TRGPLAS, RAJAUND, SCYOSTE	ST1043c2.2
Absolute	<b>522km<sup>2</sup></b>	AGONCAT, TRGPLAS, CHELLUC, MERNMER, GALOGAL, SCOPRHO, CALM, SCOPMAX, ALOS, SCYOSTE	AST522c1
Spatio-temporal		AGONCAT, TRGPLAS	AST522c1.1
		CHELLUC, MERNMER, GALOGAL, SCOPRHO, CALM, SCOPMAX, ALOS, SCYOSTE	AST522c1.2
		RAJACLA, SARDPIL, SCOMSCO, ZEUSFAB, LOLI, RAJAUND	AST522c2
		RAJACLA, SARDPIL	AST522c2.1
		SCOMSCO, ZEUSFAB, LOLI, RAJAUND	AST522c2.2
	<b>782 km<sup>2</sup></b>	CALM, SCOPRHO, ALOS, SCOPMAX, GALOGAL, SCYOSTE, AGONCAT, CHELLUC, MERNMER, TRGPLAS	AST782c1
		CALM, SCOPRHO, ALOS, SCOPMAX, GALOGAL, SCYOSTE	AST782c1.1
		AGONCAT, CHELLUC, MERNMER, TRGPLAS	AST782c1.2

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		SCOMSCO, RAJAUND, ZEUSFAB, SARDPIL, LOLI, RAJACLA	AST782c2
		SCOMSCO, RAJAUND, ZEUSFAB	AST782c2.1
		SARDPIL, LOLI, RAJACLA	AST782c2.2
<b>1043</b>		RAJACLA, SARDPIL, LOLI, SCOMSCO, RAJAUND, ZEUSFAB	AST1043c1
<b>km<sup>2</sup></b>		RAJACLA, SARDPIL	AST1043c1.1
		LOLI, SCOMSCO, RAJAUND, ZEUSFAB	AST1043c1.2
		CALM, SCYOSTE, ALOS, SCOPMAX, AGONCAT, CHELLUC, SCOPRHO, TRGPLAS, GALOGAL, MERNMER	AST1043c2
		CALM, SCYOSTE, ALOS, SCOPMAX	AST1043c2.1
		AGONCAT, CHELLUC, SCOPRHO, TRGPLAS, GALOGAL, MERNMER	AST1043c2.2

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Table S2: Parameters estimates with associated standard errors for the VAST model at a 522km<sup>2</sup>, 782km<sup>2</sup> and 1043km<sup>2</sup> scale.

Scale in Km	522		782		1043	
Parameter	Estimates	Standard Error	Estimates	Standard Error	Estimates	Standard Error
ln_H_input	-2.65E-01	1.77E-01	-1.13E+00	5.18E-01	1.67E-02	1.82E-01
ln_H_input	3.43E-01	2.28E-01	3.37E-01	4.63E-01	-7.08E-02	2.00E-01
beta1_ct	1.91E+01	1.18E+03	2.04E+01	2.23E+03	2.20E+01	4.99E+03
beta1_ct	1.81E+01	1.32E+03	1.94E+01	2.47E+03	2.07E+01	4.92E+03
beta1_ct	2.55E+01	7.81E+03	2.46E+01	4.84E+03	2.59E+01	9.59E+03
beta1_ct	2.24E+01	2.24E+03	2.41E+01	5.38E+03	2.62E+01	1.56E+04
beta1_ct	2.17E+01	5.37E+03	2.00E+01	2.31E+03	1.83E+01	9.67E+02
beta1_ct	2.63E+01	9.10E+03	7.36E+00	7.07E-01	2.52E+01	5.27E+03
beta1_ct	2.32E+01	3.48E+03	2.40E+01	5.26E+03	2.63E+01	1.62E+04
beta1_ct	2.26E+01	2.35E+03	2.46E+01	6.50E+03	2.60E+01	1.28E+04
beta1_ct	2.12E+01	3.76E+03	2.02E+01	2.26E+03	1.89E+01	1.23E+03
beta1_ct	2.17E+01	2.25E+03	2.23E+01	2.95E+03	2.45E+01	8.84E+03
beta1_ct	2.31E+01	3.10E+03	2.41E+01	5.19E+03	2.58E+01	1.25E+04
beta1_ct	1.96E+01	2.34E+03	1.97E+01	2.56E+03	1.99E+01	2.88E+03
beta1_ct	2.13E+01	3.64E+03	2.03E+01	2.25E+03	1.89E+01	1.13E+03
beta1_ct	2.17E+01	2.56E+03	2.15E+01	2.37E+03	2.10E+01	1.84E+03
beta1_ct	2.07E+01	1.81E+03	1.93E+01	8.95E+02	2.15E+01	2.61E+03
beta1_ct	2.25E+01	2.28E+03	2.43E+01	5.65E+03	2.65E+01	1.71E+04
beta2_ct	7.89E-01	9.07E-01	6.19E-01	9.49E-01	8.05E-01	9.28E-01
beta2_ct	2.89E+00	4.09E-01	2.82E+00	4.12E-01	2.99E+00	4.09E-01
beta2_ct	5.53E+00	2.09E-01	5.53E+00	1.98E-01	5.51E+00	2.26E-01



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beta2_ct	4.06E+00	1.67E-01	4.06E+00	1.55E-01	4.05E+00	1.66E-01
beta2_ct	3.54E+00	2.69E-01	3.54E+00	2.66E-01	3.52E+00	2.83E-01
beta2_ct	6.58E+00	1.40E-01	6.55E+00	1.39E-01	6.58E+00	1.47E-01
beta2_ct	4.26E+00	3.70E-01	4.27E+00	3.60E-01	4.31E+00	4.06E-01
beta2_ct	4.07E+00	1.63E-01	4.05E+00	1.62E-01	4.04E+00	1.68E-01
beta2_ct	3.50E+00	3.68E-01	3.52E+00	3.66E-01	3.53E+00	3.65E-01
beta2_ct	4.82E+00	2.62E-01	4.81E+00	2.52E-01	4.79E+00	2.64E-01
beta2_ct	5.90E+00	2.23E-01	5.91E+00	2.15E-01	5.91E+00	2.48E-01
beta2_ct	2.06E+00	7.17E-01	2.01E+00	7.20E-01	2.09E+00	7.20E-01
beta2_ct	2.28E+00	7.12E-01	2.29E+00	7.11E-01	2.28E+00	7.12E-01
beta2_ct	3.74E+00	2.45E-01	3.64E+00	2.51E-01	3.67E+00	2.58E-01
beta2_ct	3.11E+00	2.70E-01	3.08E+00	2.68E-01	3.11E+00	2.72E-01
beta2_ct	3.78E+00	1.58E-01	3.75E+00	1.56E-01	3.75E+00	1.58E-01
beta2_ct	2.79E+00	4.75E-01	2.71E+00	4.62E-01	2.62E+00	4.98E-01
beta2_ct	3.03E+00	3.78E-01	3.12E+00	3.65E-01	3.10E+00	3.82E-01
beta2_ct	5.72E+00	2.27E-01	5.69E+00	2.18E-01	5.68E+00	2.44E-01
beta2_ct	4.00E+00	1.90E-01	3.98E+00	1.81E-01	3.95E+00	1.90E-01
beta2_ct	2.56E+00	5.51E-01	2.60E+00	5.40E-01	2.56E+00	5.53E-01
beta2_ct	5.63E+00	1.67E-01	5.62E+00	1.65E-01	5.65E+00	1.72E-01
beta2_ct	4.97E+00	3.78E-01	4.98E+00	3.69E-01	4.98E+00	4.16E-01
beta2_ct	3.97E+00	1.90E-01	3.96E+00	1.89E-01	3.95E+00	1.95E-01
beta2_ct	2.50E+00	7.12E-01	2.47E+00	7.13E-01	2.50E+00	7.11E-01
beta2_ct	6.21E+00	2.74E-01	6.20E+00	2.65E-01	6.19E+00	2.76E-01
beta2_ct	5.70E+00	2.55E-01	5.71E+00	2.48E-01	5.70E+00	2.77E-01
beta2_ct	3.17E+00	4.32E-01	3.17E+00	4.27E-01	3.16E+00	4.32E-01
beta2_ct	2.46E+00	7.15E-01	2.47E+00	7.13E-01	2.47E+00	7.16E-01

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beta2_ct	3.71E+00	3.18E-01	3.74E+00	3.15E-01	3.73E+00	3.25E-01
beta2_ct	3.06E+00	4.34E-01	2.98E+00	4.33E-01	3.00E+00	4.36E-01
beta2_ct	3.07E+00	3.71E-01	3.01E+00	3.72E-01	3.04E+00	3.72E-01
beta2_ct	3.69E+00	3.73E-01	3.45E+00	3.68E-01	3.59E+00	3.91E-01
beta2_ct	1.95E+00	7.35E-01	2.02E+00	7.32E-01	2.00E+00	7.36E-01
beta2_ct	5.65E+00	1.98E-01	5.64E+00	1.88E-01	5.64E+00	2.17E-01
beta2_ct	4.31E+00	1.32E-01	4.27E+00	1.18E-01	4.28E+00	1.31E-01
beta2_ct	4.15E+00	2.23E-01	4.18E+00	2.18E-01	4.10E+00	2.43E-01
beta2_ct	6.63E+00	1.40E-01	6.62E+00	1.38E-01	6.63E+00	1.46E-01
beta2_ct	4.88E+00	3.57E-01	4.81E+00	3.49E-01	4.88E+00	3.97E-01
beta2_ct	4.38E+00	1.36E-01	4.34E+00	1.35E-01	4.36E+00	1.41E-01
beta2_ct	3.48E+00	2.67E-01	3.49E+00	2.64E-01	3.50E+00	2.63E-01
beta2_ct	3.41E+00	3.13E-01	3.46E+00	3.04E-01	3.46E+00	3.12E-01
beta2_ct	4.74E+00	2.43E-01	4.76E+00	2.35E-01	4.78E+00	2.66E-01
beta2_ct	2.35E+00	5.92E-01	2.36E+00	5.92E-01	2.43E+00	5.93E-01
beta2_ct	3.19E+00	3.17E-01	3.19E+00	3.17E-01	3.21E+00	3.16E-01
beta2_ct	3.74E+00	2.29E-01	3.77E+00	2.27E-01	3.80E+00	2.37E-01
beta2_ct	4.18E+00	1.74E-01	4.13E+00	1.68E-01	4.14E+00	1.73E-01
beta2_ct	3.99E+00	1.36E-01	3.99E+00	1.35E-01	4.01E+00	1.36E-01
beta2_ct	2.43E+00	4.42E-01	2.39E+00	4.32E-01	2.47E+00	4.56E-01
beta2_ct	2.50E+00	4.87E-01	2.55E+00	4.77E-01	2.61E+00	4.91E-01
beta2_ct	5.43E+00	2.07E-01	5.37E+00	1.98E-01	5.44E+00	2.24E-01
beta2_ct	4.09E+00	1.59E-01	4.06E+00	1.49E-01	4.08E+00	1.59E-01
beta2_ct	2.97E+00	4.04E-01	2.93E+00	4.04E-01	2.96E+00	4.12E-01
beta2_ct	6.84E+00	1.43E-01	6.77E+00	1.41E-01	6.83E+00	1.49E-01
beta2_ct	4.69E+00	3.61E-01	4.63E+00	3.53E-01	4.78E+00	3.98E-01

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beta2_ct	4.18E+00	1.56E-01	4.18E+00	1.55E-01	4.16E+00	1.61E-01
beta2_ct	3.36E+00	2.86E-01	3.39E+00	2.82E-01	3.42E+00	2.78E-01
beta2_ct	4.39E+00	2.97E-01	4.33E+00	2.90E-01	4.35E+00	2.99E-01
beta2_ct	4.82E+00	2.42E-01	4.77E+00	2.36E-01	4.84E+00	2.64E-01
beta2_ct	2.77E+00	5.14E-01	2.79E+00	5.11E-01	2.79E+00	5.18E-01
beta2_ct	3.49E+00	2.66E-01	3.47E+00	2.67E-01	3.57E+00	2.64E-01
beta2_ct	3.37E+00	2.61E-01	3.39E+00	2.59E-01	3.38E+00	2.70E-01
beta2_ct	3.44E+00	2.73E-01	3.39E+00	2.69E-01	3.39E+00	2.74E-01
beta2_ct	3.73E+00	1.79E-01	3.72E+00	1.78E-01	3.72E+00	1.80E-01
beta2_ct	2.78E+00	4.17E-01	2.82E+00	4.02E-01	2.87E+00	4.28E-01
beta2_ct	2.39E+00	4.57E-01	2.47E+00	4.51E-01	2.46E+00	4.66E-01
beta2_ct	5.53E+00	1.97E-01	5.57E+00	1.86E-01	5.56E+00	2.16E-01
beta2_ct	4.28E+00	1.39E-01	4.29E+00	1.25E-01	4.31E+00	1.38E-01
beta2_ct	3.92E+00	2.22E-01	3.90E+00	2.21E-01	3.86E+00	2.40E-01
beta2_ct	6.91E+00	1.35E-01	6.90E+00	1.33E-01	6.91E+00	1.42E-01
beta2_ct	5.03E+00	3.48E-01	5.09E+00	3.37E-01	5.11E+00	3.89E-01
beta2_ct	4.20E+00	1.40E-01	4.19E+00	1.38E-01	4.20E+00	1.45E-01
beta2_ct	3.00E+00	3.89E-01	3.04E+00	3.84E-01	2.99E+00	3.87E-01
beta2_ct	4.64E+00	2.51E-01	4.70E+00	2.38E-01	4.66E+00	2.53E-01
beta2_ct	5.01E+00	2.27E-01	5.07E+00	2.19E-01	5.05E+00	2.52E-01
beta2_ct	2.51E+00	4.70E-01	2.70E+00	4.59E-01	2.71E+00	4.65E-01
beta2_ct	3.63E+00	2.40E-01	3.64E+00	2.37E-01	3.67E+00	2.37E-01
beta2_ct	3.84E+00	2.18E-01	3.85E+00	2.17E-01	3.90E+00	2.27E-01
beta2_ct	3.52E+00	2.18E-01	3.49E+00	2.14E-01	3.47E+00	2.21E-01
beta2_ct	3.70E+00	1.53E-01	3.69E+00	1.51E-01	3.69E+00	1.53E-01
beta2_ct	2.58E+00	4.95E-01	2.46E+00	4.92E-01	2.53E+00	5.08E-01

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beta2_ct	1.43E+00	1.02E+00	1.45E+00	1.02E+00	1.44E+00	1.02E+00
beta2_ct	5.48E+00	2.05E-01	5.47E+00	1.95E-01	5.45E+00	2.23E-01
beta2_ct	3.97E+00	1.67E-01	3.94E+00	1.56E-01	3.96E+00	1.66E-01
beta2_ct	3.61E+00	2.51E-01	3.55E+00	2.53E-01	3.60E+00	2.68E-01
beta2_ct	6.34E+00	1.40E-01	6.32E+00	1.38E-01	6.34E+00	1.47E-01
beta2_ct	4.88E+00	3.53E-01	4.87E+00	3.43E-01	4.89E+00	3.93E-01
beta2_ct	4.14E+00	1.41E-01	4.12E+00	1.40E-01	4.13E+00	1.46E-01
beta2_ct	2.85E+00	4.55E-01	2.81E+00	4.55E-01	2.85E+00	4.54E-01
beta2_ct	2.92E+00	3.29E-01	2.96E+00	3.20E-01	2.93E+00	3.29E-01
beta2_ct	3.92E+00	2.61E-01	3.88E+00	2.56E-01	3.91E+00	2.84E-01
beta2_ct	2.81E+00	3.99E-01	2.79E+00	4.00E-01	2.87E+00	4.02E-01
beta2_ct	3.09E+00	3.65E-01	3.08E+00	3.65E-01	3.07E+00	3.67E-01
beta2_ct	3.26E+00	2.53E-01	3.30E+00	2.50E-01	3.33E+00	2.61E-01
beta2_ct	3.74E+00	2.12E-01	3.79E+00	2.07E-01	3.80E+00	2.11E-01
beta2_ct	4.32E+00	1.47E-01	4.30E+00	1.46E-01	4.28E+00	1.47E-01
beta2_ct	2.81E+00	4.22E-01	2.70E+00	4.12E-01	2.81E+00	4.35E-01
beta2_ct	1.99E+00	6.01E-01	2.20E+00	5.66E-01	2.30E+00	5.66E-01
beta2_ct	5.20E+00	1.96E-01	5.18E+00	1.86E-01	5.20E+00	2.16E-01
beta2_ct	4.05E+00	1.55E-01	4.09E+00	1.42E-01	4.10E+00	1.53E-01
beta2_ct	1.97E+00	7.34E-01	2.01E+00	7.27E-01	2.11E+00	7.26E-01
beta2_ct	6.66E+00	1.35E-01	6.63E+00	1.33E-01	6.66E+00	1.42E-01
beta2_ct	4.64E+00	3.51E-01	4.60E+00	3.43E-01	4.70E+00	3.93E-01
beta2_ct	4.15E+00	1.50E-01	4.16E+00	1.49E-01	4.17E+00	1.55E-01
beta2_ct	2.86E+00	3.69E-01	2.90E+00	3.66E-01	2.88E+00	3.66E-01
beta2_ct	3.97E+00	2.73E-01	3.99E+00	2.63E-01	4.00E+00	2.75E-01
beta2_ct	4.57E+00	2.28E-01	4.56E+00	2.21E-01	4.64E+00	2.53E-01

*Supplemental of spatio-temporal patterns in communities*

beta2_ct	1.91E+00	7.23E-01	2.00E+00	7.19E-01	2.01E+00	7.22E-01
beta2_ct	2.80E+00	4.59E-01	2.85E+00	4.56E-01	2.86E+00	4.58E-01
beta2_ct	3.24E+00	2.77E-01	3.23E+00	2.76E-01	3.19E+00	2.87E-01
beta2_ct	3.55E+00	2.47E-01	3.55E+00	2.43E-01	3.51E+00	2.49E-01
beta2_ct	4.09E+00	1.20E-01	4.06E+00	1.19E-01	4.08E+00	1.19E-01
beta2_ct	3.08E+00	4.08E-01	3.04E+00	3.95E-01	3.08E+00	4.23E-01
beta2_ct	2.61E+00	4.65E-01	2.67E+00	4.66E-01	2.78E+00	4.66E-01
beta2_ct	5.87E+00	1.96E-01	5.85E+00	1.86E-01	5.92E+00	2.14E-01
beta2_ct	4.29E+00	1.34E-01	4.32E+00	1.20E-01	4.36E+00	1.31E-01
beta2_ct	3.66E+00	2.53E-01	3.62E+00	2.51E-01	3.63E+00	2.71E-01
beta2_ct	6.65E+00	1.35E-01	6.63E+00	1.34E-01	6.67E+00	1.42E-01
beta2_ct	5.20E+00	3.48E-01	5.20E+00	3.39E-01	5.34E+00	3.88E-01
beta2_ct	4.24E+00	1.31E-01	4.23E+00	1.29E-01	4.23E+00	1.36E-01
beta2_ct	2.96E+00	3.71E-01	2.93E+00	3.70E-01	2.96E+00	3.70E-01
beta2_ct	3.12E+00	3.32E-01	3.16E+00	3.21E-01	3.10E+00	3.34E-01
beta2_ct	4.44E+00	2.44E-01	4.42E+00	2.37E-01	4.48E+00	2.67E-01
beta2_ct	3.32E+00	3.15E-01	3.28E+00	3.18E-01	3.37E+00	3.19E-01
beta2_ct	3.68E+00	1.98E-01	3.66E+00	2.01E-01	3.76E+00	1.96E-01
beta2_ct	3.46E+00	2.27E-01	3.44E+00	2.27E-01	3.43E+00	2.41E-01
beta2_ct	3.51E+00	2.20E-01	3.44E+00	2.18E-01	3.43E+00	2.26E-01
beta2_ct	4.00E+00	1.18E-01	3.99E+00	1.16E-01	3.99E+00	1.18E-01
beta2_ct	3.11E+00	4.00E-01	2.90E+00	3.96E-01	3.00E+00	4.18E-01
beta2_ct	3.95E+00	3.18E-01	3.96E+00	3.32E-01	4.06E+00	3.39E-01
beta2_ct	5.83E+00	1.97E-01	5.79E+00	1.87E-01	5.80E+00	2.16E-01
beta2_ct	3.95E+00	1.54E-01	3.96E+00	1.43E-01	3.96E+00	1.53E-01
beta2_ct	2.10E+00	6.26E-01	2.09E+00	6.24E-01	2.05E+00	6.37E-01

Chapter 2

beta2_ct	7.34E+00	1.36E-01	7.30E+00	1.34E-01	7.34E+00	1.43E-01
beta2_ct	4.58E+00	3.49E-01	4.54E+00	3.40E-01	4.58E+00	3.90E-01
beta2_ct	4.54E+00	1.29E-01	4.52E+00	1.28E-01	4.52E+00	1.35E-01
beta2_ct	3.07E+00	3.47E-01	3.06E+00	3.48E-01	3.06E+00	3.48E-01
beta2_ct	2.75E+00	3.52E-01	2.79E+00	3.42E-01	2.80E+00	3.49E-01
beta2_ct	3.92E+00	2.62E-01	3.92E+00	2.54E-01	3.96E+00	2.82E-01
beta2_ct	3.35E+00	2.93E-01	3.42E+00	2.88E-01	3.45E+00	2.99E-01
beta2_ct	3.44E+00	2.50E-01	3.51E+00	2.46E-01	3.50E+00	2.49E-01
beta2_ct	3.93E+00	2.21E-01	3.92E+00	2.19E-01	3.93E+00	2.32E-01
beta2_ct	2.96E+00	3.27E-01	2.90E+00	3.23E-01	2.91E+00	3.28E-01
beta2_ct	4.01E+00	1.29E-01	3.98E+00	1.28E-01	3.99E+00	1.29E-01
beta2_ct	2.65E+00	4.90E-01	2.58E+00	4.82E-01	2.52E+00	5.13E-01
beta2_ct	3.07E+00	3.57E-01	3.22E+00	3.42E-01	3.16E+00	3.63E-01
beta2_ct	5.84E+00	2.01E-01	5.81E+00	1.91E-01	5.79E+00	2.20E-01
beta2_ct	4.44E+00	1.47E-01	4.41E+00	1.37E-01	4.41E+00	1.48E-01
beta2_ct	2.09E+00	7.21E-01	2.10E+00	7.19E-01	2.09E+00	7.26E-01
beta2_ct	6.92E+00	1.36E-01	6.92E+00	1.35E-01	6.91E+00	1.43E-01
beta2_ct	4.16E+00	3.64E-01	4.14E+00	3.54E-01	4.12E+00	4.05E-01
beta2_ct	4.15E+00	1.47E-01	4.14E+00	1.45E-01	4.14E+00	1.51E-01
beta2_ct	3.08E+00	3.69E-01	3.09E+00	3.67E-01	3.12E+00	3.66E-01
beta2_ct	3.44E+00	3.17E-01	3.44E+00	3.09E-01	3.36E+00	3.23E-01
beta2_ct	4.67E+00	2.44E-01	4.68E+00	2.36E-01	4.65E+00	2.68E-01
beta2_ct	3.41E+00	2.91E-01	3.56E+00	2.68E-01	3.56E+00	2.77E-01
beta2_ct	3.49E+00	2.50E-01	3.49E+00	2.43E-01	3.50E+00	2.42E-01
beta2_ct	3.52E+00	2.33E-01	3.57E+00	2.28E-01	3.50E+00	2.45E-01
beta2_ct	3.16E+00	2.48E-01	3.13E+00	2.45E-01	3.15E+00	2.49E-01

*Supplemental of spatio-temporal patterns in communities*

beta2_ct	3.79E+00	1.55E-01	3.77E+00	1.54E-01	3.76E+00	1.55E-01
beta2_ct	3.49E+00	3.83E-01	3.46E+00	3.65E-01	3.40E+00	4.02E-01
beta2_ct	2.21E+00	5.40E-01	2.34E+00	5.32E-01	2.32E+00	5.47E-01
beta2_ct	5.62E+00	1.95E-01	5.63E+00	1.85E-01	5.64E+00	2.15E-01
beta2_ct	4.17E+00	1.40E-01	4.17E+00	1.27E-01	4.19E+00	1.39E-01
beta2_ct	2.41E+00	4.82E-01	2.41E+00	4.80E-01	2.39E+00	4.90E-01
beta2_ct	6.97E+00	1.33E-01	6.95E+00	1.32E-01	6.97E+00	1.41E-01
beta2_ct	5.17E+00	3.44E-01	5.19E+00	3.34E-01	5.27E+00	3.85E-01
beta2_ct	4.58E+00	1.23E-01	4.56E+00	1.22E-01	4.56E+00	1.29E-01
beta2_ct	3.25E+00	3.03E-01	3.31E+00	2.95E-01	3.31E+00	2.94E-01
beta2_ct	3.18E+00	3.08E-01	3.19E+00	2.99E-01	3.18E+00	3.09E-01
beta2_ct	4.81E+00	2.32E-01	4.85E+00	2.24E-01	4.86E+00	2.57E-01
beta2_ct	3.44E+00	3.36E-01	3.52E+00	3.29E-01	3.60E+00	3.29E-01
beta2_ct	3.59E+00	2.24E-01	3.64E+00	2.21E-01	3.69E+00	2.21E-01
beta2_ct	3.88E+00	2.07E-01	3.91E+00	2.04E-01	3.89E+00	2.18E-01
beta2_ct	3.36E+00	2.48E-01	3.32E+00	2.44E-01	3.34E+00	2.48E-01
beta2_ct	3.98E+00	1.20E-01	3.96E+00	1.18E-01	3.96E+00	1.19E-01
beta2_ct	2.76E+00	4.36E-01	2.65E+00	4.30E-01	2.62E+00	4.61E-01
beta2_ct	1.67E+00	7.43E-01	1.77E+00	7.39E-01	1.67E+00	7.51E-01
beta2_ct	5.24E+00	2.03E-01	5.19E+00	1.94E-01	5.17E+00	2.23E-01
beta2_ct	3.97E+00	1.46E-01	4.03E+00	1.33E-01	4.04E+00	1.45E-01
beta2_ct	2.95E+00	3.69E-01	2.99E+00	3.62E-01	2.99E+00	3.77E-01
beta2_ct	6.53E+00	1.34E-01	6.50E+00	1.32E-01	6.50E+00	1.41E-01
beta2_ct	4.05E+00	3.62E-01	4.00E+00	3.53E-01	4.00E+00	4.03E-01
beta2_ct	4.38E+00	1.29E-01	4.37E+00	1.28E-01	4.38E+00	1.35E-01
beta2_ct	1.46E+00	1.00E+00	1.50E+00	1.00E+00	1.52E+00	1.00E+00

Chapter 2

beta2_ct	3.50E+00	2.88E-01	3.53E+00	2.76E-01	3.51E+00	2.88E-01
beta2_ct	4.67E+00	2.33E-01	4.66E+00	2.26E-01	4.65E+00	2.60E-01
beta2_ct	2.54E+00	4.39E-01	2.59E+00	4.38E-01	2.54E+00	4.54E-01
beta2_ct	3.80E+00	2.02E-01	3.78E+00	2.02E-01	3.84E+00	2.00E-01
beta2_ct	3.89E+00	2.13E-01	4.01E+00	2.05E-01	4.02E+00	2.19E-01
beta2_ct	4.05E+00	1.89E-01	4.06E+00	1.83E-01	4.04E+00	1.89E-01
beta2_ct	4.03E+00	1.28E-01	4.00E+00	1.28E-01	4.03E+00	1.29E-01
beta2_ct	1.45E+00	6.82E-01	1.40E+00	6.81E-01	1.34E+00	7.05E-01
beta2_ct	3.45E+00	2.58E-01	3.57E+00	2.41E-01	3.55E+00	2.65E-01
beta2_ct	5.43E+00	2.08E-01	5.43E+00	1.98E-01	5.41E+00	2.26E-01
beta2_ct	4.15E+00	1.50E-01	4.13E+00	1.38E-01	4.14E+00	1.50E-01
beta2_ct	3.51E+00	2.76E-01	3.52E+00	2.71E-01	3.55E+00	2.88E-01
beta2_ct	6.44E+00	1.37E-01	6.42E+00	1.34E-01	6.44E+00	1.43E-01
beta2_ct	5.02E+00	3.54E-01	5.01E+00	3.44E-01	5.01E+00	3.95E-01
beta2_ct	4.46E+00	1.34E-01	4.44E+00	1.33E-01	4.46E+00	1.39E-01
beta2_ct	3.44E+00	2.94E-01	3.47E+00	2.90E-01	3.49E+00	2.90E-01
beta2_ct	4.11E+00	2.75E-01	4.14E+00	2.65E-01	4.10E+00	2.78E-01
beta2_ct	4.51E+00	2.44E-01	4.54E+00	2.36E-01	4.52E+00	2.67E-01
beta2_ct	2.84E+00	3.74E-01	2.84E+00	3.73E-01	2.87E+00	3.80E-01
beta2_ct	3.30E+00	3.44E-01	3.27E+00	3.43E-01	3.28E+00	3.44E-01
beta2_ct	3.82E+00	2.08E-01	3.82E+00	2.05E-01	3.82E+00	2.19E-01
beta2_ct	3.64E+00	1.91E-01	3.62E+00	1.81E-01	3.63E+00	1.91E-01
beta2_ct	4.03E+00	1.05E-01	4.02E+00	1.02E-01	4.03E+00	1.04E-01
beta2_ct	3.02E+00	4.14E-01	2.99E+00	4.05E-01	2.94E+00	4.37E-01
beta2_ct	2.01E+00	7.28E-01	2.09E+00	7.25E-01	2.03E+00	7.35E-01
beta2_ct	5.68E+00	1.99E-01	5.69E+00	1.89E-01	5.68E+00	2.18E-01



*Supplemental of spatio-temporal patterns in communities*

beta2_ct	4.20E+00	1.37E-01	4.21E+00	1.24E-01	4.23E+00	1.35E-01
beta2_ct	3.50E+00	3.00E-01	3.43E+00	3.02E-01	3.45E+00	3.17E-01
beta2_ct	6.18E+00	1.39E-01	6.16E+00	1.38E-01	6.20E+00	1.47E-01
beta2_ct	4.96E+00	3.51E-01	4.96E+00	3.42E-01	4.96E+00	3.93E-01
beta2_ct	4.60E+00	1.19E-01	4.58E+00	1.18E-01	4.58E+00	1.25E-01
beta2_ct	3.08E+00	3.74E-01	3.14E+00	3.67E-01	3.11E+00	3.69E-01
beta2_ct	3.25E+00	3.18E-01	3.23E+00	3.12E-01	3.28E+00	3.19E-01
beta2_ct	3.94E+00	2.57E-01	3.96E+00	2.50E-01	4.00E+00	2.78E-01
beta2_ct	3.12E+00	2.88E-01	3.24E+00	2.81E-01	3.24E+00	2.87E-01
beta2_ct	2.63E+00	5.10E-01	2.63E+00	5.10E-01	2.65E+00	5.09E-01
beta2_ct	3.47E+00	2.35E-01	3.51E+00	2.32E-01	3.48E+00	2.45E-01
beta2_ct	4.15E+00	1.63E-01	4.16E+00	1.56E-01	4.12E+00	1.64E-01
beta2_ct	4.52E+00	9.16E-02	4.50E+00	8.94E-02	4.50E+00	9.16E-02
beta2_ct	3.17E+00	3.69E-01	3.16E+00	3.52E-01	3.13E+00	3.88E-01
beta2_ct	1.83E+00	7.39E-01	1.98E+00	7.31E-01	1.89E+00	7.46E-01
beta2_ct	5.37E+00	2.01E-01	5.40E+00	1.91E-01	5.39E+00	2.20E-01
beta2_ct	4.46E+00	1.34E-01	4.48E+00	1.21E-01	4.49E+00	1.33E-01
beta2_ct	2.80E+00	3.36E-01	2.76E+00	3.33E-01	2.79E+00	3.45E-01
beta2_ct	6.95E+00	1.37E-01	6.95E+00	1.35E-01	6.95E+00	1.44E-01
beta2_ct	4.90E+00	3.49E-01	5.00E+00	3.39E-01	5.02E+00	3.90E-01
beta2_ct	4.60E+00	1.29E-01	4.59E+00	1.28E-01	4.57E+00	1.35E-01
beta2_ct	2.57E+00	4.31E-01	2.61E+00	4.26E-01	2.64E+00	4.24E-01
beta2_ct	3.02E+00	3.30E-01	3.04E+00	3.22E-01	3.00E+00	3.32E-01
beta2_ct	3.46E+00	2.98E-01	3.52E+00	2.91E-01	3.55E+00	3.16E-01
beta2_ct	2.51E+00	5.19E-01	2.53E+00	5.16E-01	2.63E+00	5.18E-01
beta2_ct	3.41E+00	2.47E-01	3.45E+00	2.45E-01	3.48E+00	2.45E-01

Chapter 2

beta2_ct	3.31E+00	2.50E-01	3.30E+00	2.49E-01	3.24E+00	2.62E-01
beta2_ct	4.07E+00	1.77E-01	4.02E+00	1.72E-01	4.04E+00	1.77E-01
beta2_ct	4.20E+00	1.04E-01	4.20E+00	1.01E-01	4.20E+00	1.03E-01
beta2_ct	3.05E+00	3.87E-01	3.07E+00	3.69E-01	3.03E+00	4.06E-01
beta2_ct	3.16E+00	3.97E-01	3.36E+00	3.89E-01	3.31E+00	4.05E-01
beta2_ct	5.20E+00	2.01E-01	5.19E+00	1.91E-01	5.19E+00	2.20E-01
beta2_ct	3.96E+00	1.47E-01	3.97E+00	1.35E-01	3.99E+00	1.46E-01
beta2_ct	2.88E+00	3.56E-01	2.87E+00	3.53E-01	2.83E+00	3.69E-01
beta2_ct	6.65E+00	1.36E-01	6.62E+00	1.34E-01	6.63E+00	1.43E-01
beta2_ct	5.39E+00	3.43E-01	5.43E+00	3.33E-01	5.45E+00	3.85E-01
beta2_ct	4.44E+00	1.22E-01	4.42E+00	1.21E-01	4.45E+00	1.27E-01
beta2_ct	3.02E+00	3.64E-01	3.02E+00	3.63E-01	3.01E+00	3.64E-01
beta2_ct	4.23E+00	2.57E-01	4.24E+00	2.47E-01	4.20E+00	2.61E-01
beta2_ct	3.76E+00	2.54E-01	3.79E+00	2.47E-01	3.76E+00	2.77E-01
beta2_ct	2.94E+00	3.62E-01	3.03E+00	3.52E-01	2.97E+00	3.63E-01
beta2_ct	2.67E+00	4.59E-01	2.67E+00	4.59E-01	2.64E+00	4.61E-01
beta2_ct	3.95E+00	2.08E-01	3.97E+00	2.05E-01	3.97E+00	2.19E-01
beta2_ct	3.92E+00	1.96E-01	3.87E+00	1.89E-01	3.90E+00	1.96E-01
beta2_ct	3.86E+00	1.23E-01	3.83E+00	1.21E-01	3.82E+00	1.23E-01
beta2_ct	3.74E+00	3.42E-01	3.58E+00	3.30E-01	3.71E+00	3.60E-01
beta2_ct	2.42E+00	5.38E-01	2.49E+00	5.31E-01	2.44E+00	5.46E-01
beta2_ct	5.31E+00	2.03E-01	5.29E+00	1.93E-01	5.29E+00	2.22E-01
beta2_ct	4.24E+00	1.42E-01	4.22E+00	1.30E-01	4.25E+00	1.41E-01
beta2_ct	2.71E+00	3.98E-01	2.69E+00	3.97E-01	2.70E+00	4.07E-01
beta2_ct	6.11E+00	1.38E-01	6.11E+00	1.36E-01	6.11E+00	1.45E-01
beta2_ct	5.00E+00	3.49E-01	4.94E+00	3.41E-01	5.02E+00	3.91E-01

*Supplemental of spatio-temporal patterns in communities*

beta2_ct	4.54E+00	1.23E-01	4.52E+00	1.22E-01	4.53E+00	1.28E-01
beta2_ct	3.03E+00	3.14E-01	3.01E+00	3.16E-01	3.05E+00	3.12E-01
beta2_ct	3.78E+00	2.90E-01	3.82E+00	2.79E-01	3.81E+00	2.91E-01
beta2_ct	3.68E+00	2.63E-01	3.70E+00	2.57E-01	3.71E+00	2.84E-01
beta2_ct	3.29E+00	2.80E-01	3.37E+00	2.71E-01	3.37E+00	2.80E-01
beta2_ct	2.86E+00	3.90E-01	2.79E+00	3.93E-01	2.86E+00	3.91E-01
beta2_ct	4.11E+00	2.14E-01	4.04E+00	2.16E-01	4.07E+00	2.27E-01
beta2_ct	3.57E+00	2.43E-01	3.54E+00	2.38E-01	3.52E+00	2.43E-01
beta2_ct	4.15E+00	1.07E-01	4.13E+00	1.05E-01	4.14E+00	1.06E-01
beta2_ct	3.18E+00	3.90E-01	3.14E+00	3.74E-01	3.14E+00	4.07E-01
beta2_ct	3.01E+00	3.68E-01	3.01E+00	3.60E-01	3.08E+00	3.71E-01
beta2_ct	5.08E+00	2.07E-01	5.06E+00	1.97E-01	5.03E+00	2.26E-01
beta2_ct	4.07E+00	1.39E-01	4.08E+00	1.26E-01	4.08E+00	1.38E-01
beta2_ct	2.98E+00	3.25E-01	2.96E+00	3.25E-01	2.96E+00	3.39E-01
beta2_ct	6.37E+00	1.41E-01	6.34E+00	1.39E-01	6.35E+00	1.48E-01
beta2_ct	4.68E+00	3.53E-01	4.68E+00	3.43E-01	4.71E+00	3.93E-01
beta2_ct	4.87E+00	1.07E-01	4.87E+00	1.06E-01	4.88E+00	1.13E-01
beta2_ct	3.75E+00	1.82E-01	3.76E+00	1.78E-01	3.78E+00	1.79E-01
beta2_ct	2.81E+00	3.40E-01	2.82E+00	3.32E-01	2.81E+00	3.40E-01
beta2_ct	3.41E+00	2.98E-01	3.41E+00	2.92E-01	3.39E+00	3.17E-01
beta2_ct	3.17E+00	3.39E-01	3.21E+00	3.36E-01	3.20E+00	3.43E-01
beta2_ct	3.16E+00	3.65E-01	3.10E+00	3.66E-01	3.15E+00	3.65E-01
beta2_ct	3.75E+00	2.25E-01	3.76E+00	2.22E-01	3.75E+00	2.36E-01
beta2_ct	4.25E+00	1.62E-01	4.24E+00	1.53E-01	4.25E+00	1.62E-01
beta2_ct	4.47E+00	8.86E-02	4.46E+00	8.62E-02	4.45E+00	8.80E-02
beta2_ct	3.59E+00	3.53E-01	3.57E+00	3.35E-01	3.55E+00	3.72E-01

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beta2_ct	2.12E+00	7.28E-01	2.14E+00	7.25E-01	2.13E+00	7.33E-01
beta2_ct	5.31E+00	2.00E-01	5.31E+00	1.90E-01	5.33E+00	2.19E-01
beta2_ct	4.44E+00	1.31E-01	4.46E+00	1.18E-01	4.47E+00	1.31E-01
beta2_ct	2.75E+00	3.96E-01	2.71E+00	3.95E-01	2.74E+00	4.07E-01
beta2_ct	6.70E+00	1.38E-01	6.70E+00	1.36E-01	6.73E+00	1.45E-01
beta2_ct	5.68E+00	3.44E-01	5.66E+00	3.34E-01	5.67E+00	3.86E-01
beta2_ct	4.94E+00	1.13E-01	4.91E+00	1.11E-01	4.91E+00	1.19E-01
beta2_ct	3.80E+00	1.98E-01	3.81E+00	1.96E-01	3.81E+00	1.98E-01
beta2_ct	3.61E+00	3.01E-01	3.64E+00	2.91E-01	3.63E+00	3.02E-01
beta2_ct	4.05E+00	2.66E-01	4.07E+00	2.60E-01	4.12E+00	2.86E-01
beta2_ct	2.71E+00	4.28E-01	2.77E+00	4.23E-01	2.81E+00	4.28E-01
beta2_ct	2.88E+00	4.18E-01	2.88E+00	4.19E-01	2.91E+00	4.18E-01
beta2_ct	4.09E+00	2.09E-01	4.11E+00	2.06E-01	4.09E+00	2.21E-01
beta2_ct	4.02E+00	1.69E-01	4.01E+00	1.62E-01	3.99E+00	1.71E-01
beta2_ct	4.49E+00	8.53E-02	4.49E+00	8.27E-02	4.49E+00	8.47E-02
beta2_ct	2.44E+00	4.24E-01	2.33E+00	4.22E-01	2.49E+00	4.48E-01
beta2_ct	1.94E+00	7.38E-01	1.99E+00	7.36E-01	1.88E+00	7.51E-01
beta2_ct	4.99E+00	2.08E-01	5.01E+00	1.98E-01	4.94E+00	2.28E-01
beta2_ct	4.18E+00	1.49E-01	4.23E+00	1.36E-01	4.23E+00	1.49E-01
beta2_ct	3.29E+00	2.81E-01	3.33E+00	2.75E-01	3.27E+00	2.95E-01
beta2_ct	7.18E+00	1.38E-01	7.18E+00	1.36E-01	7.14E+00	1.45E-01
beta2_ct	5.79E+00	3.48E-01	5.76E+00	3.39E-01	5.77E+00	3.92E-01
beta2_ct	5.31E+00	1.05E-01	5.30E+00	1.03E-01	5.32E+00	1.11E-01
beta2_ct	3.94E+00	1.45E-01	3.95E+00	1.41E-01	3.98E+00	1.41E-01
beta2_ct	4.05E+00	2.75E-01	4.08E+00	2.65E-01	4.01E+00	2.79E-01
beta2_ct	4.68E+00	2.47E-01	4.69E+00	2.40E-01	4.63E+00	2.73E-01

*Supplemental of spatio-temporal patterns in communities*

beta2_ct	2.69E+00	4.70E-01	2.75E+00	4.65E-01	2.70E+00	4.79E-01
beta2_ct	3.59E+00	2.28E-01	3.60E+00	2.27E-01	3.60E+00	2.30E-01
beta2_ct	3.57E+00	2.24E-01	3.58E+00	2.21E-01	3.61E+00	2.33E-01
beta2_ct	4.01E+00	1.71E-01	3.98E+00	1.65E-01	3.99E+00	1.71E-01
beta2_ct	4.62E+00	8.24E-02	4.60E+00	7.93E-02	4.60E+00	8.20E-02
L2_z	1.23E+00	8.35E-02	-1.41E+00	8.57E-02	1.43E+00	8.75E-02
L2_z	-2.77E-10	1.74E-01	-3.19E-02	1.32E+00	1.38E-01	2.94E-01
L2_z	-1.37E+00	2.42E-02	1.40E+00	2.43E-02	-1.42E+00	2.41E-02
L2_z	-5.46E-01	2.69E-02	-5.98E-01	2.44E-02	-5.93E-01	2.52E-02
L2_z	5.86E-01	7.73E-02	-5.79E-01	7.52E-02	5.60E-01	7.84E-02
L2_z	1.24E+00	1.79E-02	1.24E+00	1.78E-02	-1.26E+00	1.76E-02
L2_z	2.08E+00	4.87E-02	-2.10E+00	4.84E-02	-2.15E+00	4.86E-02
L2_z	8.42E-01	2.34E-02	-8.48E-01	2.30E-02	-8.52E-01	2.28E-02
L2_z	4.07E-12	1.22E-01	1.93E-11	1.25E-01	-1.33E-10	1.29E-01
L2_z	1.77E+00	5.63E-02	1.81E+00	5.52E-02	-1.83E+00	5.47E-02
L2_z	-1.74E+00	3.95E-02	-1.76E+00	3.94E-02	1.76E+00	3.92E-02
L2_z	-4.69E-11	1.17E-01	9.39E-10	1.28E-01	3.24E-11	1.24E-01
L2_z	3.13E-12	9.69E-02	-4.74E-10	9.46E-02	3.30E-11	9.91E-02
L2_z	-9.97E-01	3.92E-02	-1.00E+00	3.90E-02	-1.02E+00	3.88E-02
L2_z	3.57E-01	5.88E-02	4.16E-01	4.78E-02	-4.28E-01	4.67E-02
L2_z	3.71E-01	2.74E-02	-3.77E-01	2.71E-02	-3.90E-01	2.64E-02
L_omega2_z	5.75E-01	1.55E-01	-5.87E-01	2.42E-01	3.32E-01	1.26E-01
L_omega2_z	1.93E-01	1.42E-01	-3.32E-01	2.25E-01	1.37E-01	1.25E-01
L_omega2_z	1.25E-01	1.20E-01	-2.60E-01	1.93E-01	1.53E-01	1.08E-01
L_omega2_z	2.19E-01	7.14E-02	-1.86E-01	1.10E-01	1.13E-01	8.16E-02
L_omega2_z	1.27E-01	1.10E-01	-6.92E-02	1.69E-01	1.33E-01	9.76E-02

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L_omega2_z	-7.83E-02	1.46E-01	-1.83E-01	9.99E-02	9.24E-02	1.12E-01
L_omega2_z	7.97E-02	6.98E-02	-4.14E-02	9.29E-02	1.56E-02	6.92E-02
L_omega2_z	2.69E-02	2.26E-01	1.63E-01	1.27E-01	-2.24E-02	1.17E-01
L_omega2_z	-1.93E-01	6.26E-02	-1.27E-01	1.59E-01	1.27E-01	6.69E-02
L_omega2_z	5.64E-02	1.21E-01	4.92E-02	1.75E-01	-8.76E-03	1.28E-01
L_omega2_z	1.82E-01	2.05E-01	-3.40E-02	2.88E-01	1.43E-01	1.66E-01
L_omega2_z	-1.54E-01	2.44E-01	-3.07E-01	1.75E-01	1.69E-01	1.74E-01
L_omega2_z	1.31E-01	7.93E-02	-1.23E-01	1.14E-01	1.20E-01	6.40E-02
L_omega2_z	-6.84E-02	2.84E-01	2.90E-01	1.16E-01	-7.40E-02	1.15E-01
L_omega2_z	-2.41E-01	1.06E-01	-8.21E-02	2.76E-01	1.17E-01	9.71E-02
L_omega2_z	2.13E-01	2.07E-01	-5.03E-01	3.31E-01	3.99E-01	2.04E-01
L_omega2_z	-7.42E-01	4.16E-01	8.71E-01	4.59E-01	-5.19E-01	2.30E-01
L_omega2_z	-3.41E-01	8.70E-01	4.33E-01	8.23E-01	2.01E-01	5.10E-01
L_omega2_z	4.17E-03	6.23E-02	3.58E-02	9.63E-02	-2.75E-02	5.52E-02
L_omega2_z	1.62E-02	1.88E-01	1.80E-01	1.03E-01	-5.90E-02	8.58E-02
L_omega2_z	-1.59E-01	5.77E-02	-8.54E-02	1.66E-01	8.87E-02	7.10E-02
L_omega2_z	-4.27E-02	1.03E-01	1.37E-01	1.53E-01	-6.47E-02	8.70E-02
L_omega2_z	1.38E-01	9.80E-02	-3.04E-02	2.02E-01	9.60E-02	7.53E-02
L_omega2_z	-3.17E-02	1.95E-01	-1.80E-01	1.58E-01	1.67E-02	1.35E-01
L_omega2_z	-5.40E-02	1.43E-01	1.99E-01	2.20E-01	-1.47E-01	1.52E-01
L_omega2_z	3.49E-01	4.68E-01	-6.68E-01	2.08E-01	3.00E-01	2.57E-01
L_omega2_z	3.98E-01	4.09E-01	-6.40E-02	5.83E-01	-2.77E-01	2.77E-01
L_omega2_z	-2.08E-02	7.55E-02	2.83E-03	1.07E-01	1.86E-02	6.66E-02
L_omega2_z	-8.31E-02	1.24E-01	7.73E-02	1.48E-01	-6.20E-02	6.37E-02
L_omega2_z	-8.96E-02	1.27E-01	1.38E-01	1.34E-01	2.78E-02	9.88E-02
L_omega2_z	-2.14E-01	1.42E-01	2.06E-01	2.15E-01	-1.32E-01	1.36E-01

*Supplemental of spatio-temporal patterns in communities*

L_omega2_z	-1.46E-01	2.18E-01	2.25E-01	2.36E-01	-1.60E-01	1.53E-01
L_omega2_z	-1.59E-01	2.06E-01	2.12E-01	3.08E-01	1.27E-01	1.72E-01
L_omega2_z	8.67E-02	1.05E-01	-3.48E-02	1.49E-01	3.99E-02	8.35E-02
L_omega2_z	6.57E-02	1.50E-01	9.85E-02	1.96E-01	3.74E-02	7.50E-02
L_omega2_z	-1.05E-01	1.26E-01	-1.83E-01	1.66E-01	2.62E-02	1.01E-01
L_omega2_z	-1.11E-01	8.62E-02	1.77E-01	1.19E-01	-1.23E-01	6.99E-02
L_omega2_z	1.30E-01	9.70E-02	-3.54E-02	1.44E-01	5.42E-02	6.59E-02
L_omega2_z	-5.67E-02	1.72E-01	-1.22E-01	1.26E-01	-1.62E-02	1.06E-01
L_omega2_z	2.49E-01	1.19E-01	-9.93E-02	1.76E-01	2.54E-02	1.18E-01
L_omega2_z	3.80E-01	1.02E-01	-3.14E-01	3.56E-01	2.97E-01	7.81E-02
L_omega2_z	2.09E-02	4.39E-01	-3.79E-01	2.95E-01	2.43E-02	2.72E-01
L_omega2_z	1.98E-01	5.28E-02	-2.31E-01	8.37E-02	1.22E-01	4.23E-02
L_omega2_z	2.57E-02	1.31E-01	4.42E-02	1.02E-01	3.41E-02	6.84E-02
L_omega2_z	-1.02E-01	6.05E-02	-8.93E-02	1.15E-01	5.47E-02	5.40E-02
L_epsilon2_z	-1.35E+00	1.57E-01	1.69E+00	4.22E-01	-9.76E-01	1.23E-01
L_epsilon2_z	-5.78E-01	1.66E-01	7.17E-01	2.70E-01	-3.78E-01	1.45E-01
L_epsilon2_z	-5.44E-01	1.69E-01	-5.97E-01	2.77E-01	-4.65E-01	1.49E-01
L_epsilon2_z	-5.73E-01	8.66E-02	7.60E-01	2.10E-01	-4.09E-01	7.89E-02
L_epsilon2_z	-6.78E-01	8.05E-02	-8.69E-01	2.18E-01	-5.32E-01	6.45E-02
L_epsilon2_z	-4.45E-01	6.14E-02	4.54E-01	1.24E-01	-2.90E-01	4.42E-02
L_epsilon2_z	-1.58E-01	6.01E-02	-1.24E-01	8.21E-02	-7.57E-02	5.19E-02
L_epsilon2_z	3.53E-01	1.59E-01	-4.63E-01	2.14E-01	3.71E-01	1.20E-01
L_epsilon2_z	2.11E-01	1.40E-01	3.42E-01	1.97E-01	2.10E-01	1.12E-01
L_epsilon2_z	7.36E-02	6.11E-02	-1.25E-01	9.77E-02	2.06E-02	5.72E-02
L_epsilon2_z	-4.92E-01	5.12E-02	-7.02E-01	1.68E-01	-3.69E-01	3.90E-02
L_epsilon2_z	-1.35E+00	1.31E-01	1.83E+00	4.41E-01	-9.63E-01	1.12E-01

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L_epsilon2_z	-4.83E-01	1.44E-01	-6.79E-01	2.65E-01	-5.13E-01	1.28E-01
L_epsilon2_z	-1.07E-01	5.21E-02	6.07E-02	7.59E-02	-4.95E-02	4.73E-02
L_epsilon2_z	2.08E-01	5.11E-02	3.02E-01	9.62E-02	2.01E-01	4.11E-02
L_epsilon2_z	1.03E-02	1.12E-01	-4.57E-02	1.48E-01	4.64E-02	9.66E-02
L_epsilon2_z	3.21E-01	1.22E-01	3.83E-01	1.83E-01	2.01E-01	9.71E-02
L_epsilon2_z	3.35E-01	1.23E-01	-4.39E-01	1.90E-01	2.04E-01	9.87E-02
L_epsilon2_z	-7.78E-01	1.15E-01	-9.57E-01	2.54E-01	-4.71E-01	8.25E-02
L_epsilon2_z	-2.11E-01	1.20E-01	2.62E-01	1.86E-01	-3.50E-03	1.13E-01
L_epsilon2_z	-8.84E-01	9.79E-02	-1.15E+00	2.94E-01	-7.39E-01	7.04E-02
L_epsilon2_z	-3.64E-01	1.25E-01	4.60E-01	2.12E-01	-2.20E-01	1.18E-01
L_epsilon2_z	-2.89E-01	1.25E-01	-3.87E-01	2.03E-01	-2.78E-01	1.13E-01
L_epsilon2_z	-3.29E-01	1.02E-01	3.56E-01	1.66E-01	-2.27E-01	9.17E-02
L_epsilon2_z	-2.18E-01	9.43E-02	-4.02E-01	1.59E-01	-1.78E-01	7.88E-02
L_epsilon2_z	4.16E-01	9.73E-02	-6.18E-01	1.95E-01	2.70E-01	8.49E-02
L_epsilon2_z	3.63E-01	9.59E-02	4.34E-01	1.60E-01	3.55E-01	7.94E-02
L_epsilon2_z	2.94E-01	9.32E-02	-3.35E-01	1.41E-01	1.47E-01	8.32E-02
L_epsilon2_z	-2.15E-03	8.41E-02	1.23E-01	1.18E-01	6.54E-02	6.89E-02
L_epsilon2_z	-4.50E-02	4.70E-02	2.21E-02	6.65E-02	-2.92E-02	4.21E-02
L_epsilon2_z	-1.46E-01	4.30E-02	-2.16E-01	7.44E-02	-9.22E-02	3.63E-02
logkappa2	-2.27E+00	1.19E-01	-1.90E+00	2.59E-01	-2.68E+00	1.11E-01



## Chapter 3. Spatio-Temporal Trends of Functional Indices for Marine Species Communities in a Changing Climate

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### **Abstract**

#### Aim

Assess how spatial and spatio-temporal functional distribution affects community resilience to anthropogenic and environmental pressures.

#### Location

Europe

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### Methods

We applied the Autoregressive Spatio-Temporal Clustering model (ASTECC) on 16 species in the Eastern English Channel using historical data from the Channel Ground Fishery Survey. For the 16 species, biological and physiological traits data were collected. Each traits represent a function within the community. First, we calculated the functional richness, evenness and divergence for each community defined by ASTECC. Second, we calculated the community-level weighted means of functional traits to determine the overall linear and cyclical trends.

### Results

The Autoregressive Spatio-Temporal Cluster model fitted on 16 species defined two spatial and spatio-temporal statistical communities. Spatial community one (S1) exhibited on average a lower functional evenness than spatial community two (S2). Spatio-temporal community one (ST1) displayed a functional evenness, similar to spatial communities. However, spatio-temporal community two (ST2) was organized differently and showed a superior functional evenness. Conversely, functional evenness and functional divergence of the spatial community was on average higher for S1 and lower for S2. ST1 exhibited close level of divergence to that of S1 and S2, whereas ST2 had a divergence significantly lower than the three other communities. We defined that quantitative traits cycles through at least two decadal year patterns.

### Main conclusion

Given the results, the status of each species and which community they belong to, we can conclude that communities with traits with narrow ranges display less resilience. Evenness in the

distribution of abundance of functional traits in the functional space is detrimental to community stability. Moreover, this study highlights how drawing conclusions from the functional divergence and functional evenness in the spatio-temporal scenario is more reliable than a time stepped spatial approach. The spatial scenario may be a good method to study the impact of habitat destruction on the ecosystem. However, for proactive conservation and management, spatio-temporal scenarios draw a clearer picture of the communities' resilience.

Keywords

Functional indices, Spatio-temporal modelling, Cluster analysis, Community resilience

## **1. Introduction**

Conservation shifted in the late 90s from being mainly species focused to ecosystem focused through community ecology (Palmer et al., 1997). However, natural resources managers and regulatory agencies are, to this day, struggling to find methods that can translate what is happening at the ecosystem level. They not only need to gather how stable the ecosystem is but also how resilient an ecosystem will be when under environmental or anthropogenic pressure. Functions within an ecosystem supports the processes maintaining stability within the ecosystem (Costanza et al., 1997; Suding et al., 2008; De Groot et al., 2010). The capacity of a system to maintain stability depends on its plasticity to environmental change, whether anthropogenically or naturally induced. Plasticity is not only based on the individual traits of a species but also on the group of traits and their organization in the communities hosted by an ecosystem (e.g., Slocum and Mendelssohn, 2008; Prober and Dunlop, 2011).

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The biotic properties of a species or a group of species determine the functional traits they express in the communities. Thus, functional traits are defined here as the species phenotypic characteristics that influence species fitness and are directly linked to community functions (Violle et al., 2007; Benedetti et al., 2015). These functional traits can be morphological, physiological, structural, phenological or behavioral (Violle et al., 2007). The resilience of a community will depend on two components. First the response traits, which affects the resistance of that community, and second the effect traits which affects the recovery within the community (Diaz and Cabido, 2001; Lavorel and Garnier, 2002; Naeem and Wright, 2003). These components are measured by the magnitude of disturbance that can be absorbed by the community without registering a change in functioning, and by the time needed for the community to return to the initial functional state, respectively (France and Duffy, 2006; Sterk, et al., 2013).

Previous studies on resilience using a functional approach focus on the species located in the studied area and look at how the species composition evolves in time. Traits can be morphological (e.g. maximum length), physiological (e.g. longevity preferred temperature), behavioral (e.g. migration, trophic level) or linked to life history (e.g. age of maturity). This mainly focuses on the number of traits present, which is directly linked with species richness. It is well assumed that the richer a community, the more resilient it is (Reich et al., 2012) as the diversity of responses to a disturbance in the environment allows for a diversity of functions to be maintained (Reich et al., 2012; Van der Linden et al., 2012). This is otherwise known as the insurance hypothesis (Naeem and Li, 1997; Yachi and Loreau, 1999).

At community level, to identify the main traits, the abundance at which these traits are found is primordial, but often dismissed. Communities can be defined as: 1) a group of species pertaining

to the same habitat (Roughgarden and Diamond, 1986), 2) a group of species that are present in the same habitat at the same time (Begon et al., 1990; Mittelbach and McGill, 2019) 3) a group of species that interact directly or indirectly within a similar habitat over time (Fauth et al., 1996; Morin, 2011; Stroud et al., 2015). To simplify terminology, our communities are the statistical units defined by the ASTEC model and can be interpreted as any of these three definitions (Vertpre et al., In press). The abundance of a trait in the community is the expression of the abundance of the various species expressing this trait. Vileger et al., (2008), computed three functional indices that potentially account for this hypothesis: functional richness, functional divergence and functional evenness. These summary indices are a good approach to visualize the range of traits present in communities and assume how resilient they might be. While these indices aim to be spatio-temporal, the hypothesis is that they are a snapshot of community functioning at different timesteps. There is a need to build indices with the ability to fully measure trends in functionality and grasp functional shifts.

Moreover, most functional studies in the marine environment due to the scarcity of data tend to pre-define the communities on which the analysis will be performed based on expert knowledge or on similarities in functionality. The latter leads to functional analysis with the strong assumption that functions within a community are homogenous. Hence, assuming all the species in that community react similarly to a disturbance. When that might be true in some instances, the resilience measured in ecosystems suggests that this is not likely the norm.

This study hopes to truly encompass how communities will respond to environmental change. To do so, it seems important not only to characterize the diversity of their traits, but also to understand which species are interacting and how similarly the abundance of species respond to

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environmental changes (Gitay and Noble, 1997; Barnett and Beisner, 2007; Vogt et al., 2013; Pomerleau et al., 2015). Summarizing this information with changes in functional trends will help predict how communities will respond to a disturbance. Studying functional trends in this framework will reveal the most stable communities, but will also reveal the least resilient community, thus emphasizing the focal point for management efforts.

To explore these questions, we studied the Eastern English Channel (EEC). EEC experiences strong changes as the environmental stressors and socio-economic developments are constantly increasing. Thus, EEC has high anthropogenic impacts, e.g. shipping, aquaculture, fisheries (Dauvin, 2008; Martin et al., 2009). Indeed, fish communities and habitats are heavily exploited (Martin et al., 2012), which directly impacts functioning of the whole ecosystem. The EEC is also a region that presently lacks sufficient information to give a comprehensive answer regarding management of endangered fish species that are of commercial importance like skates and benthic sharks (Dulvy et al., 2000; Ellis et al., 2011). For these reasons, the EEC is particularly stimulating to understand the responses of community to environmental change and human pressure. Moreover, it is a marine subregion that is a management unit of the Marine Strategy Framework Directive, in which management actions are being designed and should be implemented to maintain a good ecological status of the ecosystems (Sala et al., 2018). Consequently, there is a real need to define new functional indices for communities present in this ecosystem, and more broadly, for the marine ecosystems.

To understand the impact of environmental change on the communities of the EEC the present study will undertake the development of functional indices.

To this end, we will assess the evolution of trends in functional indices and functional traits in a new statistical framework for 16 important species of the EEC, as defined by Vert-Pré et al. (In Press). Finally, with the help of this analysis, we will give recommendations regarding the status of species of interest for conservation and fishery management.

## **2. Materials and Methods**

### **2.1. Data**

Counts, fishing hauls, area swept in km square were extracted from the yearly standardized Channel groundfish survey (CGFS) for 108 species with time series from 1988 to 2014. The Gwen Drez vessel runs 30minutes hauls, at four knots, using a 10 meters Very High Vertical Opening (VHVO) bottom trawl. The survey runs between the 15<sup>th</sup> of September and the 15<sup>th</sup> of November (Foveau et al., 2017).

We started the time series at year 1995 (year at which the survey became standardized) and eliminated 70 species with gap years and 22 species that prevented the model from converging due to extreme high variance. In these 22 species, we rejected three species (*Trisopterus minutus*, *Trisopterus luscus*, *Trachurus trachurus*) that constitute 62% of the amount of catches. That would highly skew the results of any statistical analysis. Therefore, we focused on the 16 species that represent 36% of the total sampled abundance. Finally, out of 108 species a total of 16 species were selected for the analysis. These species represent some of the most resilient and evenly distributed species of the fish and cephalopod community of the EEC. For the 16 species, biological and physiological data were collected as described in Table S1.

## 2.2. Statistical communities

We identified the statistical communities present in the EEC using the Autoregressive Spatio-Temporal Cluster (ASTECC) model described in Vert-pre et al. (In press). This model combined a zero-inflated Poisson with latent predictors using the package ‘vast’ (Thorson and Barnett, 2017) and a hierarchical clustering analysis performed with the package ‘pvclust’ (Shimodaira, 2004). We used the best fit of the spatio-temporal model corresponding to a 522km<sup>2</sup> scale (Vert-pre et al., In press).

From the VAST density output we calculated the Indices of abundance for each species:

$$I_{c,t} = \sum_{x=1}^{60} (a_x \times d_{x,c,t})$$

where  $a_x$  is the area of knot  $x$  and  $d_{x,c,t}$  is the density at knot  $x$ , for species  $c$  at time  $t$ .

## 2.3. Functional indices

Mason et al. (2005) suggests that functional diversity can be summarized by three complementary indices: functional richness, functional diversity and functional evenness. To calculate these functional indices, we first needed to set the convex hull volume (Cv), the smallest volume defined by a set of vertices in a Euclidian plane (Barber et al. 1996). These vertices represented the species location given the range of their ecological strategies (Cornwell et al., 2006). These strategies were a function of the functional traits (Tab. 1). The calculation of Cv was undertaken using a Quick



hull algorithm, which is well studied and described in full in Barber et al. (1996). As the Cv was defined we could calculate each index.

As described in Villeger et al. (2008), we computed the three indices in Rv3.4.2 using the package ‘dbFD’. Given the total functional space defined by the species of a community, functional richness represents the functional space occupied by the species of the community given the maxima and minima of each traits. The functional richness is one if all the species have highly distinctive functional traits, and zero if all the species have the same range for each functional trait.

The second index, functional divergence (*Fd*) represents how far from the traits range center of gravity are the most abundant species of the community. The *Fd* is close to zero if the most abundant species have traits that are close to the center of gravity in the volume defined by the range of traits from the species of the community. It is one in the opposite scenario. The coordinate of the center of gravity of the convex hull was defined as followed:

$$g_k = \frac{1}{V} \sum_1^v x_{ik}$$

where *V* was the number of species forming the vertices of the convex hull volume,  $x_{ik}$  was the coordinate of species *i* and trait *k*.

Then, we calculated the Euclidian distance between each species location and the center of gravity:

$$dG_i = \sqrt{\sum_k^T x_{ik} - g_k}$$

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From the Euclidian distance we calculated the average distance for species and across traits:

$$\overline{dG} = \frac{1}{S} \sum_1^S dG_i$$

The functional divergence across species was then the ratio between the sum of abundance-weighted deviances and the absolute abundance-weighted deviances from the center of gravity.

$$Fd = \frac{\sum_1^S w_i \times (dG_i - \overline{dG}) + \overline{dG}}{\sum_1^S w_i \times |dG_i - \overline{dG}| + \overline{dG}}$$

where  $w_i$  was the relative abundance of species  $i$ . The index ranged between 0 and 1 as we added  $\overline{dG}$  to the denominator and numerator.

The third index, functional evenness (Fe) measured how abundance of species was distributed in the trait volume defined by the species of the community, and how the species were distributed given the functional gradient. Fe is independent from functional richness and functional divergence. It is close to one if the abundance within the community are evenly distributed and each species in the functional trait volume is equidistant.

We calculated the Fe in two steps. First, we calculated the minimum spanning tree (MST), which is a tree that has branches linking every point contained in the volume defined by the species traits. For each branch of length  $l$  we calculated, the weighted evenness:

$$EW_l = \frac{d(i,j)}{w_i + w_j}$$

where  $d(i, j)$  was the distance between species  $i$  and species  $j$  in the functional trait volume.  $w_i$  and  $w_j$  were the relative abundance of species  $i$  and species  $j$ .

Then was calculated the Partial weighted evenness that is the proportion represented by each evenness for this tree.

$$PEW_l = \frac{EW_l}{\sum_{l=1}^{S-1} EW_l}$$

Finally, the Functional evenness is

$$F_e = \frac{\sum_1^{S-1} \min\left(PEW_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

Where the index was standardized with  $\frac{1}{S-1}$  to constrain it between 0 and 1 and to integrate out the effect of the number of species  $S$  present in the community.

#### 2.4. Traits trends.

To analyze the trends of each trait from 1995 to 2014 for each community and compare it to what trends would be seen if these communities were not detected, we calculated the community-level weighted means of functional traits using the package ‘dbFD’. Then, we fitted two models to each time series. To determine the overall trend, we fitted a linear model, then an ANOVA was performed to test the significance of the slope. To find cyclical patterns in the time series we fitted a quadratic nonparametric regression. The loess model was fitted with 75% smoothing span using the ‘loess’ package in R. (Cleveland, 1988).

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We compared these indices and mean functional traits time series for the entire 16 species, the spatial community one (S1), spatial community two (S2), spatio-temporal community one (ST1) and the spatio-temporal community two (ST2).

## 3. Results

At a 522km<sup>2</sup> scale the Autoregressive Spatio-Temporal Cluster model fitted on 16 species defined two spatial and spatio-temporal statistical communities (Fig. 1). The first spatial community (S1) constituted 98% probability of occurrence composed of *Raja clavata*, *Chelidonichthys lucernus*, *Loligo sp.*, *Scophthalmus maximus*, *Merlangius merlangus* and *Scomber scombrus*. The second spatial community (S2) constituted 93% probability of occurrence composed of *Galeorhinus galeus*, *Scophthalmus rhombus*, *Agonus cataphractus*, *Zeus faber*, *Trigloporus lastoviza*, *Alosa sp.*, *Callionymus sp.*, *Sardina pilchardus*, *Raja undulata*, *Scyliorhinus stellaris* (Fig. 1a). The accuracy in defining communities increased when considering both spatial and temporal variations. ST1 composed of *A. cataphractus*, *C. lucernus*, *M. merlangus*, *S.s rhombus*, *Alosa sp.*, *S. maximus*, *S. scombrus*, *Z. faber*, *Loligo sp.*, *S. pilchardus*. and ST2 composed of *T. lastoviza*, *G. galeus*, *S. stellaris*, *R. clavata*, *R. undulata* both represented 100% probability of occurrence. The communities differed widely in the number of species and in abundance for both the spatial and spatio-temporal communities. S1 had the least number of species, six versus ten species for S2 (Tab. 3) but represented 69% of the studied total abundance (Tab. 4). ST1 had the highest species richness, eleven versus six species for ST2 (Tab. 3) and also corresponded to 90% of the total abundance (Tab. 4).

To compare the functional distribution of each community, multiple summarizing indices were calculated. The first, functional richness, was defined to be independent of species abundance and

it follows the difference in species richness within each community. For the global community, functional richness was one. Thus, the 16 species show significantly different ranges of functional traits (Fig. 2). However, for spatial and spatio-temporal scenario the community with the least number of species showed functional richness close to zero. Thus, the range of each functional trait present in the community is narrow. The functional richness for S2 and ST1 was close to 25%.

We assumed in our study that the specific composition of these communities was stable in time. However, the relative abundance within these communities varied in time. The functional richness index, did not vary in time as it does not depend on abundance, unlike functional divergence and functional evenness. Figure 2 displays the span of values from 1995 to 2014 for functional divergence and evenness for each spatial and spatio-temporal community and for the global community. S1 exhibited on average a lower functional evenness (65%) than S2 (70%) (Fig. 3). Moreover, their range did not overlap, except in rare years (Fig. 2). ST1 presented a 60% functional evenness, similar to spatial communities. However, ST2 was organized differently, and showed a superior functional evenness averaged at 85% (Fig. 3).

Contrary to functional evenness, functional divergence of spatial community was on average higher for S1 at 92% and lower for S2 at 87% (Fig. 4). ST1 exhibited close level of divergence to that of S1 and S2, whereas ST2 had a divergence significantly lower than the three other communities set at 77%.

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Figure 4 is a time series of functional divergence from 1995 to 2014. It concurred with Figure 2 results that the functional divergence of the 16 species was constant, and on average 90% higher than of the sub-communities for spatial (Fig. 4a) and spatio-temporal (Fig. 4b) scenarios.

For community one, year 1995 and 1996 were outliers both in the spatial (Fig. 4a) and the spatio-temporal scenarios (Fig. 4b). After 1996, the functional divergence in the communities and the global community was above 85%. The S1 and S2 showed similar patterns in how functional traits range was organized. However, we saw a strong difference between the two spatio-temporal communities. The divergence index for ST1 ranged between 85% and 90%, whereas for ST2, it ranged between 65% and 80% (Fig. 2). The functional divergence grew increasingly apart from 1995 to 2014.

To analyze and compare the functional trends of each spatial and spatio-temporal communities we calculated a weighted average of quantitative traits (Fig. 5). We found cyclical patterns in the weighted average life history traits time series defined in Table 2. These quantitative traits cycled through at least two decadal year patterns. The first from 1995 to 2004, the second from 2004 to 2013 and a third that seemed to start in 2013. The cyclical pattern was more pronounced for Longevity, Age at maturity, Maximum length and Trophic level. It was less pronounced for mean preferred temperature (PT) and PT range. We found identical cyclical patterns in the spatial and spatio-temporal scenario.

In the spatial scenario the functional traits in S1 followed well defined cycles. The Age at maturity, Trophic level both increased until 2004 then decreased from 2004 to 2012 only to increase again. The Max length and Longevity showed an opposite pattern. The mean preferred temperature and

the preferred temperature range revealed a more complex pattern. The first cycle had an almost null slope, then from 2004 to 2012 the traits decreased only to increase in the third cycle (Fig. 6).

The spatio-temporal scenario presented cycles in ST1. However, the Age of maturity, Max length and Trophic level were affected in an identical manner by this cyclical climate event and the longevity was affected in an opposite fashion. The main difference in spatio-temporal communities was that traits in both communities showed patterns (Fig. 7).

## **4. Discussion**

### **4.1. Community mapping of the EEC**

ASTECC opens the door to a statistically sound definition of ecosystem health and resilience.

Resilience and stability of an ecosystem depends upon community structure and their functional distribution. In the first step, we defined with statistical accuracy, the spatial and spatio-temporal communities present in the ecosystem. Contrary to past methods, this functional analysis does not define communities a priori using expert knowledge, or constrain them to species grouped with identical functions in the same community (Villegger et al., 2008; Stroud et al., 2015). These techniques while having strengths for answering ecological questions are rarely dynamic and may lack the precision needed for fishery management and conservation (Crowder and Norse, 2008; Link, 2010). ASTECC is an efficient way to bypass these issues and rely on the statistical model to define communities (Vert-pre et al., In press). This method assumed only spatial correlation and dynamic spatio-temporal approach when drawing the functional distribution of the EEC communities.

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ASTECC defined two communities both in spatial and the spatio-temporal scenarios. However, there is more confidence in the communities defined using spatio-temporal correlation than when using spatial correlation (Vert-pre et al., In press). S1 and S2 show 98% and 93% probability of occurrence, respectively, while ST1 and ST2 both have 100% confidence in composition. This is explained by the fact that spatial communities only rely on species spatial correlation, while the spatio-temporal communities are organized given both their spatial correlation and the temporal similarities in the abundance variations. Although more rarely used in functional analysis, the latter is a more realistic community as it will not only incorporate habitat preference, but it also emphasizes species similarly impacted from external environmental and anthropogenic factors. For example, the first spatial community (S1) is composed of a sub-zonale community constituted of *R. clavata*, *C. lucernus* and *Loligo sp* that spend most of their time in the benthic zone and are moderately fished in the EEC. It also has a pelagic sub-zonal community composed of *M. merlangus* and *S. scombrus*, highly fished in the EEC and, *S. maximus* that is of moderate commercial importance. The model correctly identified that these species were from the same habitat. They were found in the same water column, and reveal more specific habitat preferences at sub-community level (Fig. 1a). Meanwhile, ST2 is composed of species whose abundance vary, and often in synchrony, *T. lastoviza*, *G. galeus*, *S. stellaris*, *R. clavata*, *R. undulata*. Moreover, the composition of this community constitutes species which are ‘near threatened’, ‘vulnerable’ or ‘endangered’ under the International Union for Conservation of Nature Red List (Fig. 1b). ASTECC emphasizes species that pertain to similar habitat, and species that react strongly to external disturbance. These disturbances can be identified as mainly anthropogenic if the species pertain to ST2, and predominantly environmental if the abundance of the species are evolving in



synchronic patterns (i.e. in ST1) or a combination of both external pressures. For example, *R. clavata* and *R. undulata* are both under high fishing effort as they are increasingly being caught as bycatch and adults are also a valuable target species (Ellis et al., 2012; Silva et al., 2012). Moreover, they show synchronic patterns in abundance, as they both show no increase from 1995 to 2006, and then a positive trend starting 2006 (Vert-pre et al., In press). This assumes that their abundance is both impacted by fishing pressure and environmental changes (Vert-pre et al. 2013). Contrary to ST1, ST2 expresses a low level of resilience to environmental and anthropogenic pressures.

#### 4.2. Functional distribution of the EEC communities

To further analyze resilience and define the functional distribution of these communities, we developed accurate measures of functional indices. We focused on three main indices that have been known to be a good descriptors of communities. Most functional indices incorporate abundance variations by weighting the functional index by abundance (Villegier et al., 2008). This method is equivalent to our method of calculating the spatial distribution, then calculating the abundance weighted functional indices. However, the spatial communities defined are mostly distributed according to habitat preference, and poorly express the effect of other external pressures. Thus, this method might not display the full potential of what can be learned from functional indices. Meanwhile, the results show that the second method that identifies communities with spatio-temporal variations, and from these calculate the abundance weighted functional indices, will give a true dynamic functional distribution and help predict community resilience. The functional richness, is always independent of abundance, contrary to the functional

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divergence and functional evenness, that are both weighted by species abundance. Functional richness does not depend on abundance but only on the number and type of functional traits present in the community (Schleuter et al., 2010). The global community shows a wide range of types of functional traits with a functional richness at 100% (Fig. 2). This confirms that our sample is representative of the high functional diversity present in the EEC ecosystem. Whereas, at the community level, the functional traits are organized in a homogenized manner. Therefore, communities exhibit low functional richness, with barely a difference between spatial and spatio-temporal scenarios. The community with the least number of species (Tab. 4) in both cases show the lowest functional richness, close to zero, and the community with the highest number of species show the highest functional richness at 25% (Fig. 2). The relevance of these results is highly dependent on the number of species present in the analysis. The sample size might hinder interpretation. This issue does not appear in Functional evenness and divergence. We could think that the choice of the species is also a factor for bias in our results. However, the functional richness of the entire community reveals that the community shows a high heterogeneity in traits richness. Thus, even if not all the traits present in the ecosystem are represented there is a high diversity of traits represented in our sample.

The functional evenness and divergence trends are different, and illustrates how these functional traits range in the global community and in the communities. The overall community functional evenness ranges between 70% and 75%, and is representative of the functional evenness of the spatial and spatio-temporal communities. The first spatial community (S1) represents species from two distinct habitats while the second spatial community (S2) does not show a distinct sub-grouping per habitat (Fig. 1). Consequently, species abundance is distributed less evenly in the

functional trait space in S1 than in S2 (Fig. 2). Higher diversity in habitat is believed to lead to higher stability in a community (Roff and Mumby, 2012). Moreover, additional information on community resilience can be driven from the spatio-temporal communities. The spatio-temporal community composed of the near threatened, vulnerable and endangered species have the highest functional evenness at an average of 85%, which is above the global community average. S1, S2, ST1, and ST2 reveal very distinctive strategies when it comes to abundance distribution in the functional traits volume. Given the status of the species within each community, we can conclude that the more evenly distributed abundance is across the functional volume, the more at risk the community. Thus, we can conclude here that evenness in abundance of functional traits in the functional space is detrimental to community stability.

Like functional evenness trends, the trends of functional divergence are similar between spatial and spatio-temporal analyses, but the difference in values between the two communities are more drastic in the spatio-temporal scenario. ST1 exhibited a closer level of divergence with ST2 than between S1 and S2, but ST2 had a divergence significantly lower than the three other communities set at 77%. For ST2, the most abundant species' traits are closer to the center of gravity of the functional traits volume. This is otherwise explained as the traits expressed in the community follows more narrow functional ranges. ST2 has less variety in ranges in functional traits and is also the community the most at risk. We can conclude from these results that a more even functional distribution impairs community's resilience.

Studying the trends in functional divergence and evenness highlights whether the communities work their way towards a more stable and more resilient functional distribution. In Figure 3, functional evenness remains quite stable in spatial communities and does not tell us much about

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what impacts the community at a biogeographic scale. If we want an accurate picture of how environment and/or anthropogenic stressors affect the functional stability of a community, we need to look at spatio-temporal communities where species are clustered, not only given their spatial affinities, but also their abundance synchronous changes. Figure 3b shows that the community comprised of all the species with a critical status are slowly recovering, leading to a less functionally even and more functionally divergent community. In other terms, leading to a more resilient community. On the other hand, ST1 tends to become more functionally even and keep the same level of divergence. The two spatio-temporal communities are converging over time to a similar functional distribution. These results lead us to believe that internal mechanisms are driving the global community to a functionally stable equilibrium (Straver et al., 2011; Miller et al., 2018). Therefore, the system may return to this equilibrium after a disturbance over the course of years if the appropriate measures are taken to reduce anthropogenic impacts, and if the environment is favorable to the species productivity (Vert-pre et al., 2013). To identify the point of focus for management, one needs to identify the stressors that will impulse a shift in the functional distribution that will disrupt this equilibrium (Hagstrom and Levin, 2017, Carpenter, 2001).

#### 4.3. Processes leading to resilience

Conservation and management require the determination of which stressors are shaping the functional distribution. Analyzing the trends of the weighted average traits (Tab. 2) in each community reveals these stressors. In the global community, traits cycles occur at least twice with a period of 10 to 11 years (Fig. 6). The first period goes from 1995 to 2004, then from 2004 to 2013 and a third starting in 2013. These cyclical patterns are consistent with the North Atlantic

Oscillation (NAO) defined by Rogers (1984) as “the temporal fluctuation of the zonal winds strength across the Atlantic Ocean due to pressure variations in both the subtropical anticyclone belt and in the subpolar low near Iceland”. Moreover, the periodic alteration of sea surface temperature and coastal runoff is particularly significant for the pelagic and benthic communities of the coastal zone (Tunberg and Nelson, 1998). By changing the productivity level of the EEC, these processes induce changes mostly in longevity, age at maturity, maximum length (i.e. the fitness of fish) and trophic level traits (Fig. 6). These cycles can be seen better at the global community scale, but can also be identified in the spatial and spatio-temporal communities. The traits of the second community however does not show cyclical patterns as defined in the first community, but instead show linear trends.

The second community presents linear trends in longevity, max length and trophic level. The overall trophic level of the community is decreasing along with the mean preferred temperature. The temperature increased by 2 degrees Celsius (Gohin et al., 2015) in the Western English Channel since 2004. However, the well mixed water of the Eastern section of the channel didn't suffer such an important increase in temperature (Gohin et al., 2015). This leads to a change in preferential habitat for species of the EEC. Species with warm affinities moved to the even warmer waters to the Western English Channel and species attracted to the slightly colder water immigrated to the EEC (Southward et al., 2005; Hawkins et al., 2008; Smale et al., 2015). Indeed, the abundance of species like *R. Clavata* and *R. Undulata*, that have a lower upper temperature limit increased in the EEC when the abundance of species with warmer preferred temperature like *G. Galeus* species decreased since 2004 (Fig. S1). Thus, this increase in biomass may not be due to a true rebuilding of the population but to a relocation of the species from West to East (Sguotti et

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al., 2016). These results plus the decreasing trends in trophic level show that the fishing effort on this community may be too high for the population to remain sustainable. Hence, the proposition for increasing the French exclusive economic zone's total allowable catch (TAC) for *R. Undulata* should be done with high precaution (ICES, 2018).

These findings have dramatic consequences for the management on these endangered species. We recommend a precautionary approach when it comes to increasing TAC or reopening the fishery for species at risk, by getting a full picture of the status of these fisheries. Stakeholder and scientists need to set in place a joint management between the Eastern and the Western part of the English Channel.

This study highlights how drawing conclusions from the functional divergence and functional evenness in the spatio-temporal scenario is more reliable than a time stepped spatial approach. Trends can be followed and scientists can identify which communities or species are in a critical state and may be less resilient to external pressure. The spatial scenario might be a good method to study the impact of habitat destruction on the communities; however, for proactive conservation and management, spatio-temporal scenarios draw a clearer picture of the communities' resilience. Hence, they can pinpoint more precisely where management and conservation efforts should be implemented. Functional analysis with spatio-temporal communities can also detect dynamics that would be missed using a non-spatially explicit species management, and thus stands as a necessary tool in spatial conservation and management. Comparing the results of this study to an analogue study on the entire English Channel or with other systems would be useful to determine management decisions for rare and endangered species.



## Tables

Table 1: Code and name for the sixteen studied species.

Code	Species name
AGONCAT	<i>Agonus cataphractus</i>
ALOS	<i>Alosa sp.</i>
CALM	<i>Callionymus sp.</i>
CHELLUC	<i>Chelidonichthys lucernus</i>
GALOGAL	<i>Galeorhinus galeus</i>
LOLI	<i>Loligo sp.</i>
MERNMER	<i>Merlangius merlangus</i>
RAJACLA	<i>Raja clavata</i>
RAJAUND	<i>Raja undulata</i>
SARDPIL	<i>Sardina pilchardus</i>
SCOMSCO	<i>Scomber scombrus</i>
SCOPMAX	<i>Scophthalmus maximus</i>
SCOPRHO	<i>Scophthalmus rhombus</i>
SCYOSTE	<i>Scyliorhinus stellaris</i>
TRGPLAS	<i>Trigloporus lastoviza</i>
ZEUSFAB	<i>Zeus faber</i>



Table 2: Functional traits classification provided to calculate functional indices. The traits are related to one or more of the three main function for an individual, Feeding (Solid line), growth and reproduction (Dashed line) and Survival (dotted line).

Trait type	Ecological function	Unit/Scale
Morphological	Maximum Length	Continuous scale
	Longevity	Maximum age
Physiological	Mean preferred temperature	Continuous scale in Celcius
	Preferred temperature Range	Maximum-Minimum preferred temperature in Celcius
		Home range or resource directed
Behavioral	Migration movement	Not directly responsive to home range or resource
		Accidental displacement
	Trophic level	Continuous scale
Life history	Iteroparity	Semelparous or Iteroparous
	Age of maturity in %	$A^* = \frac{A}{\text{Longevity}} \times 100$

Table 3: Number of species and relative abundance for spatial and spatio-temporal communities defined by the Autoregressive Spatio-Temporal Clustering model.

Community	Count
Spatial 1	6
Spatial 2	10
Spatio-temporal 1	11
Spatio-temporal 2	5

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Table 4: Sum of the predicted indice of abundance in thousands per community and the relative representation within the 16 studied species.

	S1	S2	ST1	ST2	Total
<b>Total Abundance</b>	32,245	14,481	41,988	4,738	46,726
<b>%</b>	69	31	90	10	

Table 5: Output of the linear model on traits time series, from 1994 to 2014, for the slope parameters with significance given the p-value. The significance code is, '\*' for a p-value inferior to 0.05, '\*\*' for p value inferior to 0.01 and '\*\*\*' for a p-value inferior to 0.001.

Community	Trait	Estimate	Std. Error	t value	Pr(>  t )	Significance
S1	Longevity	0.003	0.069	0.048	0.962	
	Iteroparity	0.000	0.000	-1.730	0.100	
	Age Maturity%	0.030	0.212	0.142	0.889	
	Max length	0.264	0.136	1.944	0.068	
	Trophic level	0.005	0.003	1.559	0.136	
	mean PT	-0.004	0.005	-0.814	0.426	
	PT range	-0.039	0.020	-1.909	0.072	
S2	Longevity	-0.029	0.048	-0.595	0.559	
	Iteroparity	0.000	0.000	-1.730	0.100	
	Age Maturity%	0.324	0.146	2.218	0.040	*
	Max length	0.541	0.209	2.589	0.019	*
	Trophic level	0.010	0.003	3.737	0.002	**
	mean PT	0.030	0.009	3.305	0.004	**

*Spatio-temporal trends of functional indices*

	PT range	<b>0.054</b>	0.021	2.597	0.018	*
ST1	Longevity	<b>-0.022</b>	0.057	-0.387	0.703	
	Iteroparity	<b>0.000</b>	0.000	-1.730	0.100	
	Age Maturity%	<b>0.139</b>	0.255	0.547	0.591	
	Max length	<b>0.241</b>	0.062	3.884	0.001	**
	Trophic level	<b>0.008</b>	0.002	3.569	0.002	**
	mean PT	<b>0.005</b>	0.005	0.939	0.360	
	PT range	<b>-0.013</b>	0.017	-0.737	0.471	
ST2	Longevity	<b>-0.244</b>	0.083	-2.957	0.008	**
	Iteroparity	<b>0.000</b>	0.000	-1.730	0.100	
	Age Maturity%	<b>0.141</b>	0.100	1.417	0.174	
	Max length	<b>-0.567</b>	0.218	-2.597	0.018	*
	Trophic level	<b>-0.004</b>	0.001	-3.393	0.003	**
	mean PT	<b>-0.010</b>	0.004	-2.381	0.029	*
	PT range	<b>-0.036</b>	0.024	-1.523	0.145	
All	Longevity	<b>-0.014</b>	0.057	-0.250	0.805	
	Iteroparity	<b>0.000</b>	0.000	-1.730	0.100	
	Age Maturity%	<b>0.137</b>	0.234	0.583	0.567	
	Max length	<b>0.398</b>	0.115	3.466	0.003	**
	Trophic level	<b>0.007</b>	0.002	3.434	0.003	**
	mean PT	<b>0.007</b>	0.005	1.428	0.170	
	PT range	<b>-0.010</b>	0.015	-0.658	0.519	

Figures

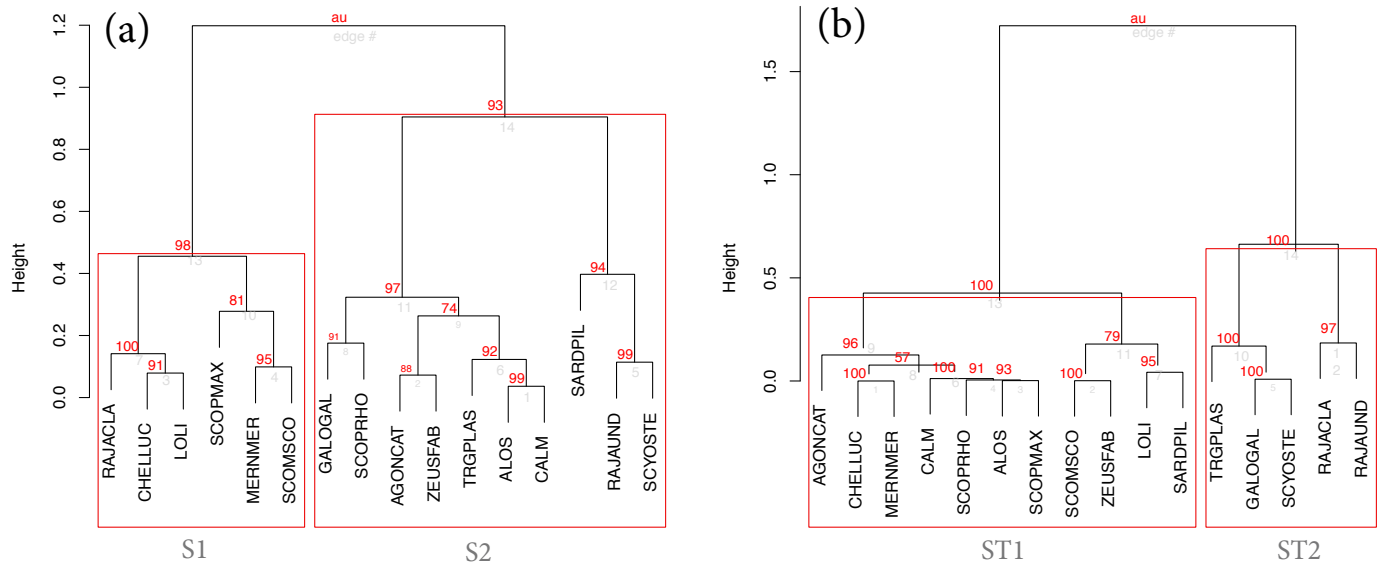


Figure 1: Spatial (a) and Spatio-temporal (b) communities defined at a 522km<sup>2</sup> scale. The communities outlined in red are found statistically significant by the Autoregressive Spatio-Temporal Clustering model (c.f. Vert-pre et al., In press)

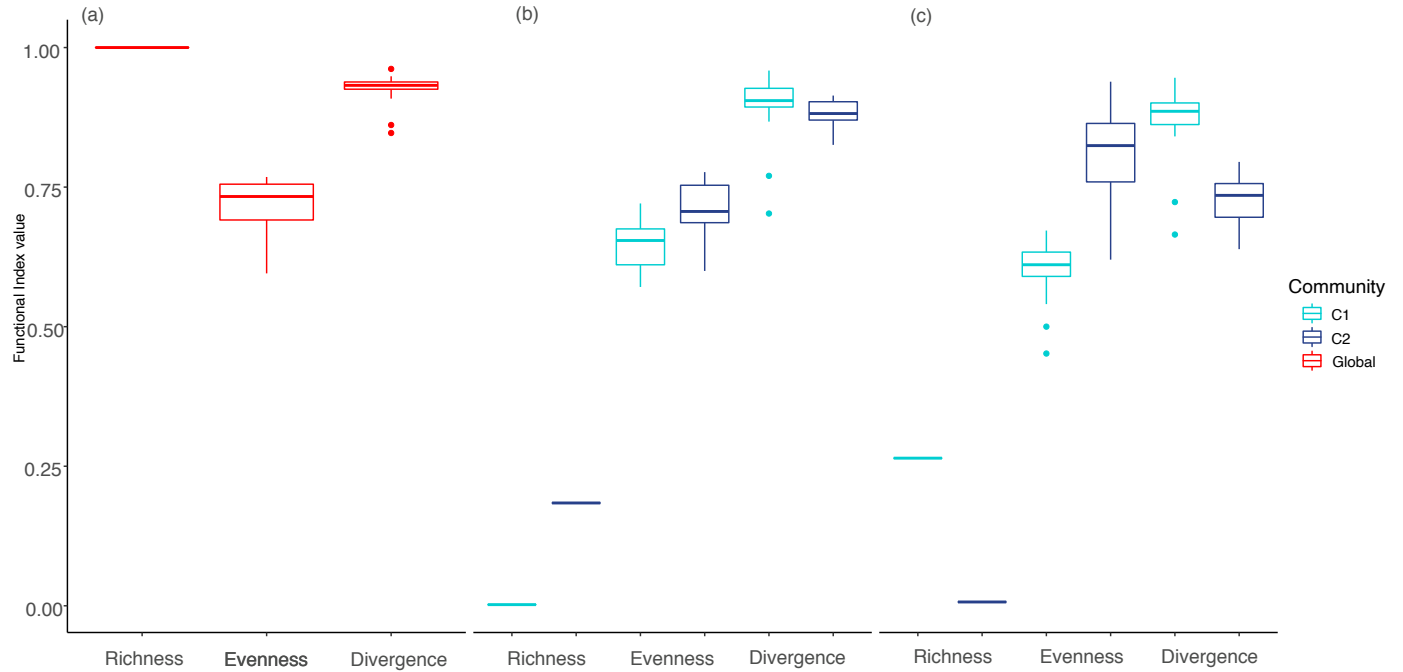


Figure 2: Distribution of functional indices calculated over 1995 to 2014 for the global community (a), spatial (b) and spatio-temporal (c) communities. The comparison within each panel is between community one (turquoise) and community two (Blue) defined by the Autoregressive Spatio-Temporal Clustering model. Each boxplot shows the outliers as solid dots, the minimum and maximum values of the distribution with the vertical bars, and the lower, middle and upper horizontal bars of the box represent 25<sup>th</sup> percentile, median and the 75<sup>th</sup> percentile respectively.

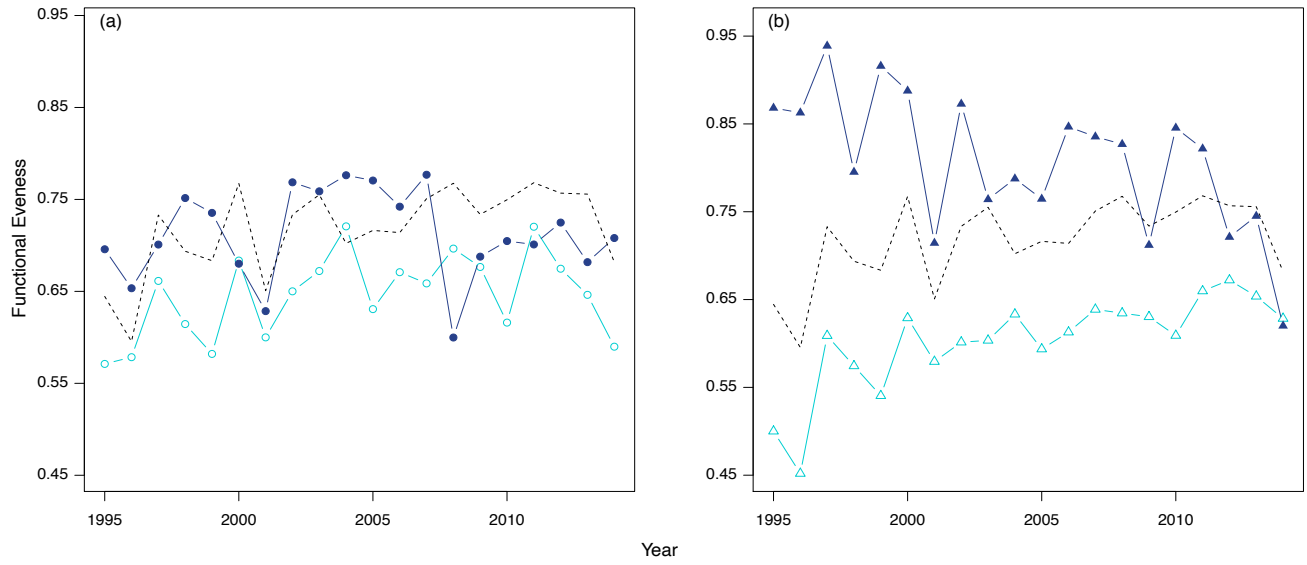


Figure 3: Temporal variations between 1995 and 2014 of functional evenness for the communities defined by the Autoregressive Spatio-Temporal Clustering model. In panel a, S1 is turquoise hollow circles and S2 is blue solid circles. In panel b, ST1 is turquoise hollow triangles and ST2 is blue solid triangles.

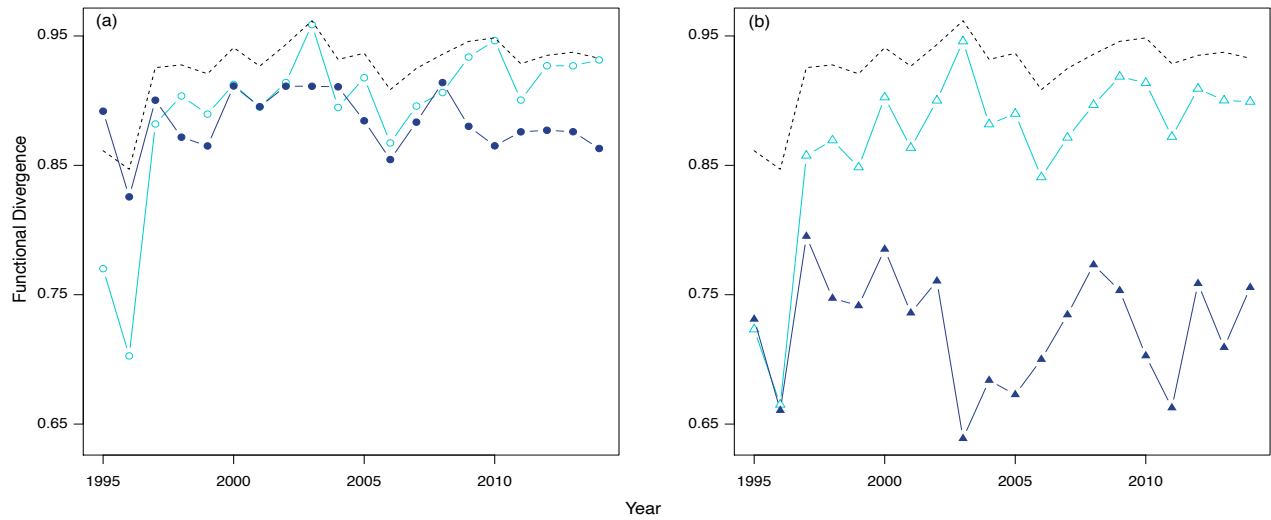


Figure 4: Temporal variations between 1995 and 2014 of functional divergence for the communities defined by the Autoregressive Spatio-Temporal Clustering model. In panel a, S1 is turquoise hollow circles and S2 is blue solid circles. In panel b, ST1 is turquoise hollow triangles and ST2 is blue solid triangles.

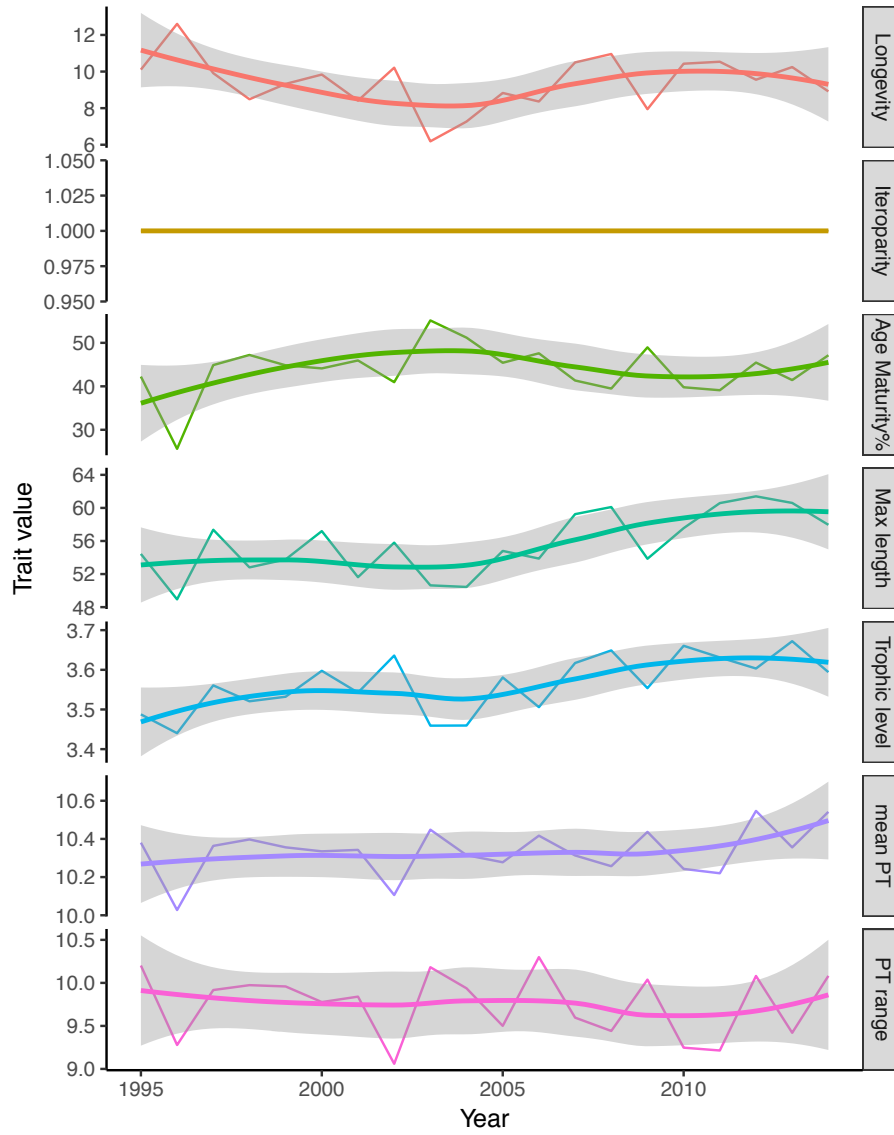


Figure 5: Temporal variations of abundance weighted average functional traits between 1995 and 2014 for all the 16 species studied.



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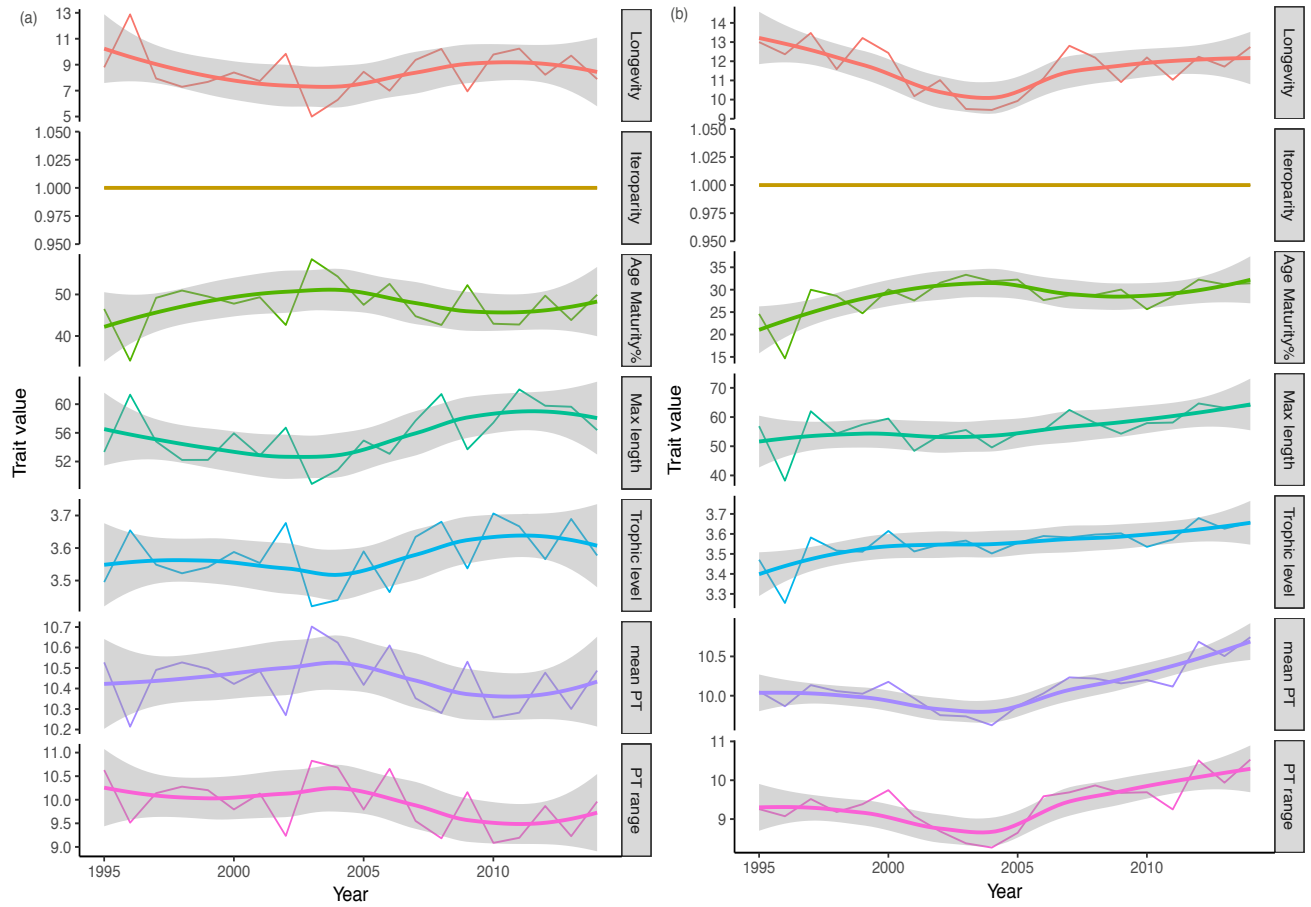


Figure 6: Temporal variations of abundance weighted average functional traits between 1995 and 2014 for the spatial community S1 (a) and spatial community S2 (b).

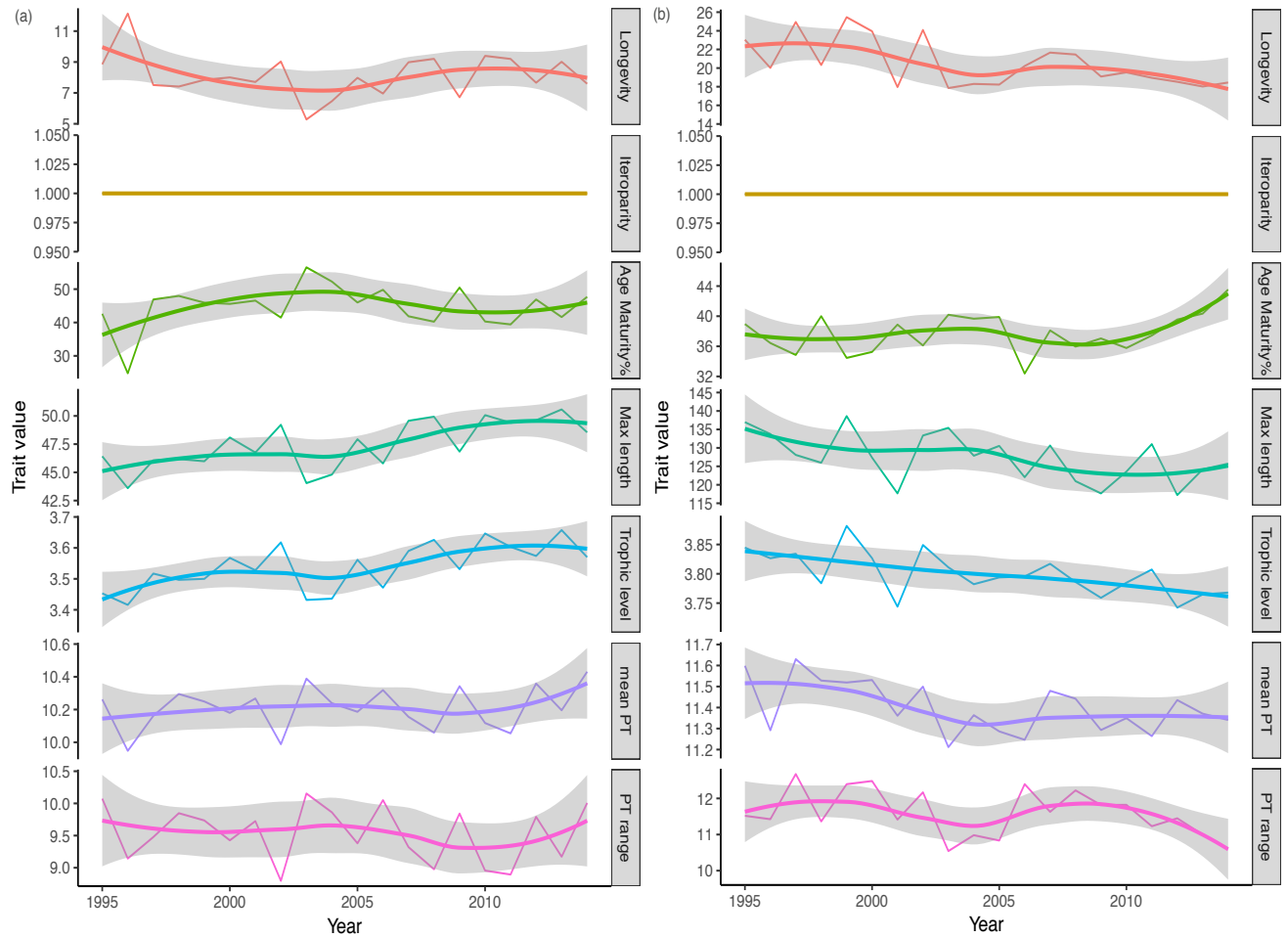


Figure 7: Temporal variations of abundance weighted average functional traits between 1995 and 2014 for the spatio-temporal community ST1 (a) and spatio-temporal community ST2 (b). To the observed data (thin line) was fitted a loess regression (thick line).

## Supplemental Materials

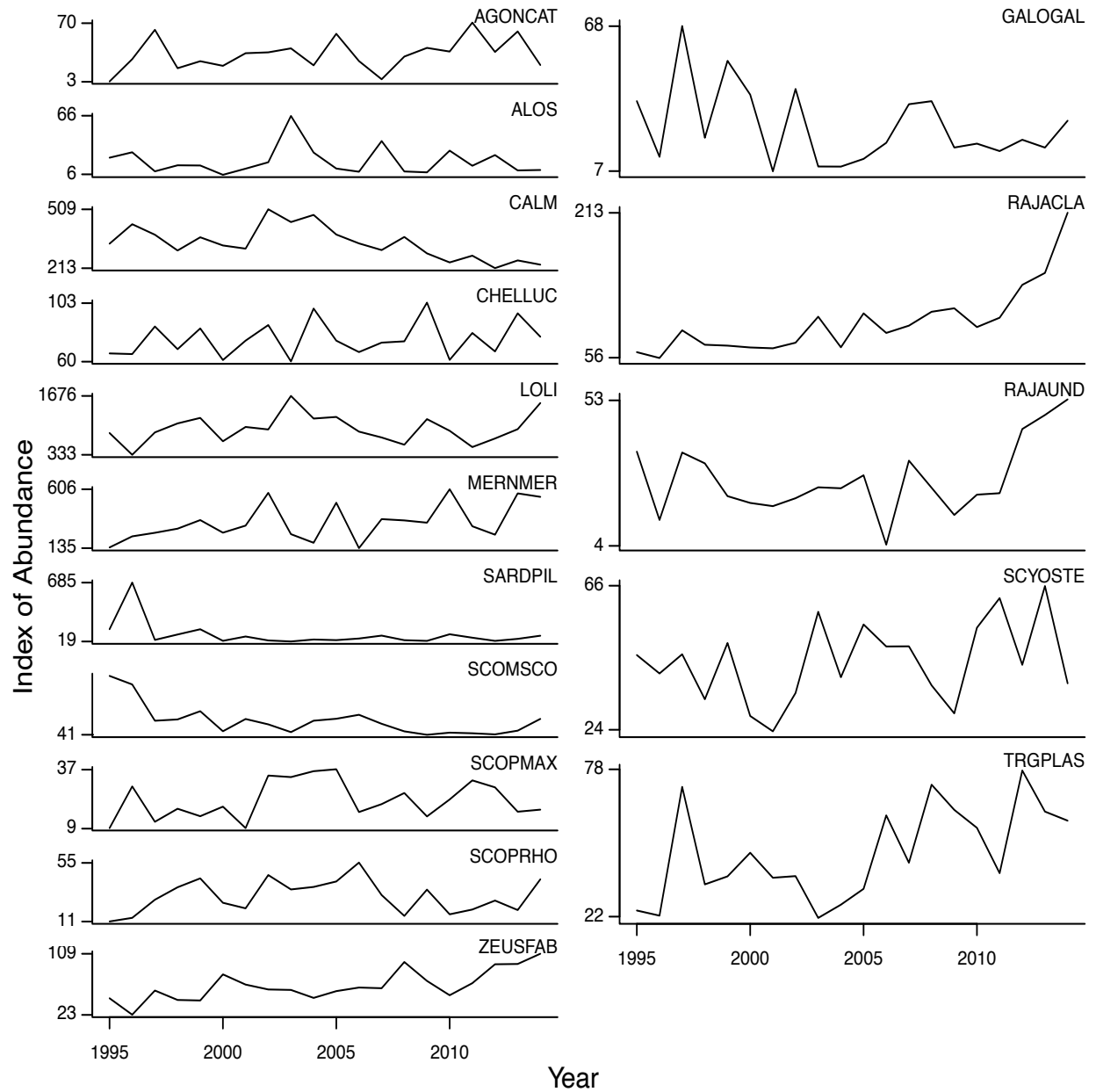
Table S1:

Code	Species	Family	Order	Feeding position	Migratory movement	Water column	Longevity	Iteroparity	Age at maturity	Age at maturity in %	Length at maturity	Max length	TL	meanPT	Vulnerability	MinPT	MaxPT	PTRange
AGONCAT	Agonus cataphractus	Agonidae	Scorpaeniformes	carnivorous	home range	demersal	3	1	1	33		21	3.4 3	9.2	26	7	11.7	4.7
ALOS	Alosa	Clupeidae	Clupeiformes	carnivorous	Not home range	pelagic-neretic	10	0	3.5	35	48.1	83	3.9	10.1	36	7	15.6	8.6
CALM	Callionymus	Callionymidae	Perciformes	carnivorous	home range	demersal	7	1			17.4	30.5	3.3	8.6	23	6.7	13	6.3
CHELLUC	Chelidonichthys lucernus	Triglidae	Scorpaeniformes	carnivorous	home range	demersal	15	1	3	20	21.6	75	3.7	9.8	40	7	16	9
GALOGAL	Galeorhinus galeus	Triakidae	Carcharhiniformes	carnivorous	Not home range	benthopelagic	55	1	13	24	45.5	193	4.3	12.3	74	6.7	23.2	16.5
LOLI	Loligo vulgaris	Teuthida	Loliginidae	carnivorous	Not home range	demersal	1	1	0.7	70		38	3.2 5	11	19	7.4	19.4	12
MERNMER	Merlangius merlangus	Gadidae	Gadiformes	carnivorous	Not home range	benthopelagic	20	1	1.5	8	27.8	70	4.4	9.2	38	7	11.9	4.9

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RAJACL A	Raja clavata	Rajidae	Rajiformes	carnivoro us	Not home range	demersal	15	1	7.5	50	76.6	139	3.8	10.7	73	7.1	15.8	8.7
RAJAUN D	Raja undulata	Rajidae	Rajiformes	carnivoro us	Not home range	demersal	13	1	9.5	73	80	100	3.5	13.2	63	9.8	17.1	7.3
SARDPIL	Sardina pilchardus	Clupeidae	Clupeiformes	carnivoro us	Not home range	pelagic- neretic	15	1	1.5	10	14.8	27.5	3.0 5	10.3	27	7.1	17.3	10.2
SCOMSC O	Scomber scombrus	Scombridae	Perciformes	carnivoro us	Not home range	pelagic- neretic	17	1	3.5	21	28.7	60	3.6	10.2	44	7	17.5	10.5
SCOPMA X	Scophthalmus maximus	Scophthalmidae	Pleuronectiformes	carnivoro us	home range	demersal	25	1	4	16	34.7	100	2.8	9.4	43	5.9	11.9	6
SCOPRH O	Scophthalmus rhombus	Scophthalmidae	Pleuronectiformes	carnivoro us	home range	demersal	6	1	3	50	33	75	4.4	11.2	32	8.4	19.5	11.1
SCYOST E	Scyliorhinus stellaris	Scyliorhinidae	Carcharhiniformes	carnivoro us	Not home range	reef associated	19	1	4	21	78	170	4	10.9	67	7.8	19.5	11.7
TRGPLA S	Trigloporus lastoviza	Triglidae	Scorpaeniformes	carnivoro us	home range	benthopela gic	18	1	3	17	15	40	3.4 9	11.8	32	8.9	26	17.1
ZEUSFA B	Zeus faber	Zeidae	Zeiformes	carnivoro us	home range	benthopela gic	12	1	4	33	32.6	90	4.5	13.6	68	6.7	23.7	17

Figure S1: abundance of all the species featured in the analysis, output of the model Vector Autoregressive Spatio-Temporal.



# Chapter 4. Neighbors helping neighbors: Protecting endangered elasmobranches with surrogate species

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## Abstract

### Aim

Forecast abundance index to manage marine rare species that are listed as vulnerable, near threatened or Endangered by the IUCN Red List.

### Location

Europe

### Methods

We applied the Autoregressive Spatial Temporal Clustering method (ASTECC) on 16 species in the Eastern English Channel using historical data from the Channel Ground Fishery Survey. We

selected from the ASTEC spatio-temporal clusters and VAST correlation matrix the paired species. Then, we ran and compared the fit of a GAM model at year lag zero to five, using generalized cross-validation.

## Results

ASTEC identified *Scophthalmus rhombus*, *Raja clavata* and *Scyliorhinus stellaris* as predictors for *Scophthalmus maximus*, *Raja undulata* and *Galeorhinus galeus*, respectively. For *S. maximus* in division 7, the 5-year lag model predicts an index of abundance varying around twenty thousand fish in 2015 with a gradual increase to twenty-eight thousand fish in 2019. The model defines that a one-year lagged model is the best predictive model for predicting *R. undulata* with values of abundance around hundred thousand fish. For *G. galeus*, the 5-year lag model estimates that the abundance will range between ten to seventy thousand fish between 2015 and 2019.

## Main conclusion

*R. undulata* seems to be steadily increasing in abundance in division 7. However, *G. galeus* and *S. maximus* abundance are extremely variable and would need a management based on environmental variations, or the use of neighboring species to get an accurate forecast. Combining the ASTEC with a GAM allowed for an accurate index of abundance prediction in intensity and trends. The GAM forecast was more accurate when stronger overall correlation occurred between indices. But also, it was more accurate the highest the number of correlated years within the time series were.

Keywords

Elasmobranchs, IUCN Red List, Surrogate species, multispecies modelling, spatiotemporal modelling, cluster analysis

## **1. Introduction**

Understanding the state of communities in data deficient systems has been a challenge in both terrestrial and marine environment. Species over-exploitation and the subsequent impact on an ecosystem remains the leading environmental focus worldwide (Myers and worm, 2003; Kappel, 2005; Venter et al., 2006). However, the required amount and quality of data needed to provide useful information for management are often lacking, especially in marine systems (McClenachan et al., 2012). Species that are rare or that are incidental catch of a non-selective fishery are more subjected to overfishing (Lewison and Crowder, 2003). Rare and cryptic species make detectability extremely hard (Vine et al. 2009), and bycatch are often mis-reported or less monitored (Brenner et al., 2009; Punt et al., 2015; Fan et al., 2019).

Data deficiency and lack of quality leads to lack of management, which ultimately leads to species being endangered or even becoming extinct. There has been an increase in biodiversity loss in the past two decades. In 2002, world leaders committed to reducing the rate of biodiversity loss via the Convention on Biological Diversity by 2010. Schneider et al. (2010), showed that the set target was not met. To correct and avoid species loss, data is needed to implement efficient management strategies. Stock assessments have informed managers efficiently on data rich stocks, but show higher uncertainty in data poor situations (Hilborn and Walters, 1992; Ludwig et al., 1993; Smith



and Addison, 2003). There is a need for data-less management (Johannes, 1998; Costello et al., 2012). Some data poor methods are being developed, e.g. FishPath, Length based integrated Mixed Effects (LIME) model (Dick and MacCall, 2011; Pilling et al. 2009; Dowling et al., 2016; Rudd and Thorson, 2017). However, many species with too little data even for these methods are thus left unmanaged (Costello et al., 2012).

The International Union for Conservation of Nature (IUCN) is composed of multiple experts that assess the level of risk for a species given several criteria (Mitcheson et al., 2013). They are separated in two groups, the taxonomic and the functional group reviews all the data available to allocate each species into a category (Rodrigues et al., 2006). The categories are: (1) Not Evaluated (NE) for when the species has not been evaluated; (2) It is Data deficient (DD), when there is inadequate information to make a direct or indirect assessment of risk of extinction; (3) It is classified as Least concern (LC) when the species does not fit in any higher category of threat; (4) when Near Threatened (NT) when the species is soon likely to be qualified as a threatened category. The high risks categories that are heading towards extinction are: (1) Vulnerable (VU); (2) Endangered (EN) and (3) Critically Endangered (CR). They are followed by (4) the Extinct in the wild (EXW) and (5) Extinct (EX) (Rodrigues et al., 2006; Mace et al., 2008). For the purpose of this study we focused on the species that pertains to the high-risk categories.

Species defined in the high-risk IUCN categories are often sparsely distributed in a local ecosystem. However, they are often of fundamental importance for the ecosystem balance. Rare species can be keystone species. Their large distribution in the ecosystem is disproportional to their local abundance (Power et al., 1996). This is often the case with top predators like sharks and skates (Ceballos and Brown, 1995; Purvis et al., 2000). The loss of predators can lead to over-abundance

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of prey that can lead to ecosystem imbalance (Webster and Parker, 2000; Anderson et al., 2001; Worm et al., 2013). Moreover, species that are less abundant can be so at various times, and show their abundance oscillate between booms and busts (Lyons et al., 2005). These species usually follow environmental triggers and play an important role in the ecosystem functioning through their changes in abundance (Courtemanche et al., 1999; Lyons et al., 2001; cf. Chapter 3).

To track changes in abundance of rare species, scientists have been using surrogate species. These surrogates are defined as population Indicator Species (Swanson, 1998; Caro and O'Doherty, 1999). Assigning surrogate species is usually done relying on life history traits assuming that these species will have similar functions in the ecosystem. Some studies used principal component analysis to group these species per traits (King and McFarlane, 2003). While this method is statistical and intuitive, it has a strong assumption that species with similar life history traits will behave in a similar fashion, which might not always be accurate. There is a need to define surrogate species statistically without a-priori upon habitat or life history traits affinity. However, that would require finding a method to define how species would be impacted by environmental and anthropogenic factors in similar intensity. To be a good predictor, the abundance of the surrogate species, as well as the predicted abundance of the other species, need to be sensitive enough to environmental or anthropogenic change.

First, this study intends to first identify surrogate species for rare species that are listed as vulnerable, Near Threatened or Endangered by the IUCN Red List. Second, it attempts to forecast abundance indices given the abundance of the selected surrogate species. Last, it hopes to provide management guidance for these species at risk in the Eastern English Channel (EEC). EEC is a heavily exploited ecosystem (Martin et al., 2012). Moreover, the EEC is a region that presently

lacks sufficient information to provide a comprehensive answer regarding management of endangered fish species that are of commercial importance like skates and benthic sharks (Dulvy et al., 2000; Ellis et al., 2011). Therefore, the European Channel represents an ideal field of study.

## **2. Materials and Methods**

### **2.1. Data**

Counts, fishing hauls, area swept in km square were extracted from the yearly standardized Channel groundfish survey (CGFS) for 114 species with time series from 1988 to 2014. The Gwen Drez vessel runs 30minutes hauls, at four knots, using a 10 meters Very High Vertical Opening (VHVO) bottom trawl. The survey runs yearly between the 15<sup>th</sup> of September and the 15<sup>th</sup> of November (Foveau et al., 2017).

We started the time series at year 1995 (year at which the survey became standardized) and eliminated 70 species with gap years and 22 species that prevented the model from converging due to extreme high variance. Out of 108 species a total of 16 species were selected for the analysis. We rejected three species (*Trisopterus minutus*, *Trisopterus luscus*, *Trachurus trachurus*) that constitute 62% of the numbers of the catches. That would highly skew the results of any statistical analysis. Therefore, we focused on the 16 species featuring 36% of the total sampled abundance. These species represent some of the most resilient and evenly distributed species of the fish and cephalopod community of the EEC. For each of these species we also collected information about the species status in the EEC and the International Union for Conservation of Nature's Red List (IUCN, 2018).

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### 2.2. Statistical communities

We identified the statistical communities present in the EEC using the Autoregressive Spatio-Temporal Cluster (ASTECC) model described in Vert-pre et al. (In press). This model combined a zero-inflated Poisson with latent predictors using the package ‘vast’ (Thorson and Barnett, 2017), and a hierarchical clustering analysis performed with the package ‘pvclust’ (Shimodaira, 2004). We used the best fit of the spatio-temporal model corresponding to a 522km<sup>2</sup> scale (Vert-pre et al., In press).

### 2.3. Derived Calculations

Using VAST we estimated the density of each given species  $d(x, c, t)$ ,

$$d(x, c, t) = r_1^*(x, c, t) \times r_2^*(x, c, t)$$

and  $I(c, t, 1)$  is the total abundance for the spatial domain for a species:

$$I_{c,t} = \sum_{x=1}^{60} (a_x \times d_{x,c,t})$$

where  $a_x$  is the area of knot  $x$  and  $d_{x,c,t}$  is the density at knot  $x$ , for species  $c$  at time  $t$ . (Thorson et al., 2015b).

## 2.4. Trend analysis

The trend analysis compared the linear trends between species detected in the ASTEC tree as highly correlated spatially and temporally. As various lags between the two time series, varying from zero years to five years we performed the following:

1) Calculated the running correlation using the function “running” from ‘ggtools v3.8.1’. Running correlation method is often used in climate change analysis (e.g. Slonosky et al. 2001; Gershunov et al., 2001). Running correlations calculate the correlation between two time series analysis at each time steps. The running correlation was ran between the Index of species 1 and species 2 of the couple identified by ASTEC. We used a running window from the second time steps to half the length of the index of species 1. 2) We tested the forecast accuracy of each model by running a Generalized Additive Model (GAM) assuming a gaussian distribution as we are dealing with continuous data (Hastie and Tibshirani, 1990). Five scenarios were compared as the sample values were 15 years of the species 2’s index lagged from 0 to 5 years. The predictor was the first 15 years of species 1’s index. Then, we forecasted the following 5 years and compared the prediction to the observed index of abundance. We assessed the best model using the generalized cross validation score (GCV);

$$GCV = \frac{nD}{(n - DoF)^2}$$

Where  $D$  is the deviance,  $n$  is the number of data,  $DoF$  is the effective degrees of freedom of the model. 3) We then reiterated the process with a GAM model with 20 years of data and forecasted

abundance index for each lag (0 to 5 years). We finally compared models using the generalized validation scores (Wood, 2004).

### 3. Results

The ASTEC model identified species for which the variation in the index of abundance showed similarities in space and time. Thus, the model defined two spatio-temporal communities with sub-groups showing strong spatio-temporal affiliation (Fig. 1-2). To identify umbrella species or predictor species, we focused on the strongest correlations (Fig. 1) aligned with the highest probability of coupling (Fig. 2). We highlighted species listed as either vulnerable, endangered, or near threatened in the IUCN Red List.

In community one, *Scophthalmus rhombus* and *Scophthalmus maximus* were classified as least concerned and near threatened, respectively (Table 1), with 100% spatio-temporal correlation (Fig. 1) and a 91% probability that they pertained to the same sub-community (Fig. 2). These species both showed significant booms and busts over time (Fig. 3). This was confirmed by the spatio-temporal mapping of the species densities (Fig. 4-5). The abundance of these species plummeted in 1995, 1996, 2001, 2008 and 2010. The spatially aggregated species abundance slightly increased overtime; however, the increase was not significant (Fig. 3). The best GAM model with 15 years of data to predict *S. maximus* abundance was the model with a three-year lag (Table 2). The model looked like a good fit between the year 2001 and 2010 (Fig. 6). Indeed, the correlation was on average the strongest between 1999 and 2007, it then became strongly negative from 2008 to 2010 and then became positive again in 2011 (Fig. 7a). As most years during this time series had a strong correlation, the GAM model was a good fit and a good model for a three-year projection

(Fig. 6). The prediction was weakened past three years and got both the trend and the index intensity wrong (Fig. 6). The GAM model using all 20 years of data was best when using a five-year lag (Table 2). The running correlation for a five-year lag showed a change in the correlation from strongly positive up to 2006, to strongly negative after this year (Fig. 7b). The five-year lag model emphasized a better fit for this second regime and predicted an index of abundance varying around twenty-two thousand fish from 2018 with an increase in 2019 to twenty-eight thousand fish (Fig. 8).

In community two *Raja clavata* and *Raja undulata* were considered near threatened and endangered, respectively, with 87% spatio-temporal correlation but a 97% probability of pertaining to the same sub-community (Fig. 1-2). The index of abundance between *R. clavata* and *R. undulata* showed positive trends with a strong drop in abundance from 2003 to 2004 in *R. clavata* and from 2005 to 2006 in *R. undulata* (Fig. 9). The spatio-temporal maps of the two species revealed that 2004 and 2006 were low abundance years for *R.clavata* and *R.undulata*, respectively (Fig 10-11). These results led to the belief that *R. clavata* could be a proxy for *R. undulata* when lagged. Therefore, we calculated the rolling correlation between the two indices at different lags. Though it visually looked like the two-year lag was a good fit, Figure 12 showed that the positive correlation is lost from year 2008 to 2011. We then ran a generalized additive model to confirm our findings and identify the best lagged model. It was determined that the best model is assuming a one-year lag model with the lowest generalized cross validation of 56.26 (Table 2). This GAM model was a good predictor for the trends from 2010 to 2015 and a good predictor for both abundance value and trend before 2010 (Fig. 13). We then fitted the GAM model to the time series data set from 1995 to 2014. The best GAM model lagged by one year could predict one year forward. The model

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predicted that the abundance of *R. undulata* in 2015 will double from 50 thousand fish to about a hundred thousand fish (Fig. 14). The residuals and qqplots didn't reveal patterns incoherent with the Poisson model pattern the index of abundance derives from (Fig. S2).

To assess the predictive power given the correlation strength between two species, we compared the power of prediction between *Galeorhinus galeus* given *Scyliorhinus stellaris* and *Galeorhinus galeus* given *Trigloporus lastoviza*. *S. stellaris* and *G. galeus* were classified as near threatened and vulnerable respectively (Table 1) and showed 98% spatio-temporal correlation (Fig. 1). *T. lastoviza*, which was classified as least concern, and had a lower spatio-temporal correlation of 85% with *G. galeus* (Fig. 1). All three species displayed a 100% probability of pertaining to the same sub-community (Fig. 2). The highest correlation between *S. stellaris* and *G. galeus* showed a better fit and higher predictive power in trend and value of *G. galeus* (Fig. 15). Moreover, the model using the highest correlation selected a model that was lagged by five years against a model lagged by four years (Table 4-5). When using the 20 years of data, the best fit was the five-year lag model (Table 4) that predicted a slightly increasing trend in *G. galeus* index of abundance with large booms and busts that set the index of abundance at twenty-five thousand fish in 2019 (Fig. 16).

## 4. Discussion

### 4.1. ASTEC pairing of species

The ASTEC model identified species for which the variation in the index of abundance showed similarities in abundance space and time variations (Vert-pre et al., In press). The model defined two spatio-temporal communities with sub-groups with strong spatio-temporal affiliation (Fig. 2). This paper relies on a statistical method to identify umbrella species and predict IUCN Red List



species. The main assumption is that species in the best health state, with a high probability of belonging to the same community, can be good umbrella species. These species would help predict abundance variations and trends to inform management decisions of the unhealthy species. In community one, the correlation matrix and tree (Fig. 1-2) and the density spatio-temporal map (Fig. 3-4) identifies *S. rhombus* as a potential predictive species for *S. maximus* abundance. In community two, the correlation matrix and tree (Fig. 2) and the density spatio-temporal map (Fig. 10-11) identifies near threatened *R. clavata* as a potential predictor for endangered *R. undulata*. ASTEC also identifies near threatened *S. stellaris* and least concern *T. lastoviza* as a potential predictor for vulnerable *Galeorhinus galeus* (Fig. 1-2). The best potential scenario is for one species to be a predictor to the other species with a lag. This allows managers to anticipate abundance changes by one year or more. Thus, we explore the dynamics of the relationship between the index of abundance between two species of a sub-community.

#### 4.2. *Schoptalamus maximus* abundance predictions

The first objective was to assess whether the predictive models are a good substitute to traditional assessment models when the data available is insufficient. *S. maximus* was part of our analysis because it is classified as near threatened, and has management advice in other areas of the European Union waters (ICES, 2018a). *S. maximus* presents specific behaviors and life history traits making it vulnerable to fishing. This species shows high level of fidelity to spawning locations making them easier to target during spawning season (Støttrup et al., 2002; Florin and Franzen 2010; Vause and Clark, 2011). Moreover, they do not travel large distances throughout their life (Aneer and Westin, 1990; Florin and Franzen, 2010). Recruitment overfishing could also be

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happening as there is no size limit on catch (ICES, 2012b). Furthermore, *S. maximus* is highly vulnerable to changes in the environment, especially El Nino and decadal oscillation. Our analysis calculated a 100% correlation between *S. maximus* and *S. rhombus* using the ASTEC model.

Coinciding with what was identified by our model, ICES provides combined advices for *S. maximus* and *S. rhombus* in some areas of the EU waters (ICES, 2017a; ICES, 2017b). Our analysis fills a gap as these species do not have recommendations for the EEC. *S. maximus* is mainly caught as bycatch of the Plaice and Sole fishery which makes it hard to monitor. However, *S. rhombus* is not only caught as bycatch, but also targeted (ICES, 2017a; ICES, 2017b). Thus, providing catch data to determine an index of abundance that can be used as a predictor for *S. maximus* abundance. Predictions can then be made to help develop well informed management recommendations for *S. maximus*.

We are focusing on the predictive abilities of our combined ASTEC and GAM models. First, predictive power is affected by how the correlation between the two species evolve over time. We tested this hypothesis by examining the correlation of 15 years of data over time. Changes in correlations not only inform on the level of trust that can be given to a forecast model, but can also detect shifts in trends in time series. We compared a three-year lag with a five-year lag running correlations (Fig. 7a and b, respectively). We then assessed the best predictive model given the proportion of high correlation years (Fig. 6). There was a higher proportion of high correlation years for the three-year lag model using 15 years of data. GCV confirmed these finding statistically (Table 2). After confirming that *S. rhombus* is a good predictor for *S. maximus*, we identified the best predictive model with the whole time series. Using 20 years of data, the best predictive model was the five-year lag model (Table 2). The model predicts an index of abundance around twenty

thousand fish in 2015 with a gradual increase to twenty-eight thousand fish in 2019 (Fig. 8). The index of abundance estimation for the division 4 from the ICES (2017a; 2017b), is thirty-two thousands and within the confidence interval of our estimation for the EEC. Our estimation is in reasonable ranges of what level of abundance are being seen in other regions. Thus, our combined ASTEC and GAM model based on sparse survey data seems to be a good predictive model that can lead to helpful recommendations for unhealthy stocks in data poor regions.

#### 4.3. *Galeorhinus galeus* abundance predictions

The strength of predictability also depends upon the overall strength of the correlation. To test this assumption, we compared the predictive abilities of the index of abundance for two stocks: *S. stellaris* and *T. lastoviza* correlated with *G. galeus* classified as vulnerable by the IUCN Red List. *S. stellaris* and *T. lastoviza* were correlated at 98% and 85% respectively with *G. galeus* (Fig. 1-2). The predictability showed both accuracy in trend and average abundance level with the strongest correlation. For *G. galeus*, though 85% seems like a strong correlation, it was not sufficient to render a good prediction of abundance (Fig. 15). To get accuracy in the prediction for abundance, we recommend using the species closest to the species of interest in the ASTEC result tree.

*G. galeus* stock of the EEC shows a slight increase in the abundance with large boom and bust over the years. The sensitivity of the species to the environment makes this species highly vulnerable and makes recommendations regarding exploitation complicated. However, the ASTEC and GAM model with five-year lagged using *S. stellaris* was selected as the best predictive model (Table 4). Stakeholders can then anticipate the impact of environment for the next couple years on this stock abundance and make appropriate recommendations. The model estimates that the abundance will

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range between ten to seventy thousand fish between 2015 and 2019 (Fig. 16). The sensitivity to the environmental changes makes this stock hard to manage and highly vulnerable to fishing.

Contrary to the other studied species the prediction of *G. galeus*' abundance index is highly variable and shows a wide confidence interval. However, when the value of the abundance is not highly accurate, the prediction of the trend in abundance is accurate.

### 4.4. *Raja undulata* abundance predictions

There has been a recurring issue with estimating the index of abundance of skates at extremely low abundance. Given the two previous hypotheses, we identify that a one-year lagged model is the best predictive model for predicting *R. undulata* given *R. clavata* index of abundance (Table 3). This small lag is to be expected as these species are highly correlated. The model predicts that the abundance of *R. undulata* in 2015 will double from 50 thousand fish to about 100 thousand fish (Fig. 14). This increase in trends could be the results of the recent management releasing fishing pressure of the species, but can also be the effect of migration in response to climate change (cf. Chap. 3).

### 4.5. Conclusion

The *S. maximus* trend keeps increasing while the *R. undulata* seems to rebuild. However, identifying which fishing pressure *R. undulata* can sustain is difficult at this point. Reopening the fishery following a precautionary approach could be tried. Managers could allow the fishing pressure to increase a small amount of the increase in abundance and monitor the stock's response.

*R. maximus*, levels are comparable to other regions and thus EU waters of ICES Division 2.a and Subarea 4 management decisions can be used as a proxy for the EEC. Indeed, not having a total allowable catch (TAC) could lead to overfishing the stock in the EEC (ICES, 2017a; ICES, 2017b). *G. galeus* is a species that is highly impacted by the changes in the environment (e.g. temperature, productivity shifts, food availability). It results in abundances that oscillates in booms and busts given how favorable the environment is to the species. This makes it harder to provide a management decision. However, it seems that the overall trend starting in 2015 for the next five years is slightly increasing. Due to the variability of abundance in the stock, we advise not to use yearly management (ICES, 2017a; ICES, 2017b), but to use all five years of projections to make an informed decision. This would be the precautionary approach. Note that at the time the study was conducted, only data pre-dating 2015 was available. However, this study could get ulteriorly updated with data from 2016 and 2017. However, the given protocols for management advice are still relevant. Moreover, the method is a great alternative to missing stock assessments.

Coupling ASTEC output with a lagged GAM has been proven efficient in predicting population abundance for most species of rare encounter. The power of prediction however depends not only on the overall spatio-temporal correlation between the two species, but also on the stability of correlation over time. As the proportion of high correlation years increases, the model becomes better at forecasting. Running correlation also helps anticipate weak predictive years which is essential for making accurate recommendations. Moreover, this method presents strong advantages as it can be done with extremely sparse survey data. This issue is extremely relevant for stocks that are already experiencing unsustainable levels of biomass. In conclusion, this method is a valuable

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alternative for managers to provide recommendations and take management decisions when traditional stock assessments have limited data.

## Tables

Table 1: Code, scientific name and IUCN status for the 16 species studied in the Eastern English Channel.

Code	Species name	IUCN
AGONCAT	<i>Agonus cataphractus</i>	Least Concern
ALOS	<i>Alosa sp.</i>	Vulnerable
CALM	<i>Callionymus sp.</i>	Not Evaluated
CHELLUC	<i>Chelidonichthys lucernus</i>	Least Concern
GALOGAL	<i>Galeorhinus galeus</i>	Vulnerable
LOLI	<i>Loligo sp.</i>	Not Evaluated
MERNMER	<i>Merlangius merlangus</i>	Least Concern
RAJACLA	<i>Raja clavata</i>	Near Threaten
RAJAUND	<i>Raja undulata</i>	Endangered
SARDPIL	<i>Sardina pilchardus</i>	Least Concern
SCOMSCO	<i>Scomber scombrus</i>	Least Concern
SCOPMAX	<i>Scophthalmus maximus</i>	Near Threaten
SCOPRHO	<i>Scophthalmus rhombus</i>	Least Concern
SCYOSTE	<i>Scyliorhinus stellaris</i>	Near Threaten
TRGPLAS	<i>Trigloporus lastoviza</i>	Least Concern
ZEUSFAB	<i>Zeus faber</i>	Least Concern

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Table 2: Comparison of generalized additive model fit with zero to five-year lag using the Generalized Cross Validation score for *Scophthalmus rhombus* index of abundance as predictor and *Scophthalmus maximus* as predicted.

Lag	0	1	2	3	4	5
Score 15years	111.5164	101.1619	104.9046	<b>73.59201</b>	99.46093	77.38391
Score 20years		87.49684	89.79927	86.79246	94.45211	<b>77.38391</b>

Table 3: Comparison of generalized additive model fit with zero to five-year lag using the Generalized Cross Validation score for *Raja clavata* index of abundance as predictor and *Raja undulata* as predicted.

Lag	0	1	2	3	4	5
Score 15years	97.59365	<b>56.25733</b>	67.09873	57.33106	90.62633	123.2621
Score 20years		<b>108.4975</b>	136.1677	180.1404	147.8932	123.2621



Table 4: Comparison of generalized additive model fit with zero to five-year lag using the Generalized Cross Validation score for *Scyliorhinus stellaris* index of abundance as predictor and *Galeorhinus galeus* as predicted.

Lag	0	1	2	3	4	5
Score 15years	380.8471	409.0166	365.8373	195.2066	244.3247	<b>171.0407</b>
Score 20years		316.03	326.8495	173.8113	225.109	<b>171.0407</b>

Table 5: Comparison of generalized additive model fit with zero to five-year lag using the Generalized Cross Validation score for *Trigloporus lastoviza* index of abundance as predictor and *Galeorhinus galeus* as predicted.

Lag	0	1	2	3	4	5
Score 15years	323.4822	401.4225	403.1071	226.7876	<b>113.6153</b>	162.931
Score 20years		307.3742	328.9232	196.9953	<b>121.6147</b>	162.931

Figures

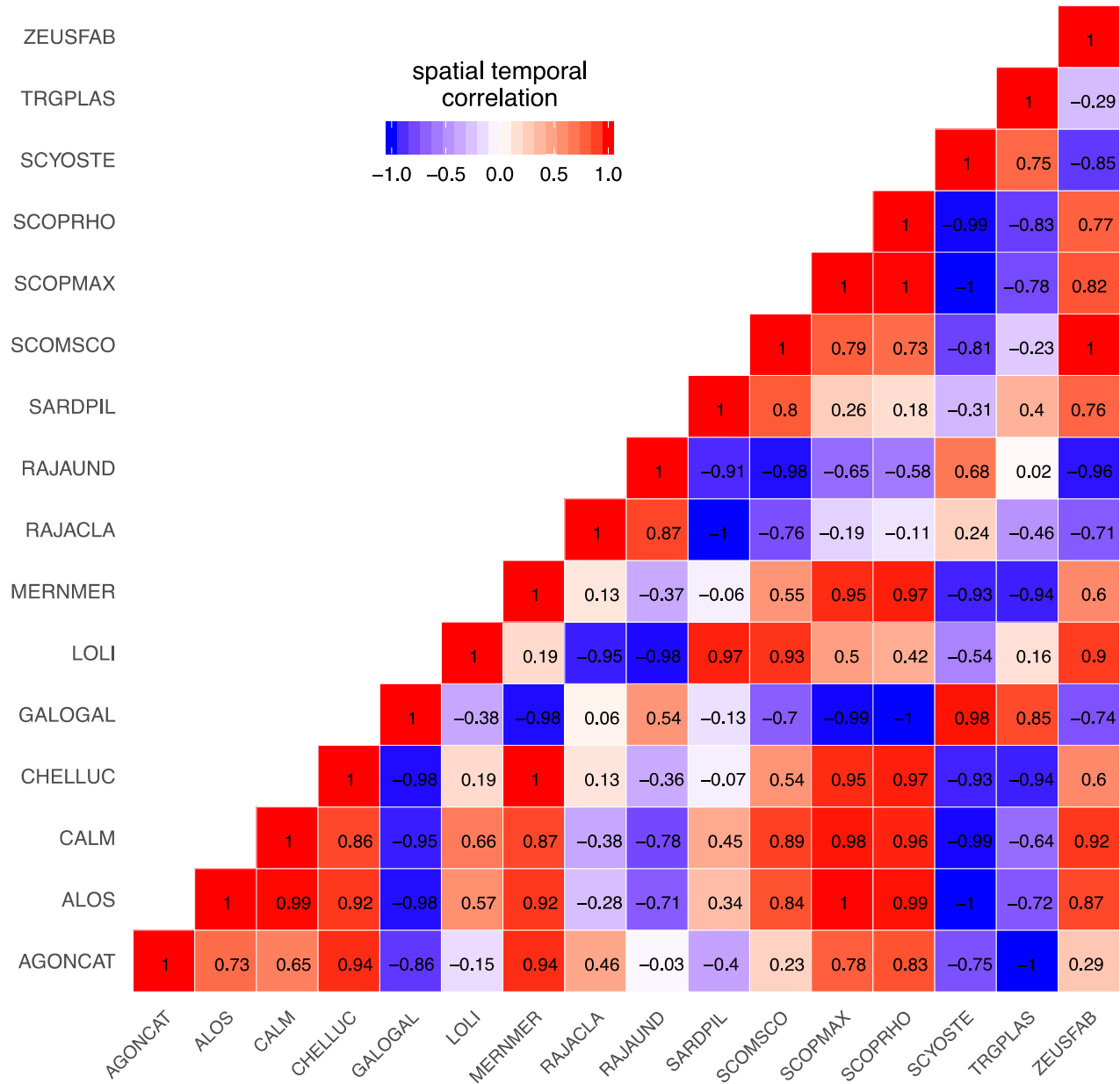


Figure 1: Spatio-temporal correlation matrix at a 522km<sup>2</sup> scale displaying correlation from strongly negative (dark blue) to strongly positive (dark red).

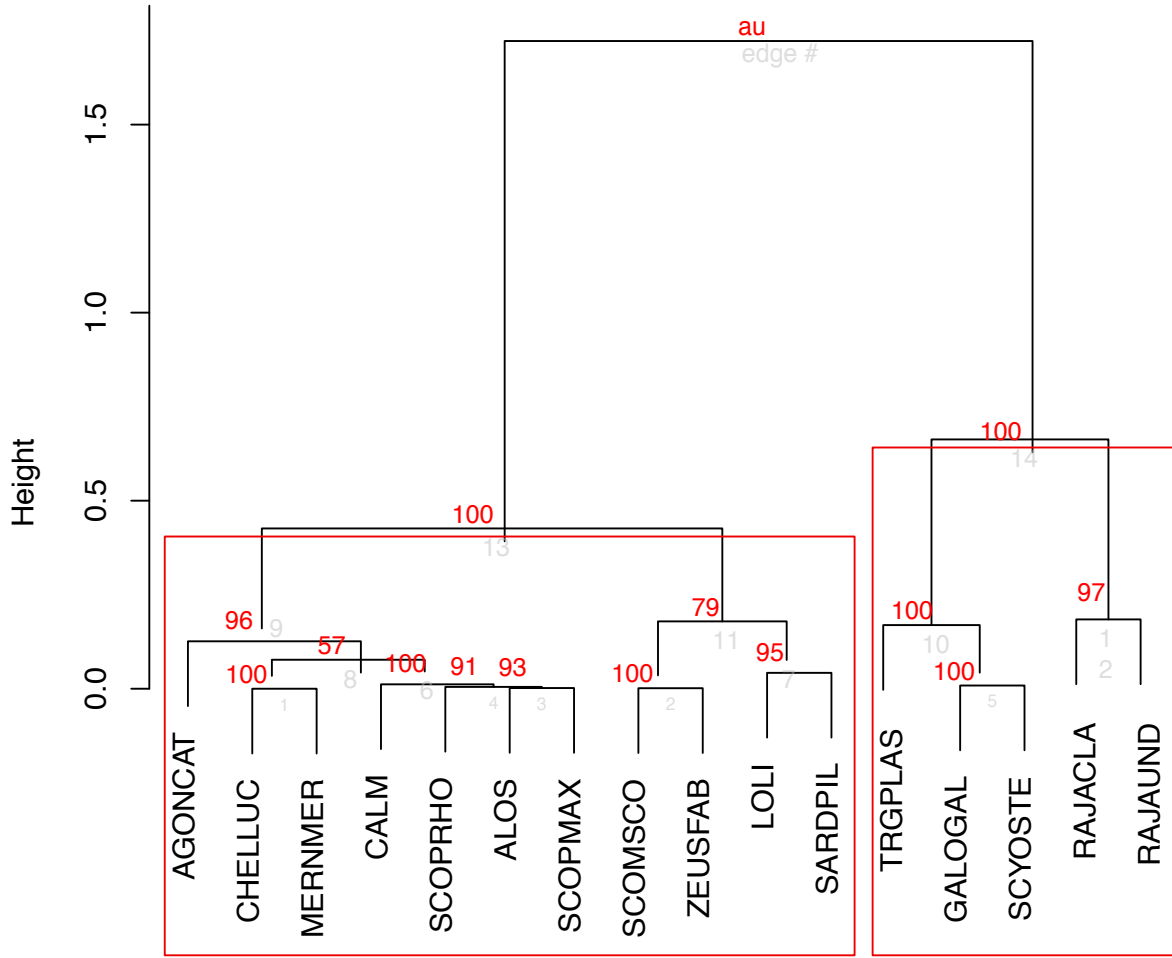


Figure 2: Spatial-temporal hierarchical clustering at a 522km<sup>2</sup> scale. The rectangle outlines the communities that were found statistically significant by ASTEC given the approximately unbiased p-values in percentage (red). The light grey numbers represent the edge number of the tree.

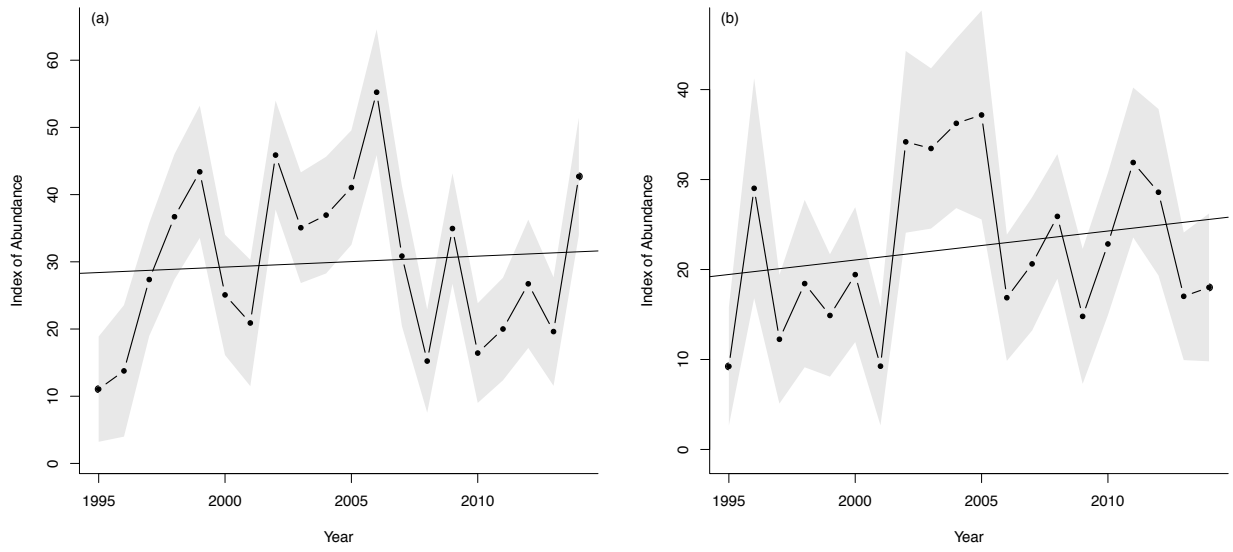


Figure 3: Index of abundance estimated by VAST in thousands for *Scophthalmus rhombus* (a) and *Scophthalmus maximus* (b) from 1995 to 2014.

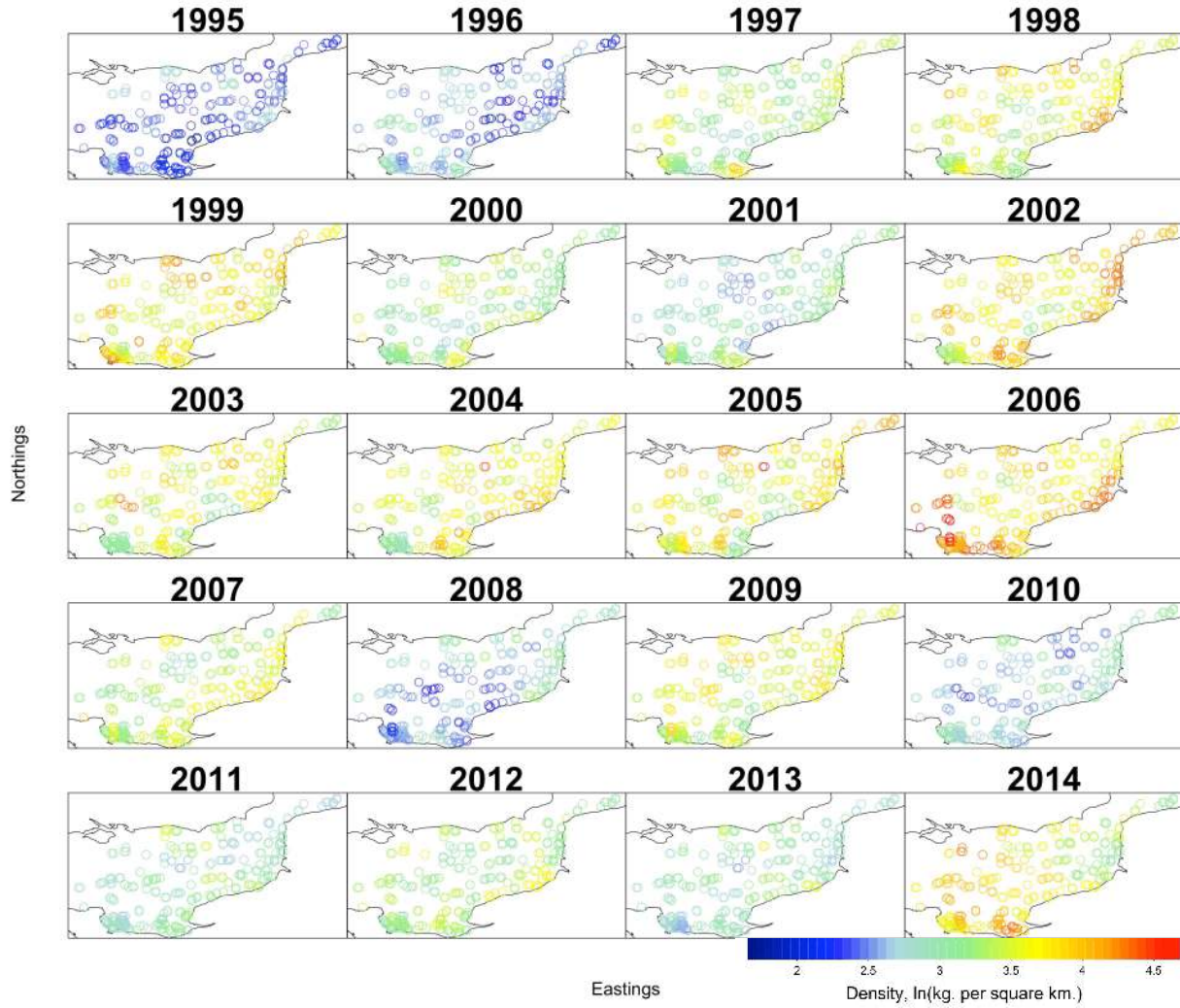


Figure 4: *Scophthalmus maximus* spatial distribution in the Eastern English Channel from low (blue) to high (red) densities in numbers/ km<sup>2</sup> in log scale.

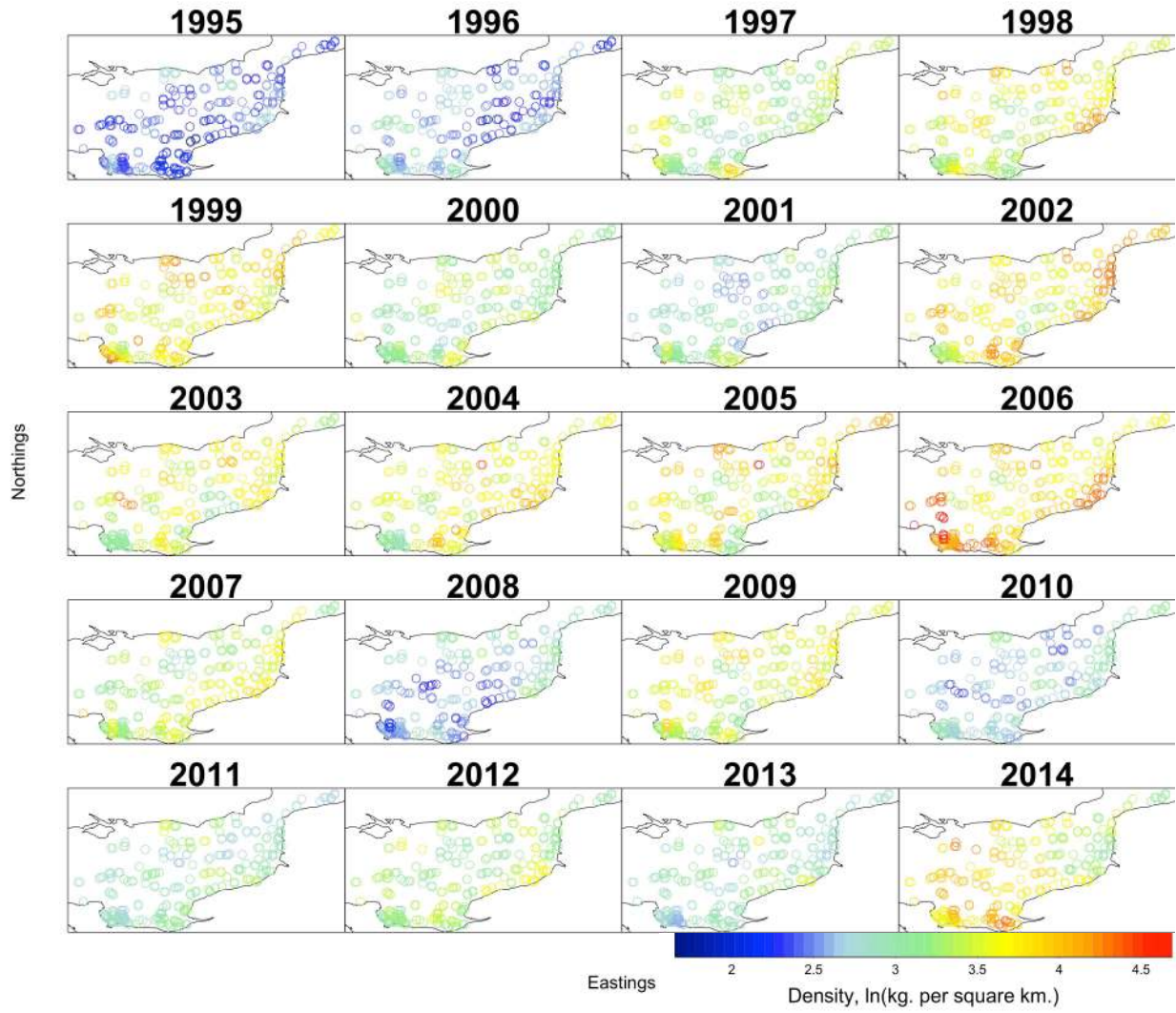


Figure 5: *Scophthalmus rhombus* spatial distribution in the Eastern English Channel from low (blue) to high (red) densities in numbers/  $\text{km}^2$  in log scale.

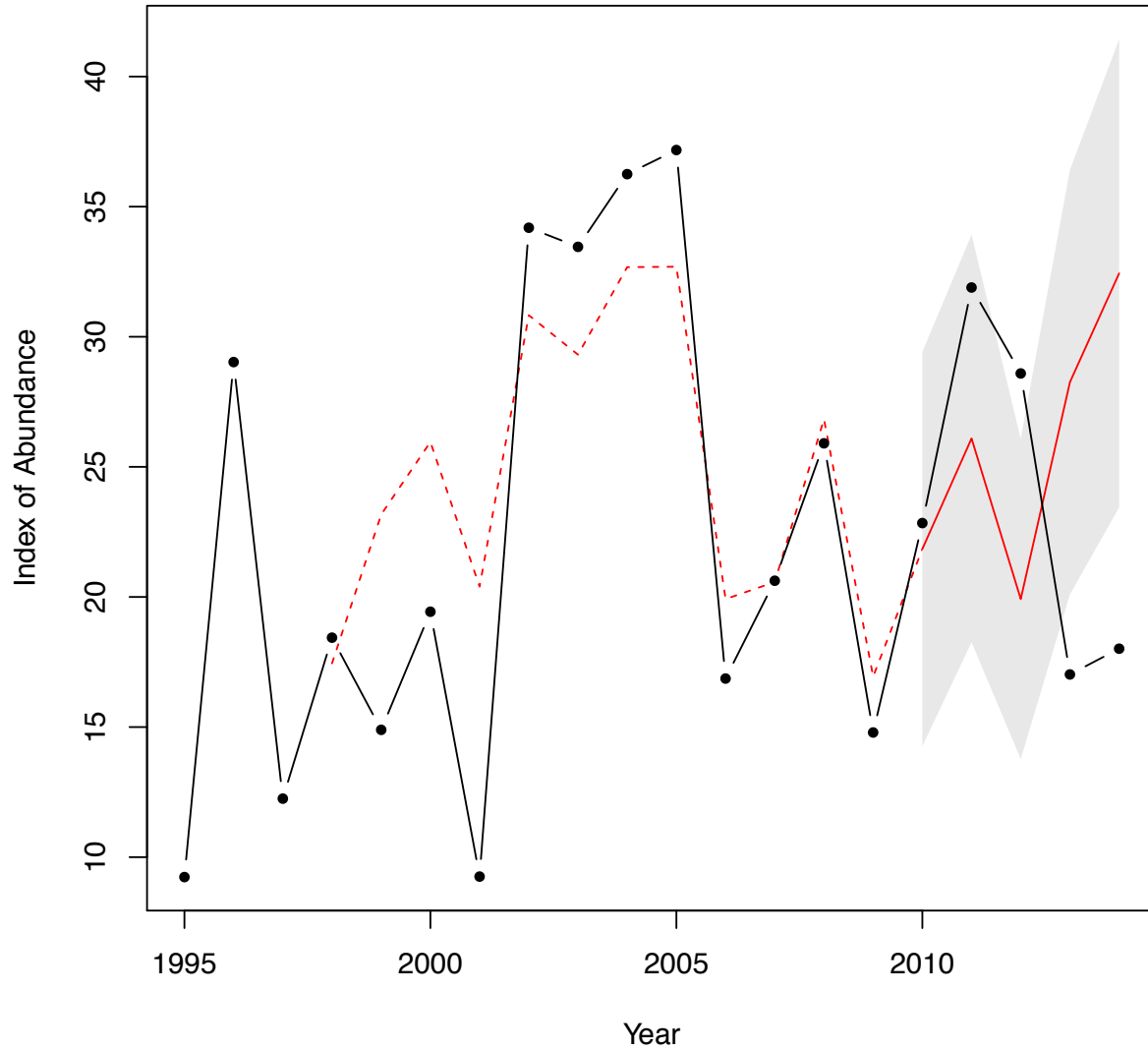


Figure 6: Cross-validation for the predicted 2010 to 2014 years of *Scophthalmus maximus* index of abundance (solid red line) given *Scophthalmus rhombus* index of abundance lagged by three years. The black line is the observed index of abundance of the *Scophthalmus maximus*, the Red dashed line is the generalized additive model prediction. The grey shaded area represents the 95% confidence interval for the prediction.

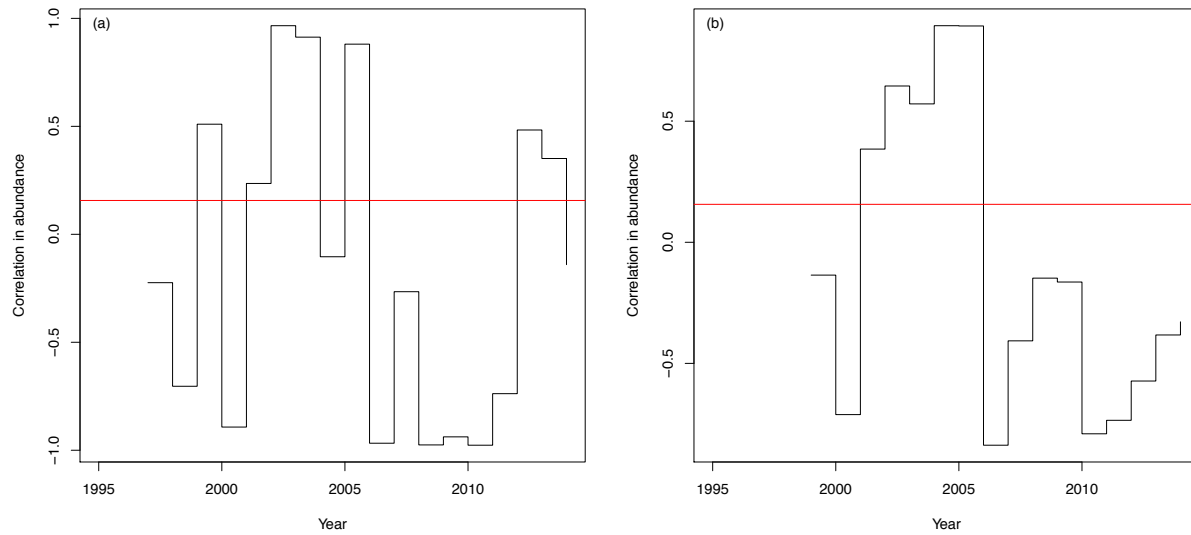


Figure 7: Rolling correlation (black line) and average correlation (red line) calculated between the index abundance of *Scophthalmus rhombus* and *Scophthalmus maximus* from 1995 to 2014 with a three-year lag (a) and a five-year lag (b).



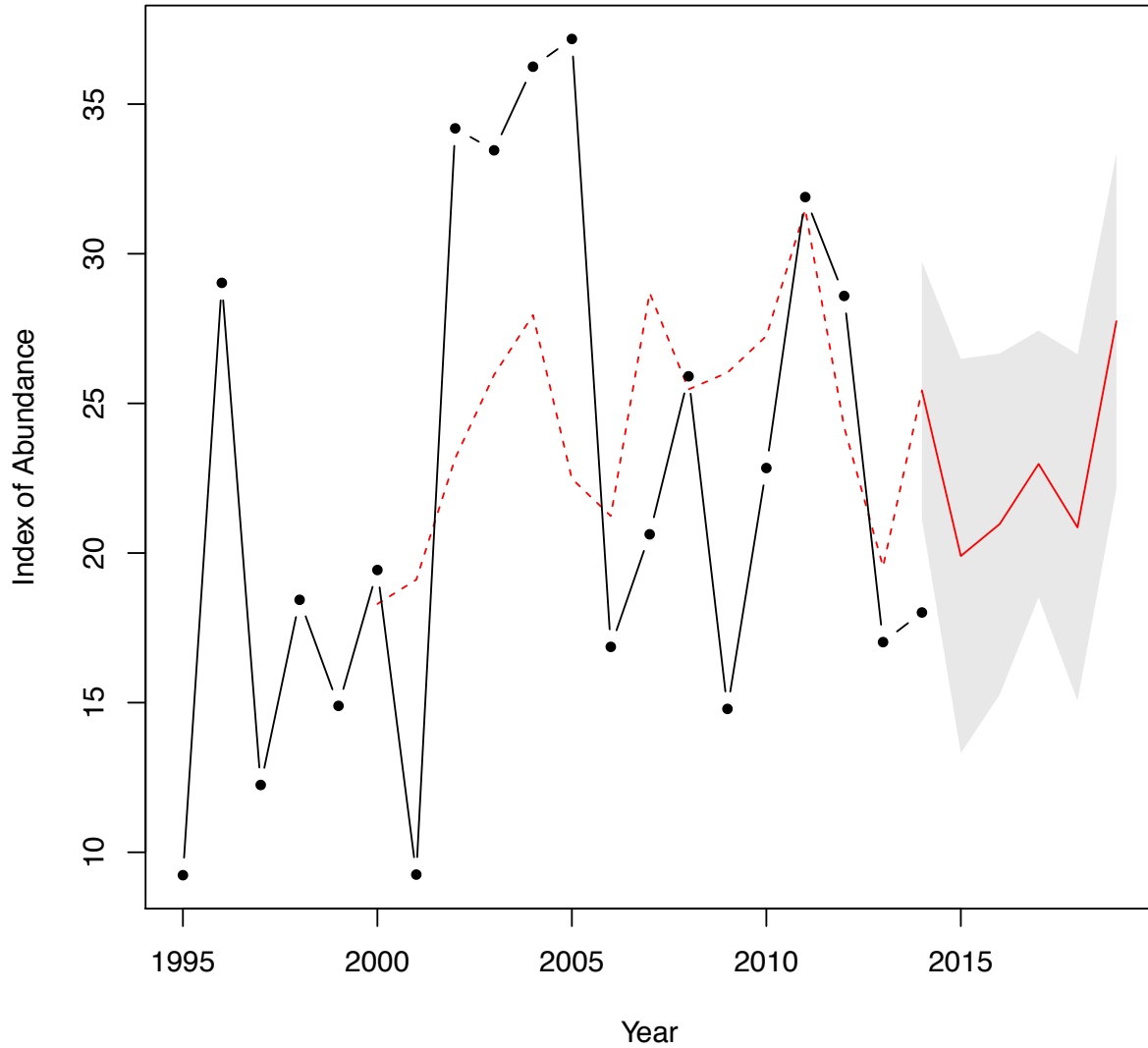


Figure 8: Projection of *Scophthalmus maximus* index of abundance for year 2015 to 2019 with the associated confidence intervals (grey shade) The projection was obtained using a generalized additive model with *Scophthalmus rhombus* index of abundance lagged by five years as a predictor.

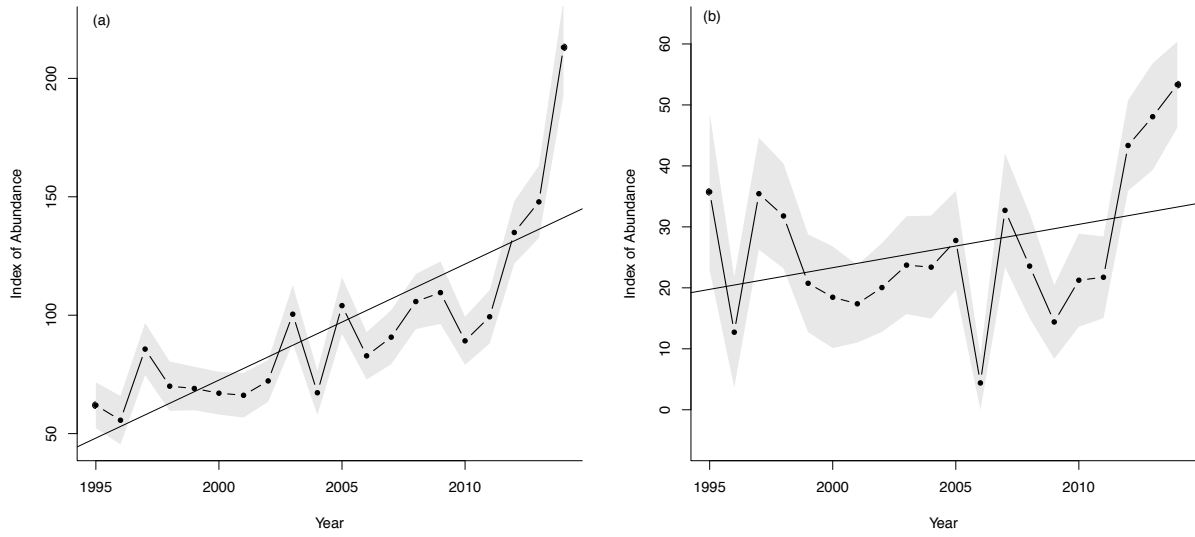


Figure 9: Index of abundance estimated by VAST in thousands for *Raja Clavata* (a) and *Raja Undulata* (b) from 1995 to 2014.

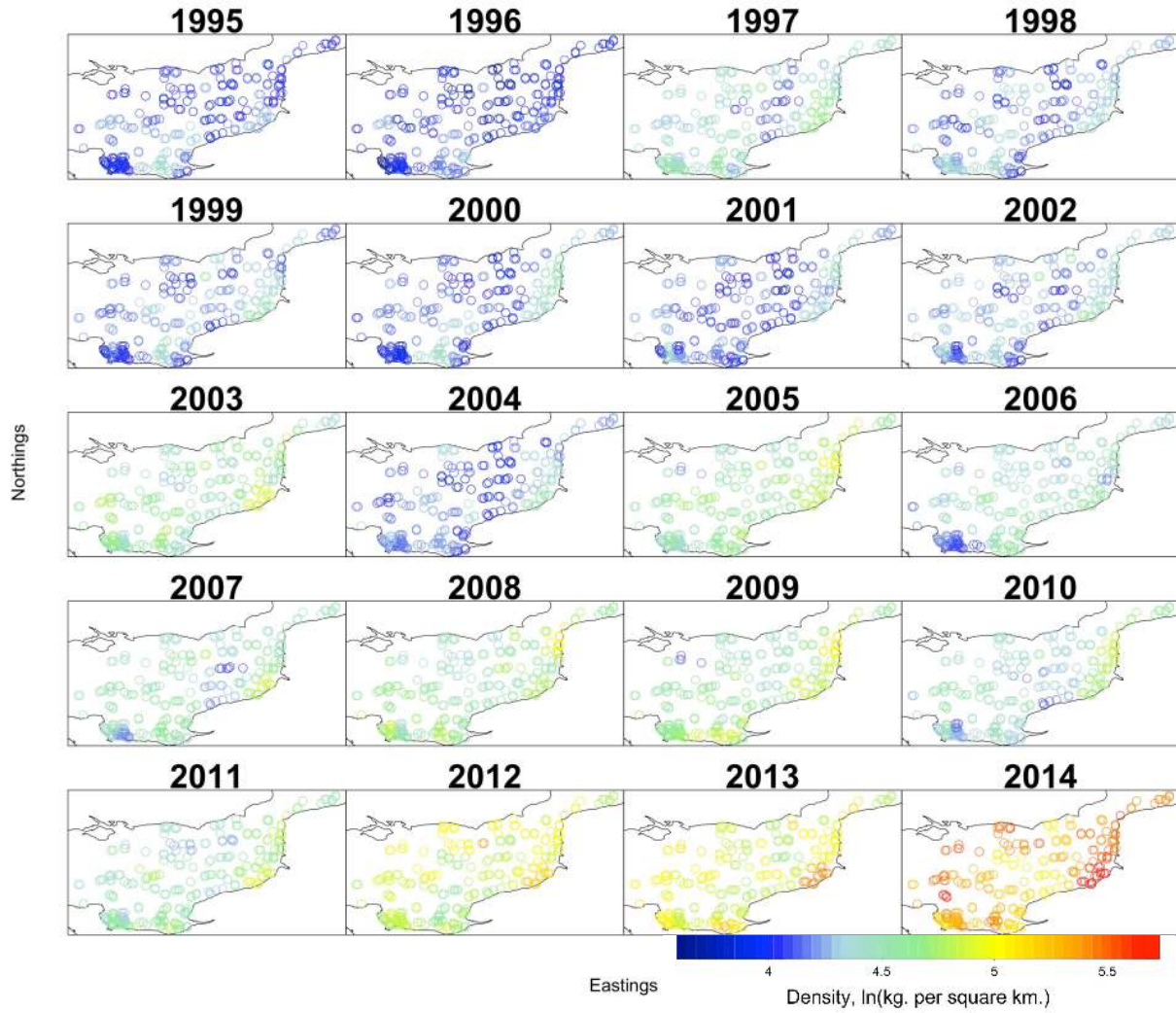


Figure 10: *Raja Clavata* spatial distribution in the Eastern English Channel from low (blue) to high (red) densities in numbers/  $\text{km}^2$  in log scale.

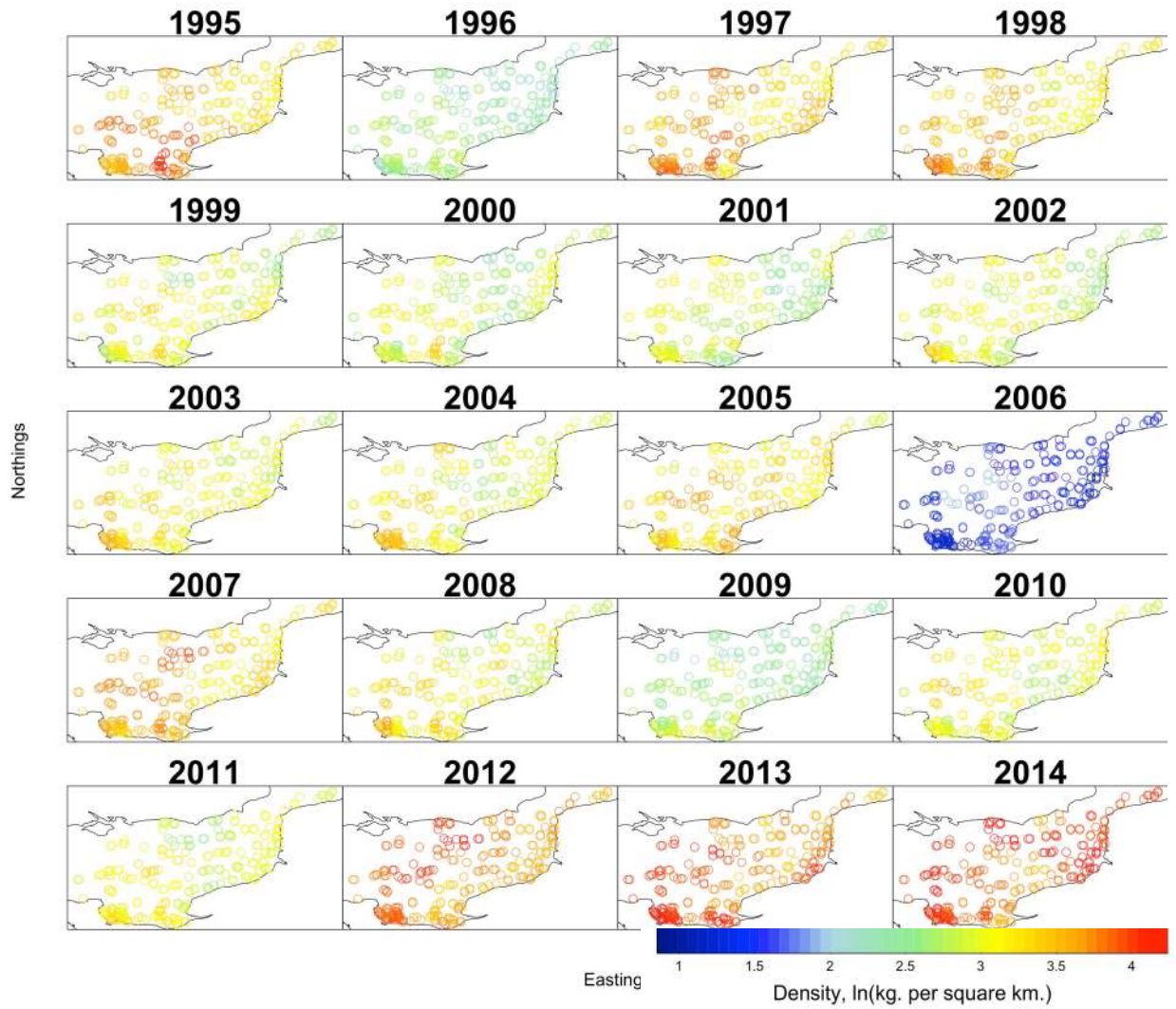


Figure 11: *Raja Undulata* spatial distribution in the Eastern English Channel from low (blue) to high (red) densities in numbers/ km<sup>2</sup> in log scale.

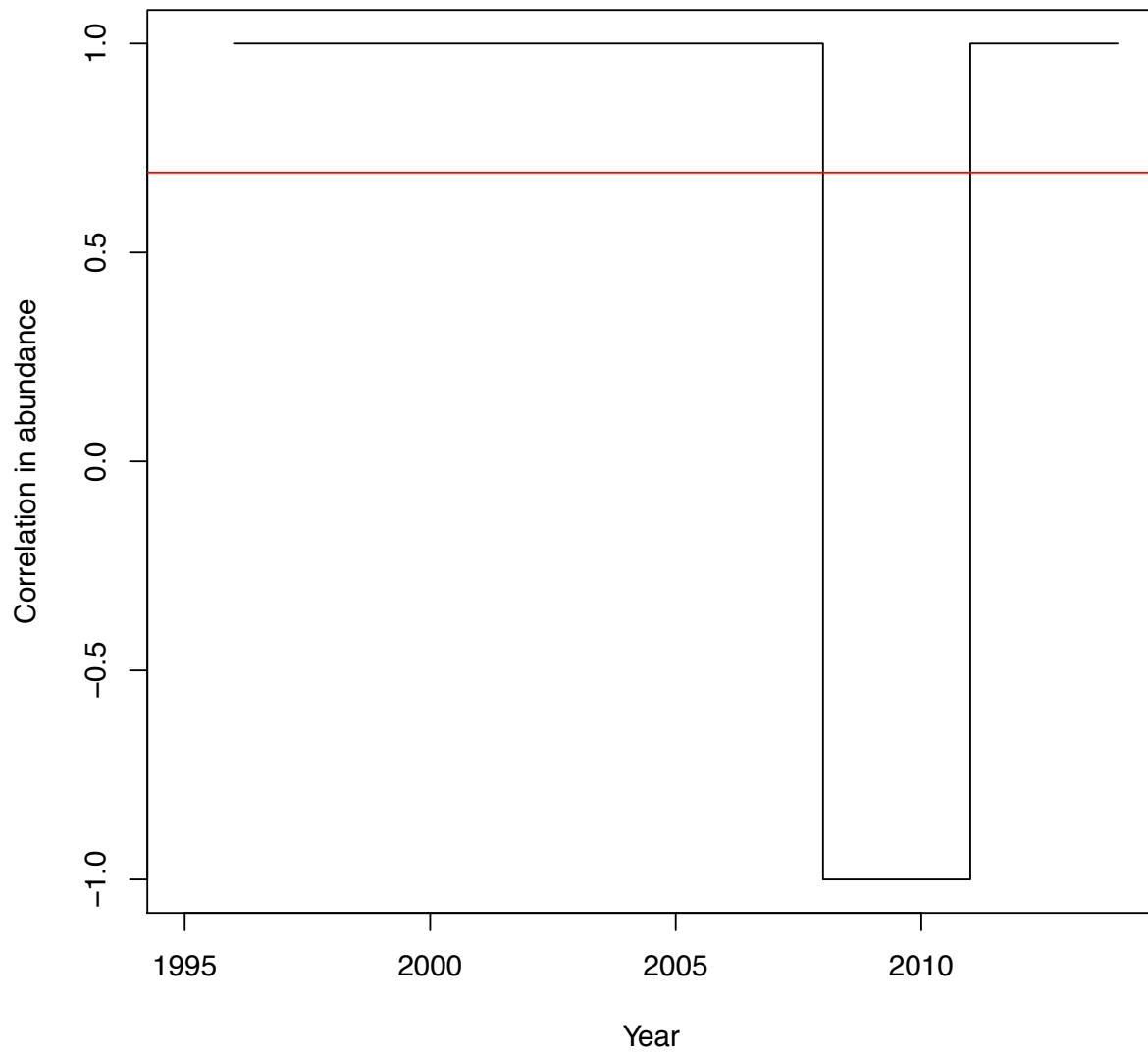


Figure 12: Running correlation (black line) and average correlation (red line) calculated between the index abundance of *Raja Clavata* and *Raja Undulata* from 1995 to 2014.

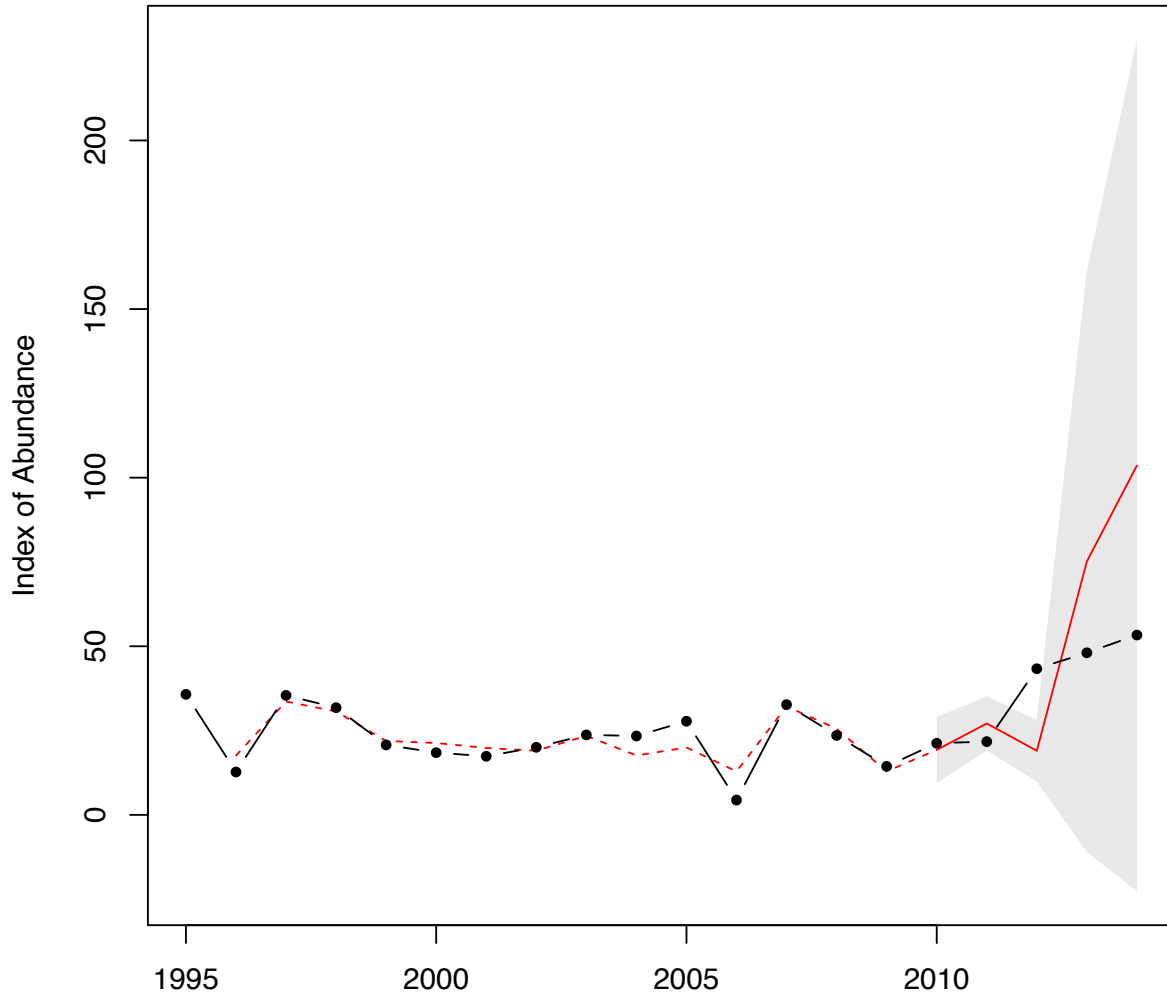


Figure 13: Crossvalidation for the predicted 2010 to 2014 years of *Raja Undulata* index of abundance (solid red line) given *Raja Clavata* index of abundance lagged by one years. The black line is the observed index of abundance of the *Raja Undulata*, the Red dashed line is the generalized additive model prediction. The grey shaded area represents the 95% confidence interval for the prediction.

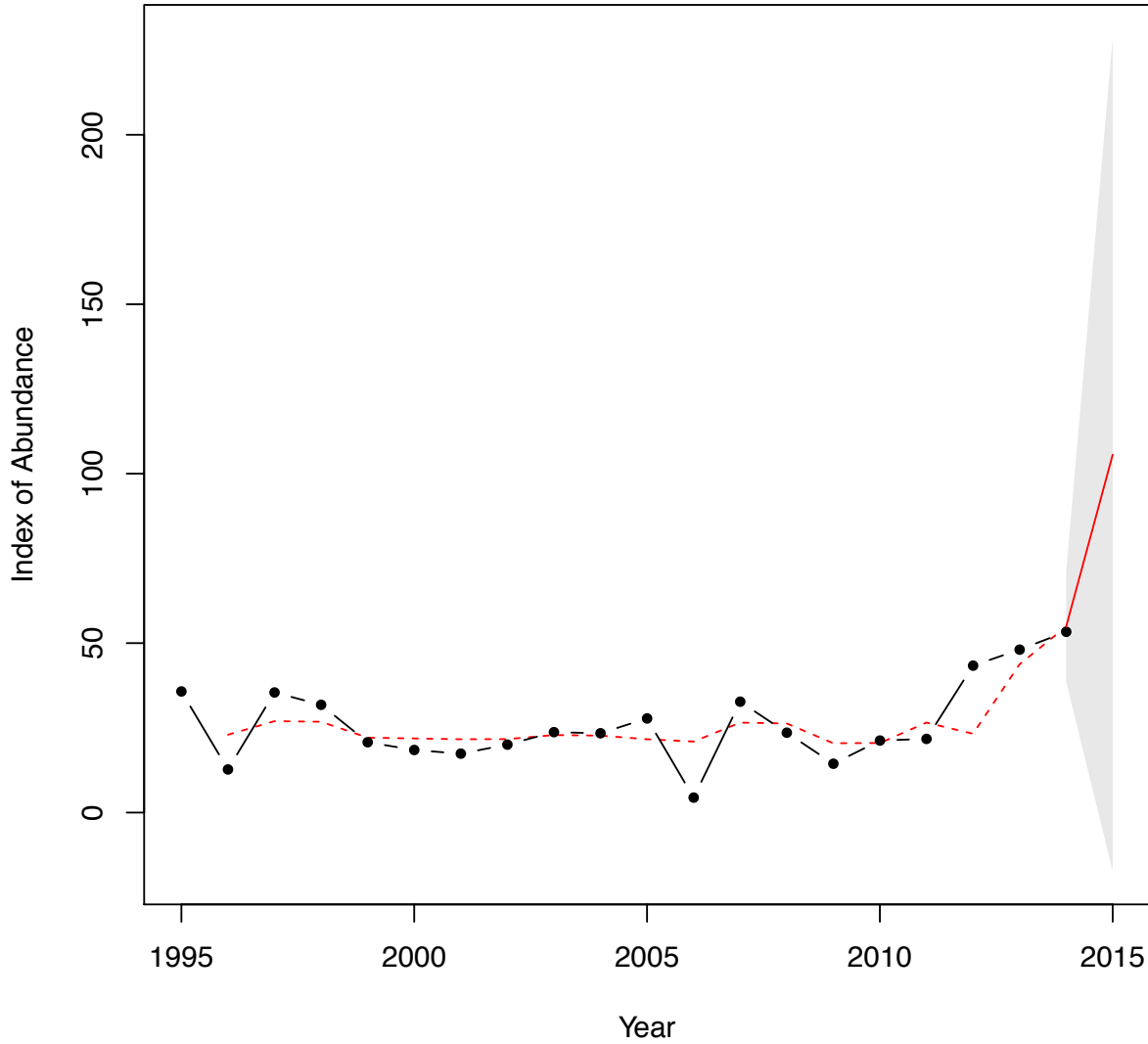


Figure 14: Projection of *Raja Undulata* index of abundance for year 2015 with the associated confidence intervals (grey shade) The projection was obtained using a generalized additive model with the *Raja Clavata* index of abundance lagged by one year as a predictor.

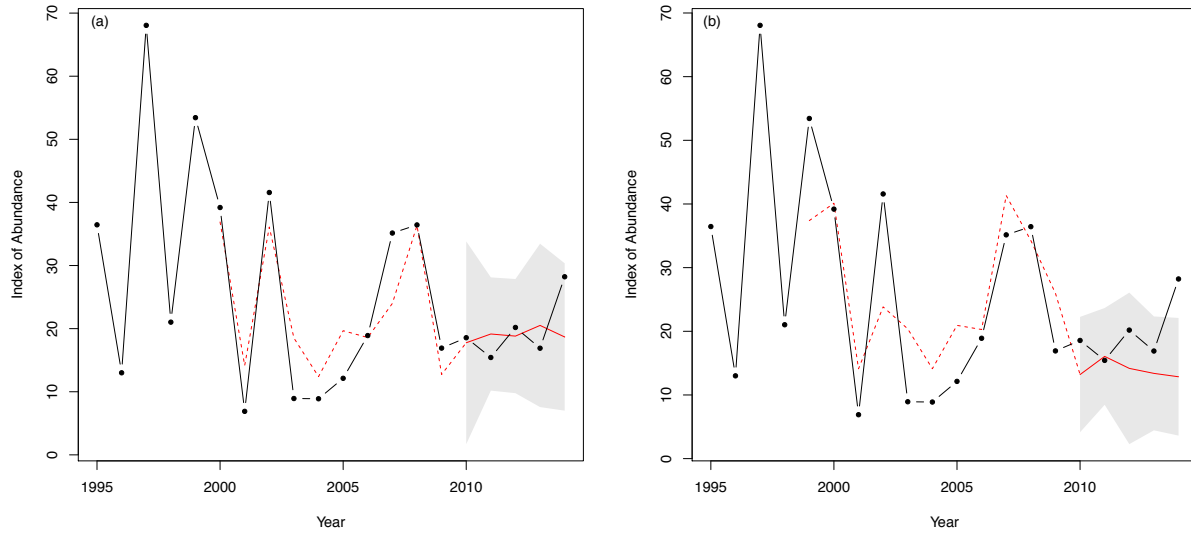


Figure 15: Cross-validation for the predicted 2010 to 2014 years of *Galeorhinus galeus* index of abundance (solid red line) given *Scyliorhinus stellaris* index of abundance lagged by five years (a) and given *Trigloporus lastoviza* lagged by four years. The black line is the observed index of abundance of the *Galeorhinus galeus*, the Red dashed line is the generalized additive model prediction. The grey shaded area represents the 95% confidence interval for the prediction.



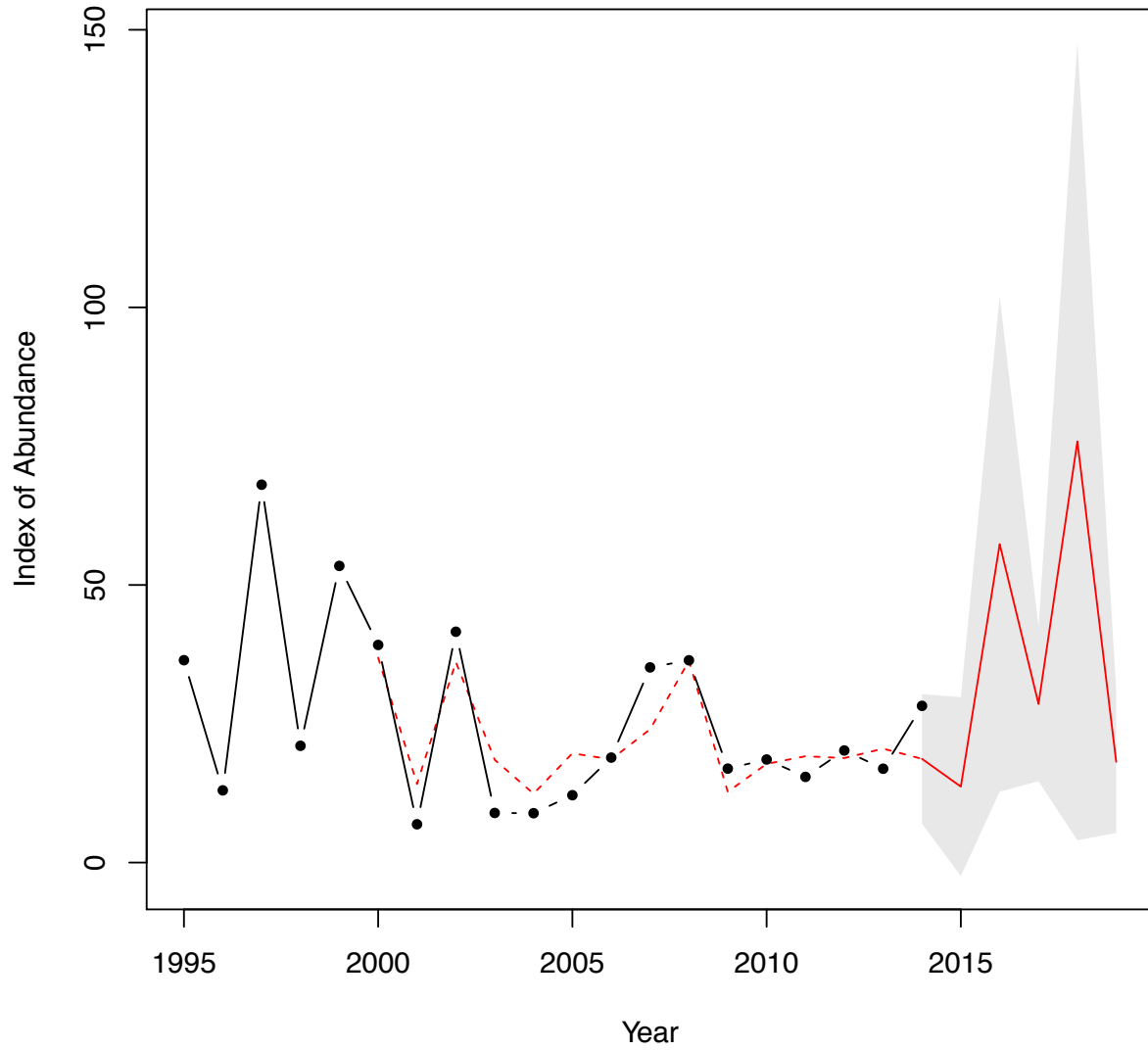


Figure 16: Projection of *Galeorhinus galeus* index of abundance for year 2015 to 2019 with the associated confidence intervals (grey shade) The projection was obtain using a generalized additive model with *Scyliorhinus stellaris* index of abundance lagged by five years as a predictor.

## Supplemental Materials

Table S1: Comparison of generalized additive model fit with zero to five-year lag using the Generalized Cross Validation score for *Trigloporus lastoviza* index of abundance as predictor and *Scyliorhinus stellaris* as predicted.

Lag	0	1	2	3	4	5
Score 15years	122.8784	<b>117.536</b>	155.5866	195.3635	188.1008	149.1782
Score 20years		<b>140.8941</b>	176.5572	195.9607	189.5349	149.1782

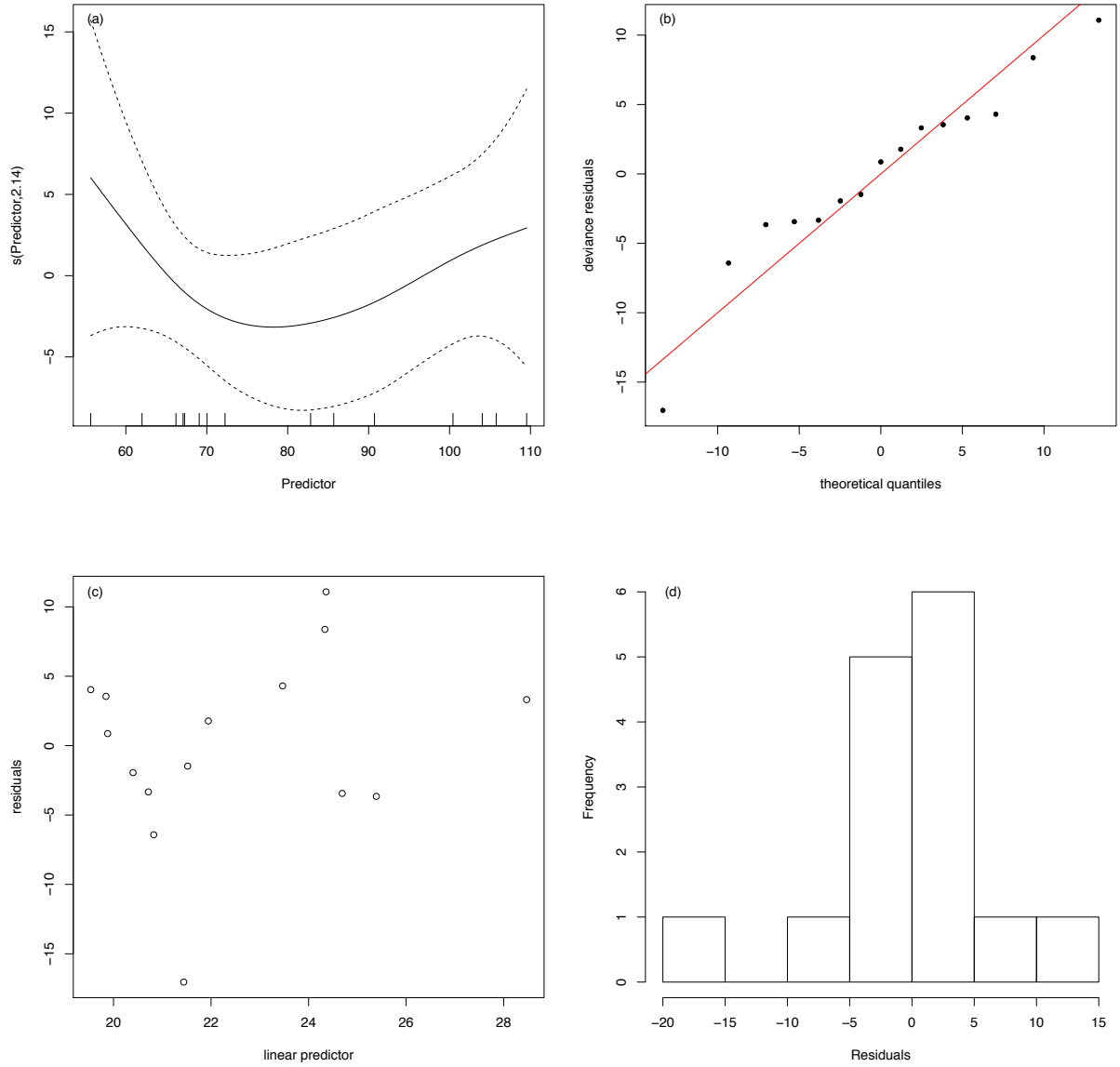


Figure S1: Residuals analysis for the generalized additive model *Raja Undulata* index of abundance.

## Conclusion

In this dissertation the focus was driven towards the most resilient species of the ecosystem. These 16 species represent 15% of the total number of species in the Eastern English Channel (EEC) and 36% of the total abundance in the ecosystem. Relying on this low proportion of selected species to draw conclusions on the community structure and resilience raises questions. From early on ecologists have focused on the most dominant species to define how stable ecosystems are (Reid and Buckley, 2011; Lynch and Neufeld, 2015). These usually do not bring enough contrast to statistical analysis but also prevent management of species at risk.

Recently the focus shifted to rare species as they are recognized crucial for the ecosystem (Lyons et al., 2005; Mouillot et al., 2013; Soliveres et al., 2016). Rarity can be defined in different ways including local abundance, geographical distribution or habitat specificity (Rabinowitz, 1981; Jousset et al., 2017). Rare species present low detectability which renders statistical analysis difficult.

Our analysis did not distinguish between rare and non-rare species but rather focused on what species of the ecosystem are the most resilient. Thus, species in this analysis are either vastly distributed in the ecosystem even in rare local abundances, in modest abundance in most habitat or are in modest abundance in rare locations. The range of abundance in these species, the fact that they represent close to 40% of the total abundance of the samples when removing the top three species and the fact that they are widely present in the study area makes them good candidates to depict significant community patterns.

The ASTEC model opened the door to answering many ecological impasses. First, ASTEC defines the spatial and spatio-temporal community structure within the EEC. Past studies used expert knowledge to determine communities, while ASTEC provides a non-biased statistical framework to do so. The spatial and spatio-temporal matrices are the output of the first part of ASTEC, a zero-inflated Poisson with latent predictors (Thorson and Barnett, 2017). The spatial matrix expresses similarities in presence-absence in the area of study and the spatio-temporal matrix pairs species with similarities in spatial presence-absence, combined with similarities in trends of abundance. The second part of ASTEC is a hierarchical clustering analysis that organizes the species in statistical clusters (Shimodaira, 2004). Joining these two analyses provides a new statistical framework that opens new possibilities in the realm of spatial and spatio-temporal species distribution analysis.

Most studies focused on spatial relationships, identifying distribution of species assemblages or predicting outcomes from species interactions (Magnuson *et al.*, 1998; Olden and Jackson, 2002; Oberdorff *et al.*, 2001). Studying spatial community structure reveals species affinities, as well as habitat preferability. This information is essential to implement valid spatial conservation measures (e.g. marine protected areas). However, it lacks summarizing the effect of a strong influencer, the environmental changes (vert-pre *et al.*, 2013). By adding covariation in abundance over time to spatial variations one can jointly predict communities in space and time. Thus, understanding how environmental drivers shapes community patterns.

## *Conclusion*

Second, ASTEC tackles the issue of spatial scales. Geographical scales are essential in spatial management but are often disregarded. To efficiently implement a spatial closure size, managers require to know the target species distribution (i.e. connectivity between functional habitat) and the distribution of other species upon which target species depend (predator-prey relationships or other sympatric relationships). To identify the correct spatial management scale, managers need to estimate the nature and variability of the interactions given the scale of the study. ASTEC does not only identify the nature of interactions given the scale but it also reveals the scale that fits the sampled data the best.

From the smallest to the largest scale, the ecological niches are more compartmented. These niches are the result of heterogeneity in abiotic and biotic factors defining community specific habitat structure (Chesson, 2000). On different scale, the ecological niches are not only different, but the species composition of the identified statistical communities is also highly variable. In a spatial framework, due to results variability, managers can use the most parsimonious model to assess ecological realized niches and define appropriate habitat conservation tools given the spatial distribution of communities. For the EEC, 522km<sup>2</sup> is the scale at which the model best fit the CGFS survey data.

Given the variability of the results in a spatial framework, it is best to use spatio-temporal framework for community studies. Spatio-temporal communities are constant in composition regardless of the scale of the study. The species within a spatio-temporal community pertains to the same fundamental niche and their abundance responds in a similar fashion to external pressure. The spatio-temporal framework revealed two main biogeographic areas from East to West of the Seine river. The Eastern community (ST1) has highest abundance in the shallower estuaries and

areas with muddy sediments. The western community (ST2) has abundance peaks in the Bay of Veys, the entrance of the Seine river and the center of the channel. ASTEC identifies the hotspots of abundance that are mainly in local areas with high disturbance. This confirms that disturbance not only affects the abundance of species through limiting or increasing food availability and modifying habitat quality (Grime, 1977), but is also defined as temporal persistence of habitat structure (Foveau *et al.*, 2017). To protect a particular species within a community, managers have to monitor that the abundance of the species does not decline in the community hotspot (blue striped in ST1 and purple vertical striped in ST2), does not decline as they could be the most resilient habitat of the community. If there is abundance decline in these resilient areas, habitat conservation plans should be implemented.

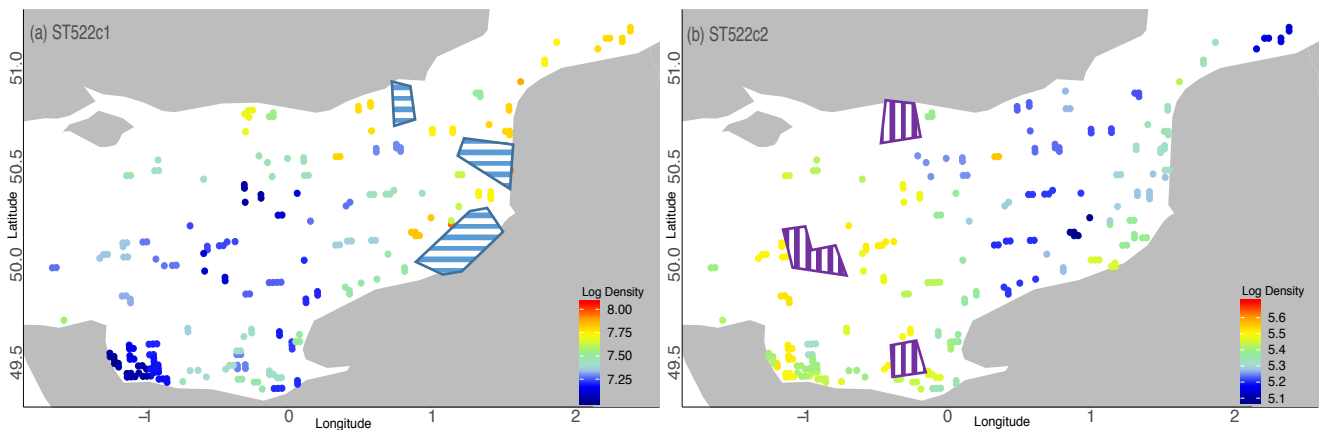


Figure 1: Eastern English Channel spatio-temporal communities with their abundance hotspots (blue horizontal striped in ST1 and purple vertical striped in ST2). Hotspots are defined by selecting the areas with highest densities. From low (blue) to high (red) median densities of numbers/ km<sup>2</sup> in log scale for communities ST1 (a), ST2 (b).

## *Conclusion*

The resilience of the communities lies also in the species dynamics shifts. By coupling the spatial and spatio-temporal variations we capture species dynamics within communities. These dynamics reflect species shifts spatially which provides crucial information about species replacement in time according to oceanographic regime shifts. ASTEC can capture the relative impact of global environmental change on community patterns. These results become crucial when studying resilience of an ecosystem to climate change, environmental shifts or strong anthropogenic pressures. Replacement species maintain a stable productivity at the community level. Thus, management should focus on the following species. *Sardina pilchardus* and *Scophthalmus scombrus* shifts in an aphasic period with *Raja clavata* and *Raja undulata*. This shift will ultimately have consequences not only on the ecosystem but also on the fisheries of the area. As the abundance of *S. pilchardus* and *S. scombrus* decrease and the abundance of *R. clavata* and *R. undulata* increase, fishing effort might shift from *S. pilchardus* and *S. scombrus* to *R. clavata* and *R. undulata*. In identifying these shifts, ASTEC can help managers anticipate the shift of fishing effort and set a more focused management on *R. clavata* and *R. undulata*.

Third, ASTEC enhances functional analysis by truly adding temporal dynamics to these already useful functional analysis. Scientists and managers shifted from a species management to a functional approach to move towards ecosystem conservation. Indeed, community functions linked with functional traits are essential to the stability within an ecosystem (Costanza et al., 1997; Suding et al., 2008; De Groot et al., 2010). Most studies capture a snapshot of the functional structure within an ecosystem per unit of time. Our comparative study concludes that these methods do not integrate the true functional temporal variability within an ecosystem and



can lead to erroneous conclusions. ASTEC via identifying spatio-temporal communities and their associated functional indices provides a dynamic functional spatio-temporal variability.

In the EEC, the overall community shows a wide range in types of functional traits. Moreover, ST1 and ST2 scenarios reveal very distinct strategies when it comes to abundance distribution in the functional traits volume. The community constituting of the most “at risk” species, show more evenly distributed abundance across the functional volume. Thus, evenness in the abundance of functional traits, and reduced variety in ranges in functional traits is detrimental to community stability and impairs community’s resilience. Moreover, the spatio-temporal communities within the ecosystem are converging over time to a similar functional distribution. These results lead us to believe that internal mechanisms are driving the community to a functionally stable equilibrium (Straver et al., 2011; Miller et al., 2018). If, in a good environmental regime and with appropriate management measures, the system can return to this equilibrium after a disturbance.

The overall trophic level of the community is decreasing along with the mean preferred temperature. Indeed, the abundance of species with lower, upper temperature limit increased in the Easter English Channel when the abundance of species with warmer preferred temperature decreased along the study period. The important spatial restructuring of the community with species migration from West to East or East to West, along with decreasing trends in trophic level indicate that these communities are under high fishing and environmental pressure.

Last, with the high statistical certainty in spatio-temporal community composition, ASTEC succeeds where traditional management model fails. Indeed, ASTEC identifies surrogate species

## *Conclusion*

that can forecast the abundance of rare at-risk species under the IUCN Red List. The predictive power of our analysis is strong when it comes to trends. However, predictive power of abundance estimates is variable given the species.

*S. maximus* trend is increasing and *Raja undulata* seems to rebuild. The projections over the next five years, and one year, respectively, predict that this increase will remain. Our analysis shows that the abundance levels of *Scophthalmus maximus* in the EEC are similar to that of the EU waters of ICES Division 2.a and Subarea 4. This area's management decisions could be used as proxy for the EEC division. Given the results of the functional trait analysis and abundance predictions, the proposition for increasing the French Exclusive Economic Zone's Total Allowable Catch (TAC) for *R. Undulata* could be done but with high precautions (ICES, 2018). Stakeholder and scientists need to set in place a joint management between the Eastern and the Western part of the English Channel. Identifying which fishing pressure *R. undulata* can sustain is difficult at this point for multiple reasons. First, the abundance can only be predicted one year in advance. Second, the species is likely driven by both fishing pressure and environmental changes, which makes it more vulnerable. Third, this species is also caught as bycatch, which makes it harder to account for real landings. However, reopening the fishery following a precautionary approach could be tried. Managers can allow the fishing pressure to be set as a small percentage of the increase in abundance between the current year and the projected year while monitoring closely the stock's response. ASTEC abundance level still proves difficult to predict for species like *Galeorhinus galeus* when the abundance of a species is mainly environmentally driven and oscillates in booms and busts. However, it still can predict the overall trend of the abundance over a few years.

Due to abundance variability in the stock abundance, our advice on allowed landings would be not to use yearly management but instead, to use all five years of projections to make an informed decision.

ASTECC possesses strength not only in spatial management but also in monospecific and multi-specific management strategies. While it is quite heavy to compute, ASTEC's power resides in that it requires very little data compared to other models. Furthermore, while highly impacted by anthropogenic and environmental changes, the EEC seems to be resilient and still experiences some structurally important endangered species rebuild. ASTEC draws a complete and dynamic picture of the two spatio-temporal communities identified in the EEC. However, more communities could exist within the ecosystem. Thus, expanding the method could allow to infer conclusions at the whole ecosystem level.

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