# Spatiotemporal abundance pattern of deep-water rose shrimp, Parapenaeus longirostris, and Norway lobster, Nephrops norvegicus, in European Mediterranean waters 

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#### Abstract

Summary: The main characteristics concerning the distribution of two of the most important decapod crustaceans of commercial interest in the Mediterranean Sea, the deep-water rose shrimp, Parapenaeus longirostris, and the Norway lobster, Nephrops norvegicus, are studied in the European Mediterranean waters. The study is based on data collected under the MEDITS trawl surveys from 1994 to 2015 from the Gibraltar Straits to the northeastern Levantine Basin (Cyprus waters). The observed differences can be interpreted as different responses to environmental drivers related to the differing life history traits of the two species. In fact, N. norvegicus is a long-living, benthic burrowing species with low growth and mortality rates, while $P$. longirostris is an epibenthic, short-living species characterized by higher rates of growth and mortality.


Keywords: Nephrops norvegicus; Parapenaeus longirostris; distribution; trawl survey; Mediterranean Sea.

Patrón de abundancia espacio-temporal de la gamba de altura, Parapenaeus longirostris, y de la cigala, Nephrops norvegicus, en las aguas mediterráneas europeas

Resumen: Se investigaron las características de la distribución de dos de los crustáceos decápodos más importantes a nivel comercial del mar Mediterráneo, la gamba de altura, Parapenaeus longirostris y la cigala, Nephrops norvegicus, en aguas mediterráneas europeas. El presente estudio se basa en datos recopilados en las campañas de pesca experimental de arrastre MEDITS, relizadas de 1994 a 2015 desde el estrecho de Gibraltar hasta la cuenca levantina nororiental (aguas de Chipre). Las diferencias observadas en el patrón de distribución se pueden interpretar como distintas respuestas a factores ambientales relacionados con los diferentes rasgos del ciclo vital de las dos especies. De hecho, N. norvegicus es una especie bentónica de vida larga, con bajas tasas de crecimiento y mortalidad, mientras que $P$. longirostris es una especie epibentónica de vida corta, caracterizada por tasas más altas de crecimiento y de mortalidad.

Palabras clave: Nephrops norvegicus; Parapenaeus longirostris; distribución; campañas de pesca experimental de arrastre; mar Mediterráneo.

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## INTRODUCTION

The deep-water rose shrimp, Parapenaeus longirostris, and the Norway lobster, Nephrops norvegicus, are two of the most important target species of demersal fisheries on the Mediterranean continental shelf and upper slope. Their biology and population dynamics have been thoroughly studied (García-Rodríguez et al. 2009, Johnson and Johnson 2013, Kapiris et al. 2013) and the exploitation status of their stocks has been assessed in several areas of the Mediterranean Sea (GFCM 2017, STECF 2017). Because the life histories of the two species show different characteristics, especially concerning their lifespan and growth rate, the study of the spatiotemporal evolution of their abundance is of valuable interest for understanding the dynamics of deep-water ecosystems (Company et al. 2008, Ligas et al. 2011).

The deep-water rose shrimp is a fast-growing, short-living species with a thermophilic preference (Sobrino et al. 2005, Colloca et al. 2014) that inhabits the water column layers close to the seabed of muddy bottoms of the shelf break and upper slope, in a depth range of between 20 and 700 m . Its distribution area encompasses the Mediterranean Sea and the eastern North Atlantic Ocean (Ribeiro-Cascalho and Arrobas 1987, Ardizzone et al. 1990, Levi et al. 1995). It has a size-related bathymetric distribution linked to the ontogenetic migration of juveniles from the continental shelf to the slope (Ardizzone et al. 1990, Lembo et al. 2000, Politou et al. 2008). Mature females are present throughout the year (Levi et al. 1995), so the species shows a continuous recruitment pattern (Sobrino et al. 2005). A large number of fleets target the species, particularly in the eastern Mediterranean (Politou et al. 2008), but it is also exploited in the eastern Atlantic (Benchoucha et al. 2008), the Balearic Islands (Guijarro et al. 2009) and the Tyrrhenian Sea (Sbrana et al. 2006, Milisenda et al. 2017).

Along the NW coasts of the Mediterranean, the species forms small and highly fluctuating populations and shows the largest abundances in warmer waters, with a decreasing south-north abundance gradient (Abelló et al. 2002, Sobrino et al. 2005). A positive correlation between sea surface temperature (SST) and abundance of deep-water rose shrimp was observed in Morocco (Benchoucha et al. 2008). In the Ligurian and northern Tyrrhenian Seas, Ligas et al. $(2010,2011)$ and Colloca et al. (2014) underpinned the positive effect of SST on the temporal trend of stock abundance and commercial catches of $P$. longirostris. The deep-water rose shrimp in the Ligurian and northern Tyrrhenian Seas are one of the few stocks in the western and central Mediterranean to be exploited sustainably, exhibiting a sharp increase in abundance in the last few years (Colloca et al. 2014, GFCM 2017, STECF 2017). This increasing trend does not appear to be affected by fishing activities, because the exploitation pattern has remained the same over the last decade, as is also demonstrated by the lack of recovery of other important stocks (Colloca et al. 2014).

The Norway lobster is a long-living decapod, typically inhabiting temperate and cold waters, dwelling in burrows and exerting territorial behaviour (Aguzzi et al. 2003). Its bathymetric distribution is very wide, ranging from a few metres down to 900 m in depth (Johnson and Johnson 2013). In the Mediterranean Sea, the highest densities are found between 200 and 500 m , although high catch rates are also reported between 500 and 800 m depth (Abelló et al. 2002). In areas with a wide continental shelf, such as the Adriatic Sea or close to the Ebro Delta, the Norway lobster can be found in shallow waters (Abelló et al. 2002, Morello et al. 2009), as in the eastern Atlantic and the North Sea (Campbell et al. 2009). The Norway lobster is a sedentary species inhabiting burrows built in muddy bottoms at the shelf break and on the upper slope of the northeastern Atlantic and Mediterranean (Aguzzi


Fig. 1. - GSAs included in the study.
and Sardà 2008). The species spends most of the time in its burrows. Its behaviour when it emerges makes it vulnerable to bottom trawling, and is associated with light and other environmental and demographic factors (food availability, size, mating, etc.) (Morello et al. 2007, Aguzzi and Sardà 2008). Gonad maturation usually starts in January-March, and the breeding season is between May and September (Orsi Relini et al. 1998, Mente et al. 2009). In the Mediterranean Sea, The Norway lobster is mostly exploited by bottom trawling (Sardà 1998), and only in the Adriatic Sea are there some fisheries using pots and creels (Morello et al. 2009). The species has relatively low importance in terms of landings for the Mediterranean fisheries, but has a leading role in view of its economic value (Sbrana et al. 2003).

Due to these contrasting characteristics, it was hypothesized that the two species show different behaviours in relation to changes in environmental factors. The aim of the present paper is to analyse the distribution pattern of both $P$. longirostris and $N$. norvegicus in the European Mediterranean waters. All data used in the present study were collected from different areas of the Mediterranean with identical fishing gear and sampling procedures, thus allowing combined analysis of data from the different areas.

## MATERIALS AND METHODS

The data analysed originate from a total of 23144 hauls carried out during daylight hours in the second/ third quarter of the year between 10 and 800 m depth under the framework of the EU Project MEDITS for the period 1994-2015. The surveys took place in the European waters of the Mediterranean Sea and cover the FAO-GFCM geographic sub-areas (hereafter GSAs) reported in Figure 1. The sampling procedures were standardized according to a common proto-
col; details on the survey methodology and defined geographical sectors are described in the MEDITS handbook (http://www.sibm.it/MEDITS\ 2011/ principaledownload.htm).

The area swept in each haul was calculated from direct measurements of the horizontal opening of the net detected by ScanMar (or SIMRAD) equipment. If such instruments were not available, the measuring procedures reported in the MEDITS handbook were applied. Biomass and density indices of deep-water rose shrimp and Norway lobster were calculated from each haul as biomass and number of individuals per swept area (kg $\mathrm{km}^{-2}$ and $\mathrm{N} \mathrm{km}^{-2}$, respectively) (Sparre and Venema 1998). Stratified mean biomass and density indices by species and year were also calculated for each GSA, as well as the frequency of occurrence per depth stratum (10-200 m, 200-800 m). The Spearman Rho nonparametric test was applied to the biomass and density indices to evaluate statistical significance in the trends of the various GSA data series (Hamed 2016). Mean depth (m) and mean geographical position (latitude and longitude) were recorded at each station during the surveys.

The effects of abiotic variables on the spatiotemporal variations in the abundance of deep-water rose shrimp and Norway lobster were determined using generalized additive models (GAMs) (Hastie and Tibshirani 1990). The density index of shrimps was modelled on the $\log$ scale. By means of an exploratory analysis, a change in spatial distribution of the two species over the years was observed, suggesting a non-separable effect of space and time that was used as a basis for the modelling approach. Explanatory variables in deep-water rose shrimp and Norway lobster abundance models were latitude and longitude, SST, depth, and time (years). Satellite data at a fine spatial scale ( $0.063 \times 0.063$ degrees) for SST (degrees Celsius) were collected (MyOcean follow-on project, http://
marine.copernicus.eu); monthly data were averaged to obtain the mean SST for the first quarter of each year from 1994 to 2015. Mean depth (m) and geographical position (latitude and longitude) were recorded at each station during the surveys.

Multicollinearity between the explanatory variables was analysed by means of pair-plots, a matrix of scatter plots that shows the bivariate relationships of variables, and variance inflation factor (VIF) values (Zuur et al. 2007). Variables with a high Pearson correlation coefficient (r) ( $>0.8$, absolute value) and a high VIF value ( $>3$ ) were considered correlated, and one of the pair was removed.

GAM models with Gaussian distribution (and identity link) were used to describe the relationship between the abundance of deep-water rose shrimp and Norway lobster and explanatory variables.

The initial model included a smooth term accounting for spatial (latitude and longitude) and temporal (years) interaction. Later, a smooth term for depth and for the interaction between depth and time was added. The best model was used to introduce a smooth term for SST. Finally, the models were compared using the Akaike information criterion (AIC) and deviance explained. The model with the lowest AIC was selected as the best model, that is, the most parsimonious model with the greatest explanatory power (which best fits the data). The significance of each variable in the GAM was determined by means of analysis of variance (F-test).

Data exploration and analysis were carried out with R 3.4.1 (R Core Team 2017), and the associated mgcv package (Wood 2006). An assumed significance level of $5 \%$ was used in all the statistical analyses.

The spatial analysis predictions were performed using a $0.03^{\circ}$ resolution grid, which was created through the sampling of the informative layers used in the model by means of the QGIS software (QGIS Development Team 2017). In particular, the bathymetric data were derived from the EMODnet Bathymetry portal, while the SST data were derived from MyOcean follow-on project (http://marine.copernicus.eu). The resulting model prediction maps were produced using the R software ( R Core Team 2017). In order to assess changes in the abundance and spatial distribution of the species, maps for six MEDITS surveys carried out in the years 1994, 1998, 2003, 2007, 2011 and 2015 are shown.

## RESULTS

The frequency of occurrence per depth stratum of the studied species in all the investigated GSAs is shown in Table 1. Deep-water rose shrimp was caught in $43.5 \%$ of the hauls performed in the MEDITS survey from 1994 to 2015. Its frequency of occurrence was higher on the continental slope than on the shelf ( $61.9 \%$ and $31.3 \%$, respectively). The highest frequency of occurrence was on the continental slope in GSA 23 (Crete, 94.6\%). In general, the species was more frequent in the eastern and central Mediterranean, from GSA 25 to GSA 8, while the lowest occurrences were recorded in the westernmost part of the Mediterranean (GSAs 1-7).

Table 1. - Percentage of occurrence of deep-water rose shrimp ( $P$. longirostris) and Norway lobster ( $N$. norvegicus) in the investigated GSAs.

|  | Deep-water rose shrimp |  |  | Norway lobster |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| GSA | Shelf | Slope | Total | Shelf | Slope | Total |
| 1 | 19.9 | 37.3 | 30.0 | 1.4 | 48.4 | 28.7 |
| 2 | 0.0 | 20.0 | 17.1 | 0.0 | 63.3 | 54.3 |
| 5 | 1.6 | 33.6 | 14.4 | 0.0 | 58.4 | 23.3 |
| 6 | 13.6 | 35.5 | 19.9 | 5.7 | 78.0 | 26.4 |
| 7 | 11.0 | 32.5 | 14.6 | 11.1 | 77.5 | 22.2 |
| 8 | 0.5 | 75.3 | 44.0 | 1.6 | 97.8 | 57.5 |
| 9 | 47.0 | 65.5 | 55.8 | 3.4 | 87.6 | 43.6 |
| 10 | 58.9 | 63.4 | 61.6 | 0.7 | 62.5 | 37.0 |
| 11 | 7.1 | 58.3 | 27.2 | 0.3 | 70.8 | 27.9 |
| 15 | 60.9 | 88.7 | 76.3 | 1.4 | 78.5 | 44.1 |
| 16 | 45.5 | 78.6 | 63.7 | 2.9 | 77.5 | 44.0 |
| 17 | 29.4 | 89.8 | 33.3 | 25.4 | 77.8 | 28.7 |
| 18 | 58.9 | 69.6 | 62.2 | 15.6 | 62.4 | 30.0 |
| 19 | 34.0 | 46.9 | 42.0 | 4.7 | 46.1 | 30.5 |
| 20 | 4.1 | 72.5 | 58.3 | 4.3 | 35.6 | 16.6 |
| 22 | 35.0 | 72.3 | 53.5 | 12.0 | 46.7 | 29.2 |
| 23 | 17.8 | 94.6 | 42.4 | 0.0 | 18.9 | 6.1 |
| 25 | 24.2 | 84.9 | 41.3 | 0.0 | 0.0 | 0.0 |
| All GSAs | 31.3 | 61.9 | 43.5 | 9.4 | 66.4 | 32.0 |

Norway lobster was mostly present on the continental slope (200-800 m depth). Its frequency of occurrence was higher than $10 \%$ on the shelf only in GSAs $7,17,18$, and 22 (Table 1), with the highest value in GSA 17 ( $25.4 \%$, northern and central Adriatic Sea). The highest occurrences were recorded on the continental slope of the central part of the Mediterranean, from GSA 6 to 17, with frequencies higher than 70\% (97.8\% in GSA 8).

During the MEDITS surveys (1994-2015), deepwater rose shrimp showed the highest biomass and density indices in GSA 23 in 2003 ( $45.128 \mathrm{~kg} \mathrm{~km}^{-2}$ and $9866.32 \mathrm{~N} \mathrm{~km}^{-2}$. Supplementary material, Table S1). In the case of the Norway lobster, the highest abundance indices were observed in GSA 8 in 2004 (52.43 $\mathrm{kg} \mathrm{km}^{-2}$ and $1326.26 \mathrm{~N} \mathrm{~km}^{-2}$, respectively; Supplementary material, Table S2). Although characterized by the presence of large fluctuations, the deep-water rose shrimp biomass and density indices showed an increasing trend in most of the investigated areas, as shown by the positive values of the Spearman rho coefficient (Supplementary material, Table S1). In contrast, the Norway lobster biomass and density indices showed generally a decreasing pattern (Supplementary material, Table S2).

Data exploration highlighted high collinearity between the biomass and density indexes for the two species ( $\mathrm{r}=0.9$; VIF values $>3$ ). Therefore, GAM models were fitted only on the biomass index as a response variable. For the explanatory variables, no high collinearity was detected by both pair-plots (Pearson correlation coefficient. Supplementary material, Fig. S1) and VIF.

Based on the model selection procedure, the best GAM model for both species was the one containing as explanatory terms the interaction between coordinates (longitude and latitude) and time, SST, and the interaction of depth and time (Tables 2 and 3). The summary of the outputs of the best GAM models for the two species are shown in Tables 4 and 5, respectively.

Table 2. - GAMs for deep-water rose shrimp ( $P$. longirostris); $j$ is the year and $i$ is the $i$-observation in the $j$-year; $\beta_{0}$ is the intercept; $s\left(\right.$ Lon $_{i j}$, Lat $_{i j}$, Year $_{j}$ ) is the smoother for the interaction of coordinates (longitude and latitude) and year; $s\left(S S T_{i j}\right)$ is the smoother for sea surface temperature; $s\left(\right.$ Depth $\left._{i j}\right)$ and $s\left(\right.$ Depth $_{i j}$, Year $\left._{j}\right)$ are the smoothers for depth and the interaction of depth and year; $\varepsilon_{i j} \sim N\left(0, \sigma^{2}\right)$ is the error term; AIC is the Akaike information criterion and Dev. expl. (\%) is the deviance explained. The best model is given in bold.

| Model | AIC | Dev. expl. (\%) |
| :--- | :---: | :---: |
| $\beta_{0}+s\left(\right.$ Lon $_{i j}$, Lat $_{i j}$, Year $\left._{j}\right)+\varepsilon_{i j}$ | 36695.7 | 25.9 |
| $\beta_{0}+s\left(\right.$ Lon $_{i j}$ LLt $_{i j}$, Year $\left._{j}\right)+s\left(\right.$ SST $\left._{i j}\right)+\varepsilon_{i j}$ | 35942.2 | 29.9 |
| $\beta_{0}+s\left(\right.$ Lon $_{i j}$ LLt $_{i j}$, Year $\left._{j}\right)+s\left(\right.$ Depth $\left._{i j}\right)+\varepsilon_{i j}$ | 29791.4 | 55.3 |
| $\beta_{0}+s\left(\right.$ Lon $_{i j}$ Lat $_{i j}$, Year $\left._{j}\right)+s\left(\right.$ Depth $_{i j}$, Year $\left._{j}\right)+\varepsilon_{i j}$ | 29629.1 | 55.9 |
| $\boldsymbol{\beta}_{\mathbf{0}}+\boldsymbol{s}\left(\right.$ Lon $_{i j}$, Lat $_{i j}$, Year $\left._{j}\right)+\boldsymbol{s}\left(\right.$ SST $\left._{i j}\right)+\boldsymbol{s}\left(\right.$ Deph $_{i j}$, Year $\left._{j}\right)+\boldsymbol{\varepsilon}_{i j}$ | $\mathbf{2 9 5 9 6 . 8}$ | $\mathbf{5 6 . 1}$ |

Table 3. - GAMs for Norway lobster (N. norvegicus); $j$ is the year and $i$ is the $i$-observation in the $j$-year; $\beta_{0}$ is the intercept; $s\left(\right.$ Lon $_{i j}$, Lat $_{i j}$, Year $_{j}$ ) is the smoother for the interaction of coordinates (longitude and latitude) and year; $s\left(S S T_{i j}\right)$ is the smoother for sea surface temperature; $s\left(\right.$ Depth $\left._{i j}\right)$ and $s\left(\right.$ Depth $_{i j}$, Year $\left._{j}\right)$ are the smoothers for depth and the interaction of depth and year; $\varepsilon_{i j} \sim N\left(0, \sigma^{2}\right)$ is the error term; AIC is the Akaike information criterion and Dev. expl. (\%) is the deviance explained. The best model is given in bold.

| Model | AIC | Dev. expl. (\%) |
| :--- | :--- | :---: | :---: |
| $\beta_{0}+s\left(\right.$ Lon $_{i j}$, Lat $_{i j}$, Year $\left._{j}\right)+\varepsilon_{i j}$ | 37895.4 | 13.8 |
| $\beta_{0}+s\left(\right.$ Lon $_{i j}$ Lat $_{i j}$, Year $\left._{j}\right)+s\left(\right.$ SST $\left._{i j}\right)+\varepsilon_{i j}$ | 36593.0 | 21.6 |
| $\beta_{0}+s\left(\right.$ Lon $_{i j}$ Lat $_{i j}$, Year $\left._{j}\right)+s\left(\right.$ Depth $\left._{i j}\right)+\varepsilon_{i j}$ | 25597.0 | 64.9 |
| $\beta_{0}+s\left(\right.$ Lon $_{i j}$ Lat $_{i j}$, Year $\left._{j}\right)+s\left(\right.$ Depth $_{i j}$, Year $\left._{j}\right)+\varepsilon_{i j}$ | 25477.3 | 65.3 |
| $\boldsymbol{\beta}_{\mathbf{0}}+s\left(\right.$ Lon $_{i j}$, Lat $_{i j}$, Year $\left._{j}\right)+s\left(\right.$ SST $\left._{i j}\right)+s\left(\right.$ Depth $_{i j}$, Year $\left._{j}\right)+\varepsilon_{i j}$ | $\mathbf{2 5 3 7 7 . 3}$ | $\mathbf{6 5 . 6}$ |



Fig. 2. - Effects of explanatory variables on the biomass of deep-water rose shrimp, as estimated by generalized additive model (GAM). Left panel, effect of the interaction between depth and time (years); right panel, effect of SST (dashed lines represent GAM confidence intervals).

Table 4. - Summary of the outputs of the best GAM model for deep-water rose shrimp. Explanatory variables included longitude-latitude-time interaction, depth-time interaction and sea surface temperature (SST); SE, standard error; edf, estimated degrees of freedom; df, degrees of freedom.

| Parametric coefficients: | Estimate | SE | t value | Significance <br> level |
| :--- | :---: | :---: | :---: | :---: |
| Intercept | 0.73 | 0.01 | 136.10 | $\mathrm{p}<0.05$ |
| Smooth terms: | edf | df | F |  |
| Longitude, latitude, year | 103.73 | 107.65 | 61.92 | $\mathrm{p}<0.05$ |
| Depth, year | 26.81 | 28.67 | 431.42 | $\mathrm{p}<0.05$ |
| SST | 4.75 | 4.97 | 16.91 | $\mathrm{p}<0.05$ |

Deep-water rose shrimp showed a widening bathymetric range in time, from $200-400 \mathrm{~m}$ in depth at the beginning of the time series to $150-600 \mathrm{~m}$ depth in the last few years. As regards temperature, the highest abundance of the species was associated with SSTs at around $10^{\circ} \mathrm{C}$, while a second peak was observed at

Table 5. - Summary of the outputs of the best GAM model for Norway lobster. Explanatory variables included longitude-latitudetime interaction, depth-time interaction, and sea surface temperature (SST); SE: standard error; edf: estimated degrees of freedom; df: degrees of freedom.

| Parametric coefficients: | Estimate | SE | t value | Significance <br> level |
| ---: | :---: | :---: | :---: | :---: |
| Intercept | 0.55 | 0.01 | 119.10 | $\mathrm{p}<0.05$ |
| Smooth terms: | edf | df | F |  |
| Longitude, latitude, year | 99.91 | 106.79 | 23.15 | $\mathrm{p}<0.05$ |
| Depth, year | 27.02 | 28.73 | 746.88 | $\mathrm{p}<0.05$ |
| SST | 4.28 | 4.79 | 10.17 | $\mathrm{p}<0.05$ |

around $14^{\circ} \mathrm{C}$ (Fig. 2). The maps in Figure 3 present the highest abundances of deep-water rose shrimp in the southeastern Mediterranean.

Norway lobster showed no particular temporal trend in bathymetric distribution over the years. There was a negative relationship between its bio-


Fig. 3. - Maps of deep-water rose shrimp distribution.


Fig. 4. - Effects of explanatory variables on the biomass of Norway lobster, as estimated by generalized additive model (GAM). Left panel, effect of the interaction between depth and time (years); right panel, effect of bottom temperature (shaded areas represent GAM confidence intervals).
mass and SST. The highest biomass indexes of this species were associated with low temperatures, while biomass decreased with increasing SST (Fig.
4). Figure 5 shows the spatiotemporal distribution of Norway lobster, indicating a slight decrease in biomass indices over time.


Fig. 5. - Maps of Norway lobster distribution.

An inspection of the residuals of the best models for deep-water rose shrimp and Norway lobster shows that there was no evidence of a pattern within the model residuals or deviation from the assumptions of homogeneity and normality of variance (Supplementary material, Figs S2 and S3).

## DISCUSSION

Since ecosystems have changed over time due to anthropogenic and environmental factors, fisheries management should not be based only on recent studies of populations (Ligas et al. 2013). While long time series of data have been collected in the Atlantic Ocean and the North Sea, fisheries time series in the Mediterranean are available only for the last few decades. Current management advice in most cases is based on data starting in the early 1990s (Sartor 2011, Colloca et al. 2013). The availability of 22 years of standardized data obtained from the MEDITS surveys of two of the most important decapods of the demersal communities in the Mediterranean offers a unique opportunity to evaluate trends in abundance at a large scale. According to Cook (1997), data collected by means of trawl surveys are a more accurate source of information for estimating stock abundance than observations from
commercial landing data. In addition, the latter could be biased by the heterogeneous distribution of fishing effort and strategy, the selectivity of the gears, and discarding procedures influenced by market demands (Fox and Starr 1996, Quirijns et al. 2008).

A decrease in the fishing fleet size has been observed during the last years in the Mediterranean EU waters, mainly due to the EU Common Fishery Policy, although this decrease has been partially compensated by an increasing catch efficiency and changes in fleet characteristics (Rijnsdorp et al. 2006). This reduction in fishing effort has not yet produced the desired effects, as is also demonstrated by the lack of recovery of the main exploited stocks in the area (GFCM 2017, STECF 2017). In addition, it seems that the abundance of some stocks is closely linked to climate change. For example, Colloca et al. (2014) reported that the stock trend of deep-water rose shrimp in the central Mediterranean Sea did not appear to be driven by fishing effort, since the exploitation pattern has remained the same in the last two decades.

Since the 1950 s, a warming process has occurred in the Mediterranean basin, demonstrated by both environmental (Vargas-Yánez et al. 2009) and biological changes (CIESM 2008). Skliris et al. (2012) reported that for the period 1985-2008, the SST in the Mediter-
ranean Sea has increased by about $0.037^{\circ} \mathrm{C}$ per year, causing a northward expansion of native tropical and sub-tropical species (Raitsos et al. 2010) and promoting the tropicalization of the Mediterranean (Azzurro et al. 2011).

According to the different life cycles and behavioural strategies, the two studied species showed different reactions in relation to changes in environmental factors. Long-term changes in abundance of deep-water rose shrimp and Norway lobster correlated significantly with the latitudinal and longitudinal distribution, SST and bathymetric range distribution.

The core area of deep-water rose shrimp, occurring between 200 and 400 m , expanded progressively in a wider depth range. This process clearly indicated an enhancement of the habitat suitability in the centralwestern Mediterranean for the deep-water rose shrimp. The main mechanism driving the spatiotemporal dynamics of this species is the increase in water temperature (Ligas et al. 2011, Colloca et al. 2014). Moreover, this species has expanded its distribution further north, up to the northwestern Mediterranean areas. It is one of the few species showing increasing trends in both commercial catches and scientific surveys (Colloca et al. 2014). In the Catalan Sea, Cartes et al. (2009) hypothesized that the increasing temperature produced low rainfall regimes and river discharges, and consequently a reduction in the flux of organic matter. These environmental conditions lead to an increased production of suprabenthos (e.g. Lophogaster typicus), which represents the main prey of the deep-water rose shrimp. Therefore, a minor increase in temperature observed in recent years may have favoured the increase in abundance of this shrimp throughout the Mediterranean basin. In the northern Tyrrhenian Sea, Bartolino et al. (2008) demonstrated that high temperature and low wind circulation negatively affect the recruitment of European hake (Merluccius merluccius). It is known that hake juveniles prey upon juveniles of deep-water rose shrimp (Carpentieri et al. 2005), so the lower predation pressure could have further enhanced the recruitment success of the shrimp.

In contrast, Norway lobster showed a negative relationship between biomass and SST, with the highest indexes associated with low temperatures. The results confirmed the preference of this species for cold waters, with highest abundances in the northern part of the western Mediterranean. Unlike the deep-water rose shrimp, this species showed no particular trend in bathymetric distribution. The decreasing abundance related to higher temperatures is again explained by Cartes et al. (2009): benthic feeders and predators such as the Norway lobster are influenced by the reduction of the organic matter flux resulting from the decreased rainfall and river discharge. In the Atlantic Sea, in areas where minor changes in fishing pressures were observed, Fariña and González Herraiz (2003) and González Herraiz et al. (2009) recorded a decline in Norway lobster abundance associated with higher temperatures.

GAM models adequately described the effects of sea temperature on the two decapod species at a large
geographical scale. In a future scenario of increasing temperature, we can expect a further expansion of deep-water rose shrimp even in areas where the species is not yet abundant, such as the Gulf of Lions and the Catalan Sea. For Norway lobster, we could expect an opposite effect, which has already been demonstrated for some species of cold or temperate waters (e.g. Merlangius merlangius and Sprattus sprattus) distributed in the northern areas of the Mediterranean Sea, such as the Gulf of Lions, the northern Adriatic Sea and the northern Aegean Sea) (Daskalov et al. 2008, Fortibuoni et al. 2010). However, these general trends may vary at smaller scale, since environmental features may influence species' regional preferences, leading to changes in the general trend. Further analyses are therefore indispensable to understand better the relationships between variations in the abundance of the species and environmental and anthropogenic factors. Additional information on sea-floor topography, sediment composition and hydro-geographical characteristics would be a useful tool for describing further temporal changes in species abundance.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article and at the following link: http://scimar.icm.csic.es/scimar/supplm/sm04858esm.pdf

Table S1. - Stratified mean biomass and density indices $\left(\mathrm{kg} \mathrm{km}^{-2}\right.$ and $\mathrm{N} \mathrm{km}^{-2} \pm$ standard deviation, SD) per year (1994-2015) of deep-water rose shrimp ( $P$. longirostris) in the investigated GSAs. Information on the results of Spearman Rho coefficient analysis is also shown.
Table S2. - Stratified mean biomass and density indices $\left(\mathrm{kg} \mathrm{km}^{-2}\right.$ and $\mathrm{N} \mathrm{km}^{-2} \pm$ standard deviation, SD) per year (1994-2015) of Norway lobster ( $N$. norvegicus) in the investigated GSAs. Information on the results of Spearman Rho coefficient analysis is also shown.
Fig. S1. - Pair-plots for all the explanatory variables in the data set used for the analysis. The upper diagonal panel shows the Pearson correlation coefficient, and the lower diagonal panel shows the scatterplots with a smoother added to visualize the pattern. The font size of the correlation coefficient is proportional to its estimated value.
Fig. S2. - Graphs of the validation of the best GAM model for deepwater rose shrimp. From top left, residuals versus depth, residuals versus longitude, residuals versus latitude, residuals versus SST, and residuals versus time (year) to assess homogeneity; bottom right, histogram of residuals to assess normality.
Fig. S3. - Graphs of the validation of the best GAM model for Norway lobster. From top left, residuals versus depth, residuals versus longitude, residuals versus latitude, residuals versus SST, and residuals versus time (year) to assess homogeneity; bottom right, histogram of residuals to assess normality.

# Spatiotemporal abundance pattern of deep-water rose shrimp, Parapenaeus longirostris, and Norway lobster, Nephrops norvegicus, in European Mediterranean waters 

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Supplementary material
Table S1. - Stratified mean biomass and density indices ( $\mathrm{kg} \mathrm{km}^{-2}$ and N $\mathrm{km}^{-2} \pm$ standard deviation, SD ) per year (1994-2015) of deep-water rose shrimp (te results of Spearman Rho coefficient analysis is also shown.

| GSA |  | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | $\begin{gathered} \text { Spearman } \\ \text { Rho } \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\mathrm{kg} \mathrm{km}^{-2}$ | 0.0 | 0.2 | 0.8 | 1.9 | 2.1 | 1.4 | 1.6 | 1.9 | 1.7 | 0.5 | 1.3 | 0.6 | 1.0 | 0.6 | 0.7 | 4.9 | 1.5 | 2.2 | 3.6 | 1.6 | 1.1 | 1.1 | Positive |
| 1 |  | 0.0 | 0.1 | 0.2 | 1.0 | 1.0 | 0.6 | 0.5 | 1.0 | 0.3 | 0.1 | 0.5 | 0.4 | 0.6 | 0.2 | 0.3 | 1.2 | 1.0 | 0.8 | 1.2 | 0.5 | 0.3 | 0.3 | trend |
|  | $\mathrm{Nkm}^{-2}$ | 1.1 | 38.0 | 98.7 | 265.6 | 386.3 | 169.0 | 194.3 | 204.9 | 219.1 | 46.1 | 137.6 | 59.4 | 110.7 | 73.4 | 83.4 | 527.2 | 321.0 | 257.4 | 575.5 | 11265.2 | 122.4 | 100.0 | Positive |
|  | SD | 1.1 | 18.2 | 31.5 | 155.2 | 174.6 | 59.0 | 63.0 | 113.5 | 43.4 | 11.0 | 60.1 | 47.9 | 61.8 | 34.7 | 28.9 | 128.9 | 285.0 | 69.6 | 218.7 | 9029.4 | 37.4 | 25.4 | trend |
|  | $\mathrm{kg} \mathrm{km}^{-2}$ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.3 | 4.4 | 0.1 | 0.7 | 0.0 | Negative |
| 2 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.3 | 4.2 | 0.1 | 0.7 | 0.0 |  |
|  | $\mathrm{Nkm}^{-2}$ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 68.5 | 660.7 | 14.7 | 103.5 | 7.2 |  |
|  | SD |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 68.5 | 585.7 | 14.7 | 103.5 | 7.2 | Negative |
|  | $\mathrm{kg} \mathrm{km}^{-2}$ |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.2 | 0.4 | 0.5 | 0.6 | 0.1 | 0.5 | 0.8 | 0.4 | 0.2 |  |
|  | SD |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.1 | 0.2 | 0.2 | 0.3 | 0.1 | 0.2 | 0.3 | 0.2 | 0.1 | NS |
| 5 | $\mathrm{N} \mathrm{km}^{-2}$ |  |  |  |  |  |  |  |  |  |  |  |  |  | 13.5 | 46.0 | 48.2 | 44.2 | 12.0 | 59.2 | 60.1 | 45.3 | 13.0 |  |
|  | SD |  |  |  |  |  |  |  |  |  |  |  |  |  | 8.0 | 24.4 | 19.8 | 19.3 | 4.8 | 20.0 | 23.3 | 16.8 | 7.1 | NS |
|  | $\mathrm{kg} \mathrm{km}^{-2}$ | 0.1 | 0.2 | 0.3 | 0.0 | 0.2 | 0.2 | 1.0 | 1.5 | 0.2 | 0.1 | 0.6 | 0.2 | 0.2 | 0.2 | 0.1 | 0.6 | 0.9 | 0.4 | 0.7 | 0.9 | 2.1 | 1.0 | Positive |
|  |  | 0.0 | 0.1 | 0.2 | 0.0 | 0.1 | 0.1 | 0.4 | 0.7 | 0.1 | 0.0 | 0.3 | 0.1 | 0.1 | 0.1 | 0.1 | 0.2 | 0.3 | 0.1 | 0.2 | 0.3 | 0.5 | 0.2 |  |
| 6 | $\mathrm{N} \mathrm{km}^{-2}$ | 12.5 | 22.2 | 36.3 | 2.4 | 17.5 | 29.6 | 128.9 | 113.7 | 19.4 | 4.9 | 52.1 | 16.5 | 11.7 | 16.6 | 11.4 | 58.5 | 72.9 | 44.1 | 285.1 | 73.2 | 211.5 | 159.2 | Positive |
|  | SD | 5.9 | 10.6 | 27.0 | 1.7 | 9.9 | 16.5 | 67.9 | 46.4 | 7.3 | 1.8 | 26.1 | 6.2 | 3.8 | 10.2 | 6.0 | 19.6 | 27.2 | 13.3 | 239.1 | 22.7 | 61.0 | 24.6 | Positid |
|  | $\mathrm{kg} \mathrm{km}^{-2}$ | 0.6 | 0.3 | 0.0 | 0.0 | 0.0 | 0.2 | 0.1 | 0.1 | 0.0 | 0.1 | 0.2 | 0.1 | 0.1 | 0.0 | 0.0 | 0.1 | 0.4 | 0.7 | 0.6 | 0.3 | 1.0 | 1.4 | Positive |
|  | SD | 0.5 | 0.3 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 0.1 | 0.0 | 0.0 | 0.1 | 0.2 | 0.4 | 0.3 | 0.1 | 0.3 | 0.3 | trend |
| 7 | $\mathrm{Nkm}^{-2}$ | 56.4 | 31.5 | 0.3 | 0.2 | 0.5 | 17.9 | 5.6 | 4.0 | 1.9 | 5.2 | 20.8 | 5.8 | 5.1 | 2.8 | 2.6 | 7.6 | 41.2 | 46.9 | 44.6 | 25.4 | 86.1 | 353.3 |  |
|  | SD | 40.8 | 29.9 | 0.2 | 0.2 | 0.3 | 14.7 | 2.2 | 2.5 | 0.9 | 2.4 | 9.5 | 4.1 | 3.0 | 2.3 | 1.9 | 4.4 | 10.5 | 25.5 | 24.2 | 6.8 | 25.5 | 88.8 | trend |
|  | $\mathrm{kg} \mathrm{km}^{-2}$ | 0.3 | 0.3 | 0.3 | 0.2 | 0.2 | 1.1 | 1.9 | 1.1 |  | 0.8 | 0.9 | 1.1 | 1.2 | 0.7 | 1.0 | 0.5 | 2.4 | 1.8 | 2.5 | 2.5 | 2.1 | 2.3 | Positive |
|  |  | 0.1 | 0.2 | 0.1 | 0.1 | 0.1 | 0.4 | 0.4 | 0.3 |  | 0.5 | 0.3 | 0.4 | 0.3 | 0.2 | 0.3 | 0.1 | 0.9 | 0.4 | 0.3 | 0.9 | 0.4 | 0.4 | trend |
| 8 | $\mathrm{N} \mathrm{km}^{-2}$ | 21.4 | 21.1 | 21.3 | 19.8 | 25.3 | 114.6 | 124.1 | 81.7 |  | 49.7 | 86.1 | 97.5 | 84.5 | 45.1 | 83.8 | 39.9 | 226.8 | 145.2 | 239.1 | 289.9 | 246.2 | 254.7 |  |
|  | SD | 8.6 | 11.7 | 7.9 | 11.3 | 9.9 | 39.1 | 29.4 | 23.5 |  | 31.4 | 33.2 | 41.5 | 33.6 | 12.9 | 25.6 | 8.2 | 70.9 | 29.4 | 40.6 | 105.9 | 46.0 | 48.2 | trend |
|  | $\mathrm{kg} \mathrm{km}^{-2}$ | 0.6 | 0.7 | 0.5 | 0.8 | 2.5 | 4.3 | 2.8 | 1.4 | 1.6 | 1.5 | 2.7 | 3.4 | 3.8 | 1.8 | 3.6 | 3.4 | 10.5 | 7.8 | 7.5 | 8.1 | 5.1 | 10.7 | Positive |
|  |  | 0.1 | 0.1 | 0.1 | 0.1 | 0.3 | 0.5 | 0.4 | 0.2 | 0.2 | 0.2 | 0.3 | 0.5 | 0.6 | 0.2 | 0.4 | 0.4 | 1.0 | 0.8 | 0.7 | 0.8 | 0.6 | 1.3 |  |
|  | $\mathrm{Nkm}^{-2}$ | 41.8 | 56.3 | 42.2 | 129.0 | 352.8 | 397.7 | 250.4 | 126.0 | 188.3 | 196.1 | 252.4 | 368.8 | 283.6 | 173.1 | 382.2 | 407.5 | 1282.4 | 1014.4 | 779.9 | 973.7 | 754.6 | 1250.6 |  |
|  | SD | 6.0 | 9.3 | 5.9 | 17.8 | 47.5 | 37.7 | 30.1 | 14.6 | 23.2 | 26.6 | 28.1 | 62.1 | 40.8 | 16.2 | 44.6 | 51.7 | 129.2 | 118.2 | 78.2 | 119.5 | 131.4 | 180.0 | trend |
|  | $\mathrm{kg} \mathrm{km}^{-2}$ | 1.3 | 1.3 | 0.9 | 2.3 | 3.7 | 5.6 | 4.3 | 3.6 | 1.8 | 2.4 | 3.9 | 6.2 | 7.8 | 2.4 | 3.5 | 4.3 | 7.4 | 4.2 | 8.2 | 9.0 | 3.0 | 2.1 |  |
|  | SD | 0.3 | 0.2 | 0.1 | 0.3 | 0.6 | 0.6 | 0.6 | 0.4 | 0.5 | 0.4 | 0.6 | 0.6 | 0.8 | 0.4 | 0.4 | 0.5 | 0.8 | 0.4 | 0.9 | 1.3 | 0.4 | 0.3 | trend |
| 10 | $\mathrm{N} \mathrm{km}^{-2}$ | 130.8 | 228.5 | 160.0 | 411.8 | 550.9 | 954.9 | 756.1 | 507.2 | 422.2 | 533.4 | 549.2 | 1121.2 | 970.0 | 266.6 | 474.9 | 529.4 | 889.6 | 653.3 | 1377.8 | 1314.1 | 401.4 | 253.4 |  |
|  | SD | 26.2 | 44.6 | 37.4 | 65.8 | 90.3 | 116.0 | 109.5 | 68.1 | 154.1 | 80.6 | 88.6 | 126.1 | 116.8 | 36.8 | 69.2 | 71.2 | 95.4 | 74.8 | 177.9 | 202.6 | 53.6 | 38.8 | trend |
|  | $\mathrm{kg} \mathrm{km}^{-2}$ | 0.5 | 0.5 | 0.5 | 1.6 | 4.5 | 7.1 | 3.2 | 2.1 | 1.1 | 4.0 | 2.6 | 1.0 | 2.3 | 0.8 | 0.4 | 2.2 | 3.1 | 3.8 | 3.1 | 1.6 | 1.3 | 1.1 |  |
|  | SD | 0.1 | 0.1 | 0.1 | 0.4 | 1.1 | 2.1 | 0.7 | 0.5 | 0.2 | 0.9 | 0.6 | 0.3 | 0.4 | 0.2 | 0.1 | 0.6 | 0.7 | 1.0 | 0.5 | 0.4 | 0.3 | 0.4 | NS |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 41.4 | 41.7 | 62.4 | 255.0 | 730.7 | 829.0 | 291.0 | 207.5 | 130.1 | 416.9 | 247.7 | 96.6 | 193.3 | 45.5 | 47.8 | 208.5 | 338.9 | 441.7 | 330.6 | 156.9 | 115.5 | 100.3 |  |
|  | SD | 10.4 | 11.2 | 16.6 | 65.9 | 175.3 | 246.2 | 73.4 | 51.0 | 27.3 | 86.5 | 62.8 | 25.5 | 39.3 | 13.1 | 10.8 | 58.5 | 87.9 | 117.6 | 56.2 | 41.6 | 26.9 | 34.0 | NS |

Table S1 (Cont.). - Stratified mean biomass and density indices ( $\mathrm{kg} \mathrm{km}^{-2}$ and $\mathrm{N} \mathrm{km}^{-2} \pm$ standard deviation, SD) per year (1994-2015) of deep-water rose shrimp ( $P$. longirostris) in the investigated GSAs.

| GSA |  | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | Spearman Rho |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 15 | $\mathrm{kg} \mathrm{km}^{-2}$ |  |  |  |  |  |  |  |  |  |  |  | 7.5 | 16.6 | 12.1 | 22.3 | 23.1 | 14.2 | 17.1 | 17.1 | 15.4 | 11.7 | 4.1 |  |
|  | SD |  |  |  |  |  |  |  |  |  |  |  | 2.0 | 5.2 | 3.3 | 5.4 | 5.2 | 4.6 | 4.3 | 3.9 | 5.0 | 2.8 | 0.5 | NS |
|  | $\mathrm{N} \mathrm{km}^{-2}$ |  |  |  |  |  |  |  |  |  |  |  | 1029.8 | 3177.4 | 2186.8 | 4869.5 | 4295.0 | 2369.6 | 3405.7 | 3187.5 | 2183.1 | 2661.9 | 940.6 |  |
|  | SD |  |  |  |  |  |  |  |  |  |  |  | 288.6 | 1069.9 | 707.8 | 1317.5 | 1055.0 | 774.2 | 896.9 | 762.3 | 697.6 | 634.6 | 97.0 | NS |
| 16 | $\mathrm{kg} \mathrm{km}{ }^{-2}$ | 5.9 | 5.1 | 7.6 | 7.5 | 11.5 | 15.8 | 16.0 | 13.0 | 4.8 | 7.4 | 16.8 | 11.3 | 12.4 | 5.3 | 11.8 | 23.9 | 16.6 | 13.0 | 38.2 | 21.8 | 10.7 | 5.4 | Positive |
|  | SD | 2.7 | 1.8 | 2.6 | 2.2 | 3.3 | 4.6 | 5.0 | 4.4 | 1.1 | 2.4 | 6.3 | 3.8 | 5.9 | 1.9 | 4.4 | 10.1 | 6.6 | 5.5 | 11.3 | 6.3 | 4.3 | 1.8 | trend |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 793.8 | 785.2 | 1523.3 | 1461.8 | 2448.2 | 3190.3 | 2868.7 | 2548.0 | 1571.7 | 1433.3 | 4565.5 | 1858.1 | 1848.4 | 815.2 | 2286.9 | 3563.1 | 2717.9 | 2252.1 | 8012.1 | 4606.9 | 3245.1 | 948.0 | Positive |
|  | SD | 314.4 | 213.9 | 450.5 | 427.1 | 693.3 | 877.1 | 850.2 | 751.0 | 484.2 | 449.1 | 1888.5 | 654.2 | 933.9 | 284.6 | 860.1 | 1510.6 | 1124.0 | 880.1 | 2366.1 | 1354.4 | 1911.5 | 326.4 | trend |
| 17 | $\mathrm{kg} \mathrm{km}^{-2}$ |  |  |  |  |  |  |  |  | 2.2 | 3.0 | 2.4 | 2.6 | 3.4 | 2.1 | 1.4 | 0.8 | 0.9 | 0.5 | 0.7 | 0.7 | 1.6 | 3.0 |  |
|  | SD |  |  |  |  |  |  |  |  | 0.4 | 0.5 | 0.5 | 0.6 | 0.7 | 0.6 | 0.3 | 0.2 | 0.2 | 0.1 | 0.2 | 0.1 | 0.2 | 0.4 | NS |
|  | $\mathrm{N} \mathrm{km}^{-2}$ |  |  |  |  |  |  |  |  | 405.6 | 518.6 | 362.6 | 441.4 | 459.0 | 270.1 | 192.1 | 81.0 | 105.2 | 59.4 | 114.6 | 92.2 | 260.4 | 578.3 | Negative |
|  | SD |  |  |  |  |  |  |  |  | 75.6 | 81.5 | 66.7 | 92.7 | 83.9 | 70.1 | 48.2 | 20.1 | 22.8 | 13.4 | 27.4 | 18.3 | 32.3 | 99.9 | trend |
| 18 | $\mathrm{kg} \mathrm{km}{ }^{-2}$ | 0.1 | 0.3 | 4.9 | 2.1 | 4.2 | 1.9 | 2.5 | 4.2 | 4.6 | 5.6 | 7.3 | 9.8 | 7.0 | 3.3 | 9.0 | 7.3 | 5.2 | 4.2 | 5.5 | 2.1 | 4.9 | 2.2 | Positive |
|  | SD | 0.0 | 0.1 | 1.0 | 0.3 | 0.8 | 0.3 | 0.4 | 0.6 | 0.6 | 0.8 | 1.3 | 1.5 | 1.0 | 0.8 | 2.0 | 1.1 | 0.7 | 0.7 | 1.0 | 0.4 | 1.0 | 0.5 | trend |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 12.5 | 21.7 | 870.4 | 307.3 | 517.8 | 209.4 | 352.2 | 629.5 | 603.3 | 837.3 | 985.4 | 1538.7 | 798.0 | 338.6 | 890.2 | 1097.7 | 815.3 | 700.9 | 791.0 | 339.2 | 940.5 | 286.0 | Positive |
|  | SD | 4.8 | 9.6 | 208.6 | 64.0 | 105.1 | 31.4 | 62.1 | 83.5 | 70.3 | 136.9 | 218.5 | 222.1 | 119.8 | 72.0 | 186.5 | 195.5 | 145.9 | 138.7 | 147.6 | 90.0 | 216.2 | 68.8 | trend |
| 19 | $\mathrm{kg} \mathrm{km}^{-2}$ | 5.4 | 8.1 | 4.6 | 6.9 | 9.4 | 3.9 | 3.3 | 3.2 | 5.8 | 7.2 | 7.8 | 6.9 | 7.1 | 4.4 | 8.6 | 12.1 | 10.8 | 6.8 | 8.8 | 10.1 | 7.2 | 11.7 | Positive |
|  | SD | 1.1 | 1.8 | 0.8 | 1.5 | 2.1 | 1.0 | 1.4 | 0.8 | 1.1 | 1.6 | 1.3 | 1.5 | 1.3 | 0.7 | 1.5 | 1.6 | 1.6 | 1.6 | 1.3 | 2.0 | 1.4 | 1.8 | trend |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 698.1 | 1051.2 | 855.3 | 1123.8 | 1538.3 | 723.2 | 541.8 | 509.8 | 949.4 | 1403.0 | 1046.9 | 1167.4 | 1436.2 | 940.3 | 1662.8 | 2307.6 | 2066.8 | 1326.0 | 1573.4 | 2237.7 | 1561.7 | 1857.3 | Positive |
|  | SD | 177.1 | 246.8 | 198.1 | 300.0 | 453.3 | 220.6 | 192.2 | 131.1 | 186.1 | 342.1 | 181.2 | 273.7 | 371.2 | 154.5 | 421.8 | 472.0 | 340.9 | 338.2 | 303.6 | 476.3 | 351.5 | 286.8 | trend |
| 20 | $\mathrm{kg} \mathrm{km}^{-2}$ | 3.5 | 2.7 | 5.0 | 4.1 | 3.5 | 3.8 | 6.5 | 5.0 |  | 6.0 | 7.9 | 13.5 | 6.5 |  | 7.2 |  |  |  |  |  | 2.9 |  | Positive |
|  | SD | 1.4 | 0.7 | 1.6 | 1.2 | 0.9 | 0.8 | 2.2 | 1.6 |  | 1.0 | 1.9 | 3.0 | 1.8 |  | 1.8 |  |  |  |  |  | 1.0 |  | trend |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 246.3 | 437.6 | 734.0 | 449.1 | 514.2 | 810.1 | 930.1 | 697.2 |  | 1301.9 | 1580.7 | 2625.9 | 1239.0 |  | 1475.3 |  |  |  |  |  | 434.2 |  |  |
|  | SD | 96.6 | 98.6 | 309.9 | 239.7 | 161.4 | 182.6 | 284.5 | 245.4 |  | 240.3 | 398.8 | 563.0 | 350.7 |  | 362.8 |  |  |  |  |  | 158.6 |  | trend |
| 22 | $\mathrm{kg} \mathrm{km}^{-2}$ | 1.5 | 3.0 | 14.6 | 18.2 | 10.9 | 13.5 | 14.3 | 13.6 |  | 14.2 | 14.1 | 13.3 | 12.9 |  | 8.9 |  |  |  |  |  | 10.6 |  |  |
|  | SD | 0.5 | 0.8 | 2.7 | 4.4 | 1.7 | 2.0 | 2.6 | 2.6 |  | 2.4 | 2.7 | 2.2 | 2.3 |  | 2.1 |  |  |  |  |  | 1.8 |  | NS |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 125.2 | 559.2 | 2702.6 | 2305.2 | 1599.0 | 2486.9 | 2724.2 | 2139.0 |  | 2693.1 | 2464.5 | 2294.0 | 2688.0 |  | 1466.8 |  |  |  |  |  | 2233.2 |  |  |
|  | SD | 34.7 | 159.3 | 640.1 | 601.0 | 257.0 | 367.9 | 789.0 | 411.9 |  | 532.9 | 561.9 | 392.2 | 669.3 |  | 397.7 |  |  |  |  |  | 433.1 |  | NS |
| 23 | $\mathrm{kg} \mathrm{~km}^{-2}$ | 1.4 | 34.2 | 27.1 | 4.8 | 15.0 | 15.3 | 43.4 | 7.1 |  | 45.1 | 30.6 | 27.5 | 34.2 |  | 33.7 |  |  |  |  |  | 6.5 |  |  |
|  | SD | 1.1 | 6.4 | 11.4 | 1.7 | 3.3 | 4.0 | 17.4 | 1.9 |  | 17.7 | 6.7 | 7.3 | 9.0 |  | 10.0 |  |  |  |  |  | 1.6 |  | NS |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 136.3 | 5290.3 | 5071.7 | 589.7 | 2705.1 | 4181.9 | 9348.2 | 1675.1 |  | 9866.3 | 7405.4 | 8251.4 | 8632.1 |  | 5316.9 |  |  |  |  |  | 1837.4 |  |  |
|  | SD | 121.3 | 1065.6 | 1498.2 | 180.9 | 538.0 | 1092.5 | 4110.6 | 525.9 |  | 3955.3 | 2265.2 | 2486.6 | 2856.3 |  | 1838.2 |  |  |  |  |  | 399.5 |  | NS |
| 25 | $\mathrm{kg} \mathrm{km}^{-2}$ |  |  |  |  |  |  |  |  |  |  |  | 0.8 | 0.3 | 0.1 | 0.3 | 2.1 | 0.6 | 3.0 | 4.0 | 1.7 |  | 1.8 | NS |
|  | SD |  |  |  |  |  |  |  |  |  |  |  | 0.2 | 0.1 | 0.0 | 0.3 | 0.7 | 0.2 | 0.9 | 1.9 | 0.7 |  | 0.5 | NS |
|  | $\mathrm{N} \mathrm{km}^{-2}$ |  |  |  |  |  |  |  |  |  |  |  | 262.4 | 86.2 | 25.4 | 116.0 | 296.4 | 96.7 | 584.8 | 680.8 | 229.9 |  | 274.6 |  |
|  | SD |  |  |  |  |  |  |  |  |  |  |  | 50.3 | 31.9 | 12.1 | 78.0 | 80.5 | 16.6 | 171.1 | 353.5 | 63.1 |  | 64.2 | NS |


| GSA |  | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | Spearman Rho |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | $\mathrm{kg} \mathrm{km}{ }^{-2}$ | 0.6 | 1.0 | 1.8 | 3.4 | 0.6 | 0.7 | 1.0 | 1.2 | 2.9 | 6.2 | 5.7 | 2.6 | 4.4 | 2.4 | 1.4 | 2.4 | 1.5 | 1.4 | 0.6 | 1.8 | 2.2 | 2.0 |  |
|  | SD | 0.2 | 0.4 | 0.8 | 2.0 | 0.3 | 0.5 | 0.4 | 0.5 | 0.9 | 2.2 | 2.9 | 1.2 | 1.5 | 0.7 | 0.4 | 1.3 | 0.5 | 0.6 | 0.3 | 1.0 | 0.7 | 0.5 | NS |
|  | $\mathrm{N} \mathrm{km}{ }^{-2}$ | 9.6 | 19.9 | 28.4 | 69.6 | 16.5 | 21.2 | 21.5 | 20.8 | 77.3 | 134.1 | 106.2 | 49.1 | 69.9 | 24.8 | 19.1 | 44.9 | 28.1 | 20.8 | 6.2 | 21.1 | 36.3 | 33.2 |  |
|  | SD | 4.1 | 6.8 | 12.0 | 37.9 | 7.9 | 11.6 | 7.7 | 8.3 | 31.8 | 46.6 | 53.7 | 22.0 | 24.5 | 7.3 | 5.6 | 25.7 | 9.3 | 9.2 | 3.1 | 12.9 | 13.6 | 9.4 | NS |
| 2 | $\mathrm{kg} \mathrm{km}{ }^{-2}$ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1.3 | 1.6 | 1.2 | 0.8 | 1.8 |  |
|  | SD |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.5 | 0.7 | 0.8 | 0.4 | 0.9 | NS |
|  | $\mathrm{N} \mathrm{km}{ }^{-2}$ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 21.2 | 552.8 | 12.4 | 9.5 | 23.9 |  |
|  | SD |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 12.2 | 531.9 | 7.7 | 3.7 | 12.4 | NS |
| 5 | $\mathrm{kg} \mathrm{km}{ }^{-2}$ |  |  |  |  |  |  |  |  |  |  |  |  |  | 5.3 | 6.3 | 2.5 | 3.8 | 1.9 | 2.3 | 4.1 | 2.3 | 2.2 | Negative |
|  | SD |  |  |  |  |  |  |  |  |  |  |  |  |  | 2.3 | 2.8 | 1.1 | 1.6 | 1.0 | 0.9 | 1.8 | 0.7 | 0.8 | trend |
|  | $\mathrm{N} \mathrm{km}{ }^{-2}$ |  |  |  |  |  |  |  |  |  |  |  |  |  | 120.0 | 145.0 | 61.5 | 82.9 | 44.6 | 55.3 | 240.6 | 54.9 | 49.4 |  |
|  | SD |  |  |  |  |  |  |  |  |  |  |  |  |  | 59.2 | 68.3 | 34.2 | 33.8 | 24.1 | 24.5 | 135.9 | 19.2 | 18.6 | NS |
| 6 | $\mathrm{kg} \mathrm{km}^{-2}$ | 3.1 | 3.7 | 6.7 | 6.2 | 2.4 | 1.3 | 4.1 | 11.1 | 4.7 | 4.6 | 5.5 | 2.5 | 4.9 | 4.8 | 2.2 | 8.1 | 3.6 | 3.9 | 5.7 | 6.4 | 5.6 | 7.6 | Positive |
|  | SD | 1.0 | 0.8 | 1.9 | 2.1 | 1.1 | 0.4 | 1.8 | 3.0 | 1.2 | 1.3 | 2.0 | 0.9 | 1.2 | 1.4 | 0.9 | 2.8 | 1.2 | 1.3 | 1.8 | 2.1 | 1.4 | 1.9 | trend |
|  | N km ${ }^{-2}$ | 135.3 | 136.8 | 246.3 | 245.7 | 77.9 | 65.7 | 244.9 | 404.7 | 182.7 | 169.0 | 236.8 | 88.7 | 157.8 | 132.2 | 86.6 | 300.1 | 127.6 | 127.0 | 224.4 | 354.1 | 182.0 | 233.5 |  |
|  | SD | 34.7 | 31.2 | 73.5 | 88.7 | 29.8 | 31.2 | 135.8 | 119.3 | 56.0 | 49.8 | 100.0 | 31.4 | 36.4 | 46.2 | 37.3 | 115.0 | 45.0 | 42.4 | 65.0 | 154.0 | 50.1 | 61.9 | NS |
| 7 | $\mathrm{kg} \mathrm{km}{ }^{-2}$ | 4.8 | 6.2 | 4.9 | 2.0 | 4.2 | 9.3 | 14.3 | 23.2 | 18.6 | 14.6 | 6.6 | 8.8 | 10.2 | 10.7 | 9.1 | 11.5 | 10.0 | 8.3 | 4.3 | 4.9 | 7.5 | 9.6 |  |
|  | SD | 2.1 | 1.7 | 1.8 | 0.8 | 2.2 | 3.3 | 6.2 | 6.7 | 9.5 | 7.2 | 3.6 | 6.1 | 6.5 | 5.1 | 4.1 | 3.9 | 2.2 | 3.0 | 1.8 | 2.9 | 2.9 | 3.3 | NS |
|  | N km ${ }^{-2}$ | 124.4 | 186.9 | 160.4 | 66.9 | 128.3 | 196.6 | 400.1 | 582.4 | 513.7 | 315.9 | 177.3 | 204.4 | 271.5 | 284.7 | 260.2 | 383.5 | 308.3 | 221.7 | 122.6 | 167.1 | 203.2 | 260.4 |  |
|  | SD | 52.2 | 45.8 | 55.7 | 25.7 | 64.0 | 52.1 | 171.5 | 144.8 | 232.0 | 136.2 | 88.7 | 130.2 | 157.2 | 119.1 | 102.8 | 129.6 | 69.0 | 73.0 | 47.6 | 90.9 | 72.1 | 82.4 | NS |
| 8 | $\mathrm{kg} \mathrm{km}^{-2}$ | 24.2 | 11.1 | 24.5 | 15.8 | 19.3 | 18.1 | 28.6 | 28.8 |  | 46.1 | 52.4 | 38.6 | 27.1 | 22.1 | 33.1 | 40.4 | 31.7 | 33.6 | 34.1 | 17.4 | 26.8 | 15.7 |  |
|  | SD | 7.9 | 2.1 | 3.1 | 4.9 | 4.9 | 2.1 | 3.6 | 4.0 |  | 9.7 | 14.5 | 14.3 | 5.3 | 3.9 | 5.2 | 8.2 | 7.2 | 7.2 | 7.6 | 5.2 | 3.4 | 1.8 | NS |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 628.2 | 302.3 | 595.6 | 325.7 | 520.5 | 602.7 | 662.5 | 897.7 |  | 1077.6 | 1326.3 | 1143.1 | 688.5 | 527.2 | 845.4 | 1158.5 | 872.5 | 829.0 | 905.0 | 471.6 | 710.3 | 431.8 |  |
|  | SD | 199.2 | 51.8 | 82.0 | 91.9 | 134.8 | 218.2 | 92.8 | 185.5 |  | 256.4 | 375.5 | 518.3 | 147.4 | 97.7 | 134.0 | 277.9 | 290.4 | 203.1 | 222.9 | 129.6 | 97.6 | 56.7 | Positive trend |
| 9 | $\mathrm{kg} \mathrm{~km}^{-2}$ | 3.4 | 3.7 | 5.6 | 4.4 | 6.1 | 4.4 | 5.6 | 6.2 | 3.7 | 5.5 | 4.6 | 3.4 | 4.9 | 5.3 | 5.5 | 7.1 | 5.4 | 4.4 | 5.3 | 3.2 | 4.1 | 4.4 |  |
|  | SD | 0.4 | 0.4 | 0.7 | 0.6 | 0.7 | 0.6 | 0.8 | 0.9 | 0.9 | 1.2 | 0.8 | 0.6 | 0.8 | 0.9 | 0.8 | 1.1 | 0.9 | 0.8 | 1.1 | 0.5 | 0.7 | 0.7 | NS |
|  | N km ${ }^{-2}$ | 91.3 | 110.1 | 159.8 | 121.5 | 170.9 | 125.0 | 179.0 | 205.3 | 110.9 | 179.4 | 138.2 | 114.9 | 145.2 | 192.8 | 184.0 | 251.2 | 176.2 | 130.9 | 180.3 | 98.3 | 144.5 | 141.8 |  |
|  | SD | 11.9 | 16.3 | 21.0 | 15.4 | 22.1 | 17.8 | 24.7 | 30.7 | 27.6 | 40.7 | 22.7 | 19.6 | 23.6 | 34.1 | 30.6 | 46.2 | 38.1 | 23.1 | 40.2 | 15.5 | 29.2 | 25.9 | NS |
| 10 | $\mathrm{kg} \mathrm{km}{ }^{-2}$ | 1.1 | 1.1 | 0.7 | 1.1 | 1.7 | 1.6 | 0.9 | 1.1 | 0.2 | 0.5 | 1.4 | 1.3 | 1.2 | 1.2 | 1.3 | 1.0 | 1.2 | 1.2 | 1.3 | 1.0 | 0.6 | 0.8 |  |
|  | SD | 0.2 | 0.3 | 0.1 | 0.3 | 0.3 | 0.3 | 0.2 | 0.3 | 0.1 | 0.1 | 0.5 | 0.3 | 0.2 | 0.3 | 0.3 | 0.2 | 0.3 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | NS |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 26.2 | 25.9 | 15.4 | 28.4 | 42.8 | 43.0 | 26.9 | 27.7 | 5.8 | 12.9 | 30.9 | 43.8 | 27.4 | 21.7 | 21.4 | 15.0 | 23.3 | 27.0 | 23.9 | 20.5 | 11.0 | 14.3 |  |
|  | SD | 5.6 | 9.3 | 3.8 | 8.7 | 9.9 | 8.7 | 7.2 | 6.4 | 3.1 | 2.6 | 8.6 | 9.4 | 4.0 | 4.9 | 4.7 | 3.5 | 4.9 | 4.1 | 4.1 | 3.6 | 3.3 | 2.9 | trend |



| GSA |  | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | Spearman Rho |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 11 | $\mathrm{kg} \mathrm{km}^{-2}$ | 1.7 | 4.2 | 3.6 | 1.6 | 2.6 | 2.0 | 4.0 | 1.5 | 2.0 | 3.0 | 3.7 | 2.2 | 3.3 | 3.1 | 4.5 | 4.3 | 4.1 | 1.8 | 2.7 | 2.0 | 2.1 | 2.3 |  |
|  | SD | 0.5 | 1.3 | 0.8 | 0.3 | 0.6 | 0.6 | 1.4 | 0.5 | 0.7 | 0.8 | 1.1 | 0.6 | 0.7 | 0.7 | 1.1 | 1.2 | 1.0 | 0.5 | 0.7 | 0.6 | 0.6 | 0.8 | NS |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 38.4 | 102.9 | 92.7 | 40.0 | 61.6 | 45.7 | 85.6 | 31.5 | 36.6 | 87.8 | 91.4 | 71.4 | 87.9 | 92.4 | 136.1 | 100.8 | 87.9 | 37.1 | 58.8 | 45.2 | 45.3 | 47.6 |  |
|  | SD | 9.9 | 31.5 | 19.2 | 8.3 | 15.3 | 15.1 | 28.3 | 8.0 | 10.3 | 25.9 | 28.4 | 21.2 | 21.3 | 22.6 | 35.1 | 25.3 | 20.7 | 8.7 | 13.5 | 16.0 | 13.0 | 16.4 | NS |
| 15 | $\mathrm{kg} \mathrm{km}{ }^{-2}$ |  |  |  |  |  |  |  |  |  |  |  | 5.4 | 10.3 | 12.5 | 8.0 | 16.1 | 4.0 | 7.6 | 4.3 | 3.2 | 3.5 | 3.4 | Negative |
|  | SD |  |  |  |  |  |  |  |  |  |  |  | 1.9 | 4.2 | 6.8 | 2.4 | 10.0 | 1.2 | 2.3 | 1.1 | 0.9 | 1.5 | 1.3 | trend |
|  | $\mathrm{N} \mathrm{km}{ }^{-2}$ |  |  |  |  |  |  |  |  |  |  |  | 137.3 | 214.8 | 413.0 | 210.2 | 413.4 | 90.4 | 170.6 | 154.9 | 137.0 | 148.8 | 151.1 | Negative |
|  | SD |  |  |  |  |  |  |  |  |  |  |  | 53.9 | 85.5 | 213.6 | 64.6 | 278.7 | 29.0 | 59.1 | 38.6 | 40.2 | 81.6 | 51.5 | trend |
| 16 | $\mathrm{kg} \mathrm{km}^{-2}$ | 1.4 | 2.2 | 4.3 | 1.5 | 2.1 | 2.0 | 2.0 | 2.3 | 2.5 | 2.1 | 5.1 | 3.6 | 4.4 | 6.0 | 6.6 | 7.0 | 5.4 | 4.2 | 6.2 | 2.0 | 0.6 | 3.3 |  |
|  | $\mathrm{Sb} \mathrm{km}^{-2}$ | 0.5 | 1.1 | 2.0 | 0.9 | 0.9 | 0.7 | 0.8 | 0.9 | 1.2 | 0.9 | 2.0 | 2.3 | 1.7 | 2.8 | 2.9 | 3.2 | 2.3 | 1.8 | ${ }_{2} .8$ | 0.7 | 0.3 | 1.3 | NS |
|  | $\mathrm{N} \mathrm{km}{ }^{-2}$ | 48.7 | 96.2 | 175.0 | 65.1 | 76.7 | 79.7 | 86.9 | 118.9 | 106.0 | 74.5 | 142.0 | 97.7 | 128.9 | 170.7 | 215.2 | 232.4 | 158.4 | 121.4 | 183.6 | 60.2 | 15.3 | 84.6 |  |
|  | SD | 17.3 | 48.4 | 76.0 | 37.3 | 34.1 | 24.0 | 41.8 | 53.7 | 50.2 | 36.2 | 58.5 | 59.4 | 50.9 | 73.2 | 99.1 | 107.3 | 63.7 | 58.3 | 80.0 | 20.1 | 7.4 | 37.3 | NS |
| 17 | $\mathrm{kg} \mathrm{km}{ }^{-2}$ |  |  |  |  |  |  |  |  | 1.5 | 1.8 | 1.9 | 2.6 | 2.8 | 1.0 | 1.4 | 1.4 | 1.0 | 0.6 | 0.5 | 0.9 | 0.8 | 0.7 | Negative |
|  | SD |  |  |  |  |  |  |  |  | 0.4 | 0.4 | 0.3 | 0.7 | 0.6 | 0.2 | 0.2 | 0.3 | 0.2 | 0.1 | 0.2 | 0.2 | 0.1 | 0.1 | trend |
|  | $\mathrm{Nkm}{ }^{-2}$ |  |  |  |  |  |  |  |  | 56.1 | 94.6 | 72.9 | 122.7 | 145.3 | 44.4 | 52.8 | 42.9 | 28.4 | 13.6 | 18.9 | 23.6 | 26.7 | 24.2 |  |
|  | SD |  |  |  |  |  |  |  |  | 18.5 | 26.4 | 14.7 | 37.3 | 41.6 | 12.4 | 11.4 | 9.0 | 5.9 | 2.9 | 8.2 | 5.5 | 6.6 | 4.9 | trend |
| 18 | $\mathrm{kg} \mathrm{km}^{-2}$ | 1.4 | 2.0 | 2.8 | 1.4 | 1.4 | 1.4 | 1.4 | 1.8 | 1.0 | 1.3 | 1.6 | 1.7 | 1.6 | 1.1 | 3.2 | 3.1 | 1.9 | 1.3 | 0.8 | 0.8 | 0.9 | 0.5 | Negative |
|  | SD | 0.3 | 0.6 | 0.4 | 0.3 | 0.2 | 0.3 | 0.3 | 0.4 | 0.2 | 0.4 | 0.3 | 0.4 | 0.4 | 0.3 | 0.6 | 0.8 | 0.4 | 0.4 | 0.2 | 0.2 | 0.2 | 0.1 |  |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 36.7 | 64.2 | 98.3 | 40.2 | 44.3 | 45.8 | 40.5 | 57.3 | 30.4 | 40.0 | 40.8 | 43.0 | 50.1 | 26.6 | 78.5 | 118.5 | 74.0 | 47.0 | 22.4 | 21.5 | 26.9 | 19.6 | Negative |
|  | SD | 8.1 | 19.4 | 20.2 | 9.1 | 9.4 | 11.1 | 10.6 | 14.9 | 8.1 | 15.0 | 7.2 | 9.7 | 18.9 | 12.3 | 17.6 | 44.3 | 21.9 | 19.9 | 6.1 | 7.7 | 6.8 | 7.2 | Negative |
| 19 | $\mathrm{kg} \mathrm{km}^{-2}$ | 2.2 | 1.6 | 1.1 | 1.6 | 1.7 | 1.5 | 2.5 | 1.3 | 0.8 | 0.8 | 0.7 | 1.5 | 1.7 | 1.1 | 1.5 | 0.7 | 0.8 | 0.6 | 0.5 | 0.4 | 0.4 | 0.5 | Negative |
|  | SD | 0.8 | 0.5 | 0.4 | 0.4 | 0.7 | 0.3 | 0.9 | 0.3 | 0.3 | 0.2 | 0.3 | 0.9 | 0.4 | 0.3 | 0.5 | 0.2 | 0.4 | 0.2 | 0.1 | 0.1 | 0.1 | 0.1 | trend |
|  | $\mathrm{N} \mathrm{km}{ }^{-2}$ | 46.8 | 37.7 | 32.0 | 47.0 | 95.2 | 60.1 | 218.7 | 49.7 | 46.4 | 43.0 | 20.8 | 51.5 | 90.7 | 35.7 | 41.3 | 25.7 | 22.1 | 16.0 | 14.6 | 9.6 | 7.9 | 9.7 | Negative |
|  | SD | 12.6 | 9.9 | 8.2 | 13.1 | 37.2 | 15.3 | 119.6 | 15.7 | 17.6 | 15.4 | 6.4 | 23.3 | 28.2 | 9.2 | 14.3 | 10.2 | 12.6 | 5.1 | 4.3 | 3.0 | 2.6 | 2.4 | trend |
| 20 | $\mathrm{kg} \mathrm{km}^{-2}$ | 5.0 | 5.8 | 2.6 | 4.8 | 1.8 | 0.8 | 1.1 | 2.2 |  | 0.6 | 0.6 | 0.4 | 0.6 |  | 0.1 |  |  |  |  |  | 1.2 |  | Negative |
|  | SD | 3.7 | 4.8 | 1.4 | 2.1 | 0.8 | 0.4 | 0.7 | 1.1 |  | 0.3 | 0.4 | 0.3 | 0.4 |  | 0.1 |  |  |  |  |  | 1.1 |  | trend |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 285.4 | 159.2 | 73.9 | 131.8 | 50.9 | 15.3 | 18.9 | 49.5 |  | 15.9 | 16.4 | 10.0 | 12.0 |  | 4.9 |  |  |  |  |  | 34.8 |  |  |
|  | SD | 241.8 | 127.7 | 30.1 | 57.6 | 26.0 | 7.0 | 9.8 | 20.3 |  | 7.3 | 10.4 | 6.5 | 7.8 |  | 4.6 |  |  |  |  |  | 32.0 |  | trend |
| 22 | $\mathrm{kg} \mathrm{km}^{-2}$ | 5.7 | 3.1 | 2.9 | 3.9 | 3.4 | 4.5 | 2.9 | 4.0 |  | 1.1 | 1.5 | 2.1 | 1.5 |  | 1.3 |  |  |  |  |  | 1.0 |  | Negative |
|  | SD | 2.0 | 0.6 | 0.7 | 0.9 | 0.9 | 1.2 | 0.8 | 1.5 |  | 0.3 | 0.4 | 0.7 | 0.4 |  | 0.4 |  |  |  |  |  | 0.2 |  | trend |
|  | $\mathrm{N} \mathrm{km}^{-2}$ | 166.9 | 79.3 | 77.5 | 84.2 | 80.6 | 100.6 | 78.4 | 99.4 |  | 36.5 | 39.3 | 56.4 | 46.5 |  | 41.5 |  |  |  |  |  | 25.9 |  | Negative |
|  | SD | 70.3 | 19.9 | 17.1 | 19.4 | 18.1 | 27.0 | 25.3 | 40.2 |  | 13.5 | 10.0 | 21.3 | 16.0 |  | 14.7 |  |  |  |  |  | 6.9 |  | trend |
| 23 | $\mathrm{kg} \mathrm{km}^{-2}$ |  | 3.7 | 2.5 | 0.4 | 2.9 | 1.9 |  | 2.5 |  | 0.3 | 0.2 | 0.0 | 0.1 |  |  |  |  |  |  |  |  |  | Negative |
|  | SD |  | 1.9 | 1.2 | 0.4 | 2.9 | 1.9 |  | 2.5 |  | 0.3 | 0.2 | 0.0 | 0.1 |  |  |  |  |  |  |  |  |  | trend |
|  | N km-2 |  | 78.9 | 49.1 | 1.8 | 65.3 | 58.0 |  | 51.0 |  | 7.9 | 4.8 | 1.4 | 1.3 |  |  |  |  |  |  |  |  |  |  |
|  | SD |  | 39.5 | 24.6 | 1.8 | 65.3 | 58.0 |  | 51.0 |  | 7.9 | 4.8 | 1.4 | 1.3 |  |  |  |  |  |  |  |  |  | trend |
| 25 | $\mathrm{kg} \mathrm{km}^{-2}$ |  |  |  |  |  |  |  |  |  |  |  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |  | 0.0 |  |
|  | SD |  |  |  |  |  |  |  |  |  |  |  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |  | 0.0 | NS |
|  | $\mathrm{Nkm}{ }^{-2}$ |  |  |  |  |  |  |  |  |  |  |  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |  | 0.0 |  |
|  | SD |  |  |  |  |  |  |  |  |  |  |  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |  | 0.0 | NS |



Fig. S1. - Pair-plots for all the explanatory variables in the data set used for the analysis. The upper diagonal panel shows the Pearson correlation coefficient, and the lower diagonal panel shows the scatterplots with a smoother added to visualize the pattern. The font size of the correlation coefficient is proportional to its estimated value.


Fig. S2. - Graphs of the validation of the best GAM model for deep-water rose shrimp. From top left, residuals versus depth, residuals versus longitude, residuals versus latitude, residuals versus SST, and residuals versus time (year) to assess homogeneity; bottom right, histogram of residuals to assess normality.


Fig. S3. - Graphs of the validation of the best GAM model for Norway lobster. From top left, residuals versus depth, residuals versus longitude, residuals versus latitude, residuals versus SST, and residuals versus time (year) to assess homogeneity; bottom right, histogram of residuals to assess normality.

