

## Manuscript Details

<b>Manuscript number</b>	PROOCE_2016_168
<b>Title</b>	Environmentally driven synchronies of Mediterranean cephalopod populations
<b>Article type</b>	Full Length Article

### Abstract

The Mediterranean Sea is characterized by large scale gradients of temperature, productivity and salinity, in addition to pronounced mesoscale differences. Such a heterogeneous system is expected to shape the population dynamics of marine species. On the other hand, prevailing environmental and climatic conditions at whole basin scale may force spatially distant populations to fluctuate in synchrony. Cephalopods are excellent case studies to test these hypotheses owing to its high sensitivity to environmental conditions. Data of two cephalopod species with contrasting life histories (benthic octopus vs nectobenthic squid), obtained from scientific surveys carried out throughout the Mediterranean during the last 20 years were analyzed. The objectives of this study and the methods used to achieve them (in parentheses) were: i) to investigate synchronies in spatially separated populations (decorrelation analysis); ii) detect underlying common abundance trends over distant regions (dynamic factor analysis, DFA); and iii) analyse putative influences of key environmental drivers such as productivity and sea surface temperature on the population dynamics at regional scale (general linear models, GLM). In accordance with their contrasting spatial mobility, the distance from where synchrony could no longer be detected (decorrelation scale) was higher in squid than in octopus (385 vs 193 km); for comparison, the maximum distance between locations was 2620 km. The DFA revealed a general increasing trend in the abundance of both species in most areas, which agrees with the already reported worldwide proliferation of cephalopods. DFA results also showed that population dynamics are more similar in the eastern than in the western Mediterranean basin. According to the GLM models, cephalopod populations were negatively affected by productivity, which would be explained by an increase of competition and predation by fishes. While warmer years went along with declining octopus numbers, areas of high sea surface temperature showed higher abundances of squid. Our results are relevant for regional fisheries management and demonstrate that the regionalisation objectives envisaged under the new Common Fishery Policy may not be adequate for Mediterranean cephalopod stocks.

**Keywords** cephalopods; Mediterranean; MEDITS; Dynamic factor analysis; synchrony; Octopus vulgaris; Illex coindetii

**Manuscript category** Biological Oceanography

**Corresponding Author** Stefanie Keller

**Order of Authors** Stefanie Keller, Antoni Quetglas, Patricia Puerta, Isabella Bitetto, Loredana Casciaro, Danila Cuccu, Antonio Esteban, Cristina Garcia, Germana Garofalo, Beatriz Guijarro, Marios Josephide, Angelique Jadaud, Evgenia Lefkaditou, Porzia Maiorano, Chiara Manfredi, Bojan Marceta, Reno Micallef, Panagiota Peristeraki, Giulio Relini, Paolo Sartor, Maria Teresa Spedicato, George Tserpes, Manuel Hidalgo

**Suggested reviewers** Paul Rodhouse, Mary Hunsicker, Zoe Doubleday

## Submission Files Included in this PDF

### File Name [File Type]

Manuscript Keller et al.pdf [Manuscript]

Highlights.docx [Highlights]

To view all the submission files, including those not included in the PDF, click on the manuscript title on your EVISE Homepage, then click 'Download zip file'.

# 1 Environmentally driven synchronies of Mediterranean cephalopod populations

2 *Stefanie Keller*<sup>\*1</sup>, *Antoni Quetglas*<sup>1</sup>, *Patricia Puerta*<sup>1</sup>, *Isabella Bitetto*<sup>2</sup>, *Loredana Casciaro*<sup>2</sup>,  
3 *Danila Cuccu*<sup>3</sup>, *Antonio Esteban*<sup>4</sup>, *Cristina Garcia*<sup>5</sup>, *Germana Garofalo*<sup>6</sup>, *Beatriz Guijarro*<sup>1</sup>, *Marios*  
4 *Josephide*<sup>7</sup>, *Angelique Jadaud*<sup>8</sup>, *Evgenia Lefkaditou*<sup>9</sup>, *Porzia Maiorano*<sup>10</sup>, *Chiara Manfredi*<sup>11</sup>,  
5 *Bojan Marceta*<sup>12</sup>, *Reno Micallef*<sup>13</sup>, *Panagiota Peristeraki*<sup>14,17</sup>, *Giulio Relini*<sup>15</sup>, *Paolo Sartor*<sup>16</sup>, *Maria*  
6 *Teresa Spedicato*<sup>2</sup>, *George Tserpes*<sup>14</sup>, *Manuel Hidalgo*<sup>1</sup>

7  
8 <sup>1</sup> *Instituto Español de Oceanografía (IEO), Centro Oceanográfico de Baleares, Muelle de*  
9 *Poniente, s/n, Apdo. 291, 07015 Palma de Mallorca, Spain; Tel: +34971133742; fax:*  
10 *+34971404945;*  
11 *e-mail: [stefanie.keller@ba.ieo.es](mailto:stefanie.keller@ba.ieo.es)*

12 <sup>2</sup> *COISPA-Tecnologia & Ricerca, Stazione Sperimentale per lo Studio delle Risorse del Mare, Bari,*  
13 *Italy*

14 <sup>3</sup> *Dipartimento di Scienze della Vita e dell'Ambiente, Università di Cagliari, Cagliari, Italy*

15 <sup>4</sup> *IEO, Centro Oceanográfico de Murcia, San Pedro del Pinatar, Murcia, Spain*

16 <sup>5</sup> *IEO, Centro Oceanográfico de Malaga, Fuengirola, Málaga, Spain*

17 <sup>6</sup> *IAMC – Coastal Marine Environment Institute – CNR, Mazara del Vallo (TP), Italy*

18 <sup>7</sup> *DFMR – Department of Fisheries and Marine Research, Ministry of Agriculture, Rural*  
19 *Development and Environment, Nicosia, Cyprus*

20 <sup>8</sup> *Ifremer, Institut Français de Recherche pour l'Exploitation de la mer, UMR 212 Ecosystèmes*  
21 *Marins Exploités (EME), Sète, France*

22 <sup>9</sup> *HCMR, Hellenic Centre of Marine Research, Athens, Greece*

23 <sup>10</sup> *University of Bari Aldo Moro - Department of Biology, Bari, Italy*

24 <sup>11</sup> *Laboratorio Biologia Marina e Pesca, Università di Bologna, Fano (PS), Italy*

25 <sup>12</sup> *Fishery Research Institute of Slovenia, Ljubljana-Smartno, Slovenia*

26 <sup>13</sup> *Ministry for Sustainable Development, Department of Fisheries and Aquaculture, Marsa, Malta*

27 <sup>14</sup> *HCMR, Hellenic Centre of Marine Research, Heraklion, Crete, Greece*

28 <sup>15</sup> *SIBM, Società Italiana di Biologia Marina, Genova and DISTAV, Università di Genova, Genova,*  
29 *Italy*

30 <sup>16</sup> *CIBM – Centro Interuniversitario di Biologia Marina ed Ecologia Applicata, Livorno, Italy*

31 <sup>17</sup> *University of Crete, Biology Department, Heraklion, Crete, Greece*

32

## 33 Abstract

34 The Mediterranean Sea is characterized by large scale gradients of  
35 temperature, productivity and salinity, in addition to pronounced mesoscale  
36 differences. Such a heterogeneous system is expected to shape the population  
37 dynamics of marine species. On the other hand, prevailing environmental and climatic  
38 conditions at whole basin scale may force spatially distant populations to fluctuate in  
39 synchrony. Cephalopods are excellent case studies to test these hypotheses owing to  
40 its high sensitivity to environmental conditions. Data of two cephalopod species with  
41 contrasting life histories (benthic octopus vs nectobenthic squid), obtained from  
42 scientific surveys carried out throughout the Mediterranean during the last 20 years  
43 were analyzed. The objectives of this study and the methods used to achieve them (in  
44 parentheses) were: i) to investigate synchronies in spatially separated populations

45 (decorrelation analysis); ii) detect underlying common abundance trends over distant  
46 regions (dynamic factor analysis, DFA); and iii) analyse putative influences of key  
47 environmental drivers such as productivity and sea surface temperature on the  
48 population dynamics at regional scale (general linear models, GLM). In accordance  
49 with their contrasting spatial mobility, the distance from where synchrony could no  
50 longer be detected (decorrelation scale) was higher in squid than in octopus (385 vs  
51 193 km); for comparison, the maximum distance between locations was 2620 km.  
52 The DFA revealed a general increasing trend in the abundance of both species in most  
53 areas, which agrees with the already reported worldwide proliferation of  
54 cephalopods. DFA results also showed that population dynamics are more similar in  
55 the eastern than in the western Mediterranean basin. According to the GLM models,  
56 cephalopod populations were negatively affected by productivity, which would be  
57 explained by an increase of competition and predation by fishes. While warmer years  
58 went along with declining octopus numbers, areas of high sea surface temperature  
59 showed higher abundances of squid. Our results are relevant for regional fisheries  
60 management and demonstrate that the regionalisation objectives envisaged under  
61 the new Common Fishery Policy may not be adequate for Mediterranean cephalopod  
62 stocks.

63

64 **Keywords:** cephalopods, Mediterranean, MEDITS, Dynamic factor analysis,  
65 synchrony, *Octopus vulgaris*, *Illex coindetii*

66

67

68

69

70

71

72

73

74

75

## 76 **1. Introduction**

77 The Mediterranean Sea is generally shaped by large scale gradients of  
78 temperature, productivity and salinity (D'Ortenzio and d'Alcalá, 2009). However, it is  
79 also known as a complex ecosystem with contrasting regions in terms of productivity  
80 (Nieblas et al., 2014), seafloor topography and hydrography (Millot, 2005; Rossi et al.,  
81 2014). In an ecosystem with such pronounced regional differences, animal  
82 populations are prone to exhibit patchy distributions due to different habitat  
83 conditions. Such patchiness has been observed analysing feeding habitats of high  
84 trophic level species such as whales and tuna (Druon et al., 2012, 2011, 2016), the  
85 distribution of secondary consumers such as cephalopods or small elasmobranchs  
86 (Navarro et al., 2016; Puerta et al., 2016a, 2015) or nursery grounds and spawning  
87 areas of commercially important species (Colloca et al., 2015; Druon et al., 2011,  
88 2015). All these studies revealed that hydrographic conditions (Druon et al., 2011,  
89 2015), bathymetric features like depth and type of seafloor (Colloca et al., 2015;  
90 Druon et al., 2012) and productivity (Druon et al., 2012, 2011; Puerta et al., 2016a)  
91 are key drivers of distribution patterns.

92 Environmental and large-scale climatic variability may force spatially distant  
93 populations to fluctuate in synchrony (Liebhold et al., 2004). Comparing the dynamics  
94 of spatially distant populations allows detecting the main drivers of abundance  
95 fluctuations and the scale at which they operate (Descamps et al., 2013), and thus the  
96 degree of connectivity of neighbouring populations. In synchronized populations,  
97 drastic declines in population size likely affect all populations simultaneously,  
98 exposing them to a greater risk of extinction (Descamps et al., 2013 and references  
99 therein). By contrast, heterogeneous and complex populations generally show higher  
100 resilience and recovery rates and are more likely to withstand mass elimination  
101 (Schindler et al., 2010). Therefore, knowledge about the underlying mechanisms of  
102 population dynamics at large spatial scales has important implications for the  
103 management and conservation of species (Liebhold et al., 2004).

104 Large-scale synchronic fluctuations have been described in phytoplankton  
105 (Doyle and Poore, 1974), zooplankton (Batchelder et al., 2012), fish (Kelly et al.,  
106 2009) and crustaceans (Hidalgo et al., 2015; Koeller et al., 2009). However, very little  
107 is known about cephalopods. This group is considered excellent for case studies to  
108 analyze synchronic fluctuations, owing to its sensitivity to changing environmental  
109 conditions as a result of its fast growth rates and short life cycles (Pierce et al., 2008).

110 Among the environmental parameters investigated until now, sea surface  
111 temperature (SST) plays an important role in driving cephalopod abundance trends  
112 (Chen, 2010; Zuur and Pierce, 2004). Additionally, a recent study investigated local  
113 scale seasonal synchronies in Mediterranean cephalopod abundances (Puerta et al.,  
114 2016b), revealing contrasting seasonal cycles in response to local environmental  
115 conditions.

116 Due to the decline in the traditional finfish resources, European cephalopod  
117 fisheries, which were once located mostly in the Mediterranean, have grown and  
118 expanded northwards (Pierce et al., 2010). This expansion is expected to continue as  
119 a result of the increasing market demand of cephalopods, whereby regular  
120 assessments and certain management measures would be needed to ensure a  
121 sustainable exploitation. Under the current Common Fisheries Policy (CFP; [EU  
122 Regulation N° 1380/2013](#)), the regionalization approach may lead to a revision of the  
123 management areas currently in place in the Mediterranean (see below). For a  
124 successful implementation, gaining knowledge of the mechanisms controlling stock  
125 fluctuations is essential, as defining management areas merging independently  
126 fluctuating populations may result in strong miss-management. Sound scientific  
127 knowledge is necessary to implement management areas appropriately matching the  
128 biological distribution of populations as demanded by the new CFP in their  
129 regionalised ecosystem-based approach.

130 Here we analyse the population dynamics of two commercially important  
131 cephalopods (Quetglas et al., 2000; Sartor et al., 1998) with contrasting life histories,  
132 the nectobenthic broadtailed shortfin squid *Illex coindetii* and the benthic common  
133 octopus *Octopus vulgaris*, in the whole Mediterranean Sea. The data analysed were  
134 obtained from scientific surveys carried out throughout the Mediterranean during the  
135 last 20 years. The objectives of this study are three-fold. For each species, we first  
136 analyse the global correlation structure across the entire Mediterranean Sea to assess  
137 how the similarity in population abundances of spatially separated populations (or  
138 population sub-units) decreases with distance. Second, we use dynamic factor  
139 analysis to detect underlying common abundance trends over distant regions. Finally,  
140 we analyse putative influences of key environmental drivers (productivity and SST)  
141 on the population dynamics at regional scale using general linear models.

142  
143  
144

145 **2. Material and Methods**

146

147 **2.1 DATA SOURCE**

148

149 Data were obtained from the international Mediterranean bottom trawl survey  
150 MEDITS (<http://www.sibm.it/MEDITS%202011/principalemedits.htm>), which is  
151 conducted every year in spring / early summer (May-August) since 1994, covering  
152 depths from 10 m down to 800 m. The surveys are performed by all riparian EU  
153 countries, in addition to Montenegro and Albania, and are the most comprehensive  
154 data sources to investigate demersal ecosystems in the entire Mediterranean. The  
155 sampling methodology is standardized among all the countries (for details see  
156 Bertrand et al., 2002 and A.A.V.V., 2016). A stratified random sampling design is used  
157 for this survey, with bathymetric strata comprising 10-50, 51-100, 101-200, 201-500  
158 and 501-800 m. The standardized gear used is a GOC 73 trawl with a cod-end mesh  
159 size of 20 mm and a vertical and horizontal opening of the net of about 2 m and 18 m  
160 respectively (Bertrand et al., 2002). The net opening is measured by an attached  
161 underwater Scanmar or SIMRAD system, which allows calculating the swept area.  
162 Trawling is conducted at daylight, with a towing speed of about 3 knots and hauls  
163 duration of 30 and 60 minutes over shelf and slope grounds respectively. Haul  
164 catches are sorted to species level whenever possible. Abundance data for each  
165 species are standardized to number of individuals per km<sup>2</sup> using the mean stratified  
166 swept area method (Saville, 1977; Souplet, 1996).

167 The geographical sub-areas (GSA's; Fig. 1) established by the General  
168 Fisheries Commission for the Mediterranean ([www.gfcm.org](http://www.gfcm.org)) for assessment and  
169 management have been used as spatial units in the present study. Some areas  
170 sampled only in recent and/or very few years were excluded from these analyses  
171 (GSA 2, 15 and 25). Although Greece did not conduct the surveys in 2007 and 2009-  
172 2012, its data were included as they represent the easternmost data points of the  
173 time series. The final dataset included 15 GSAs and comprised between 13 and 20  
174 years depending on GSA. In total, 20463 hauls were analysed.

175

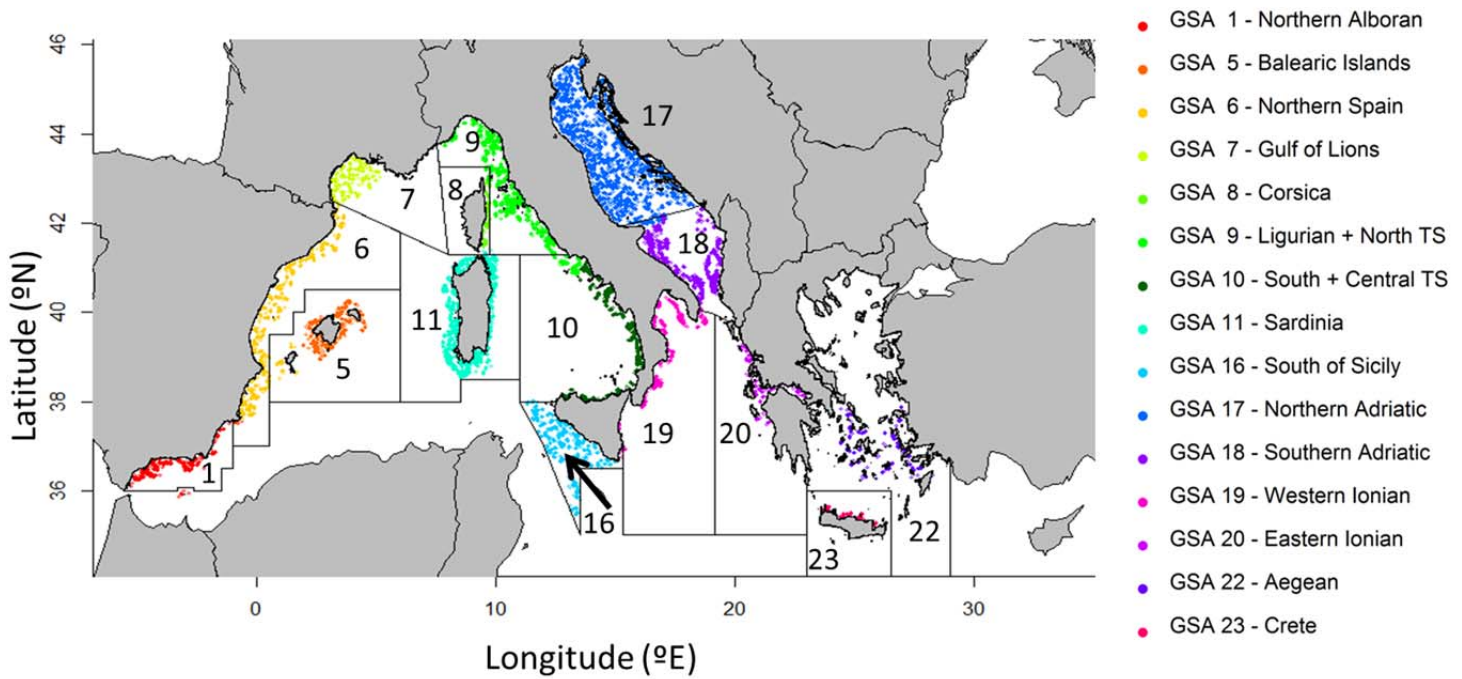
176

177

178

179

180



193

194 Figure 1: Map of the Mediterranean Sea showing the geographical sub-areas (GSAs) established by the  
 195 General Fisheries Commission for the Mediterranean (GFCM) and the MEDITS stations sampled during  
 196 1994-2013.

197

198

## 199 2.2 DATA ANALYSIS

### 200 2.2.1 Decorrelation analysis

201 For both study species (*Octopus vulgaris* and *Illex coindetii*), the Pearson's  
 202 correlation coefficient  $r$  was calculated for each pair of abundance time series and  
 203 plotted against the distance between the GSAs' centres of gravity (Woillez et al.,  
 204 2007). A centre of gravity is the mean location of an individual taken at random in the  
 205 field, and discrete summation over sampling locations divided by population density  
 206 gives the average location of a population in the respective sampling area. This  
 207 method only takes into consideration positive records, that is sampling locations  
 208 where cephalopods have been found (Woillez et al., 2007). To correct for differences  
 209 in time series lengths, each coefficient was weighted by the length of the  
 210 corresponding time series. The graphical output (spatial correlogram) shows the  
 211 decline of synchrony with distance (Kelly et al., 2009) and the spatial scale of  
 212 synchrony. The distance from where synchrony can no longer be detected is referred  
 213 to as "decorrelation scale". Points were fitted by non-linear least squares estimation  
 214 using an exponential fit:

215

216  $q_d = q_0 e^{-d/v}$

217 with  $q_d$  being the Pearson's  $r$  correlation coefficient between CPUE time series of a  
218 pair of locations,  $q_0$  the estimated correlation between CPUEs at zero distance,  $d$   
219 stands for the distance between locations (km), and  $1/v$  ( $\text{km}^{-1}$ ;  $v > 0$ ) is the decay rate  
220 that estimates spatial correlation scale as the e-folding scale of the exponential fit, i.e.,  
221 the distance at which  $q_d = e^{-1}$  (Kelly et al., 2009).

222

### 223 2.2.2 Dynamic Factor Analysis (DFA)

224 To identify underlying common trends in abundance among time series, a  
225 Dynamic Factor Analysis (DFA, Zuur et al., 2003) was used. This technique can cope  
226 with non-stationary data, short time series and also missing values (Zuur et al., 2003),  
227 and has already been implemented for the identification of temporal trends of  
228 exploited species in various studies (Chen and Lee, 2013; Chen et al., 2008; Erzini,  
229 2005; Zuur et al., 2003). DFA is a dimension reduction technique in which a set of  
230 time series are modelled as a linear combination of underlying common trends +  
231 factor loadings (+ covariates) + error terms to explain temporal variability. Factor  
232 loadings indicate how much each time series resembles each common trend.  
233 Covariates can be included, but only one yearly value per model. As this is not  
234 appropriate in a heterogeneous and extensive environment like the Mediterranean  
235 Sea, the effect of covariates will be unmasked separately by means of General Linear  
236 Models (see below). The correlation of observation errors can be modelled using  
237 different error matrices: i) same variance and no covariance (diagonal-equal); ii)  
238 different variances and no covariance (diagonal-unequal); iii) same variance and  
239 covariance (equalvarcov); and iv) different variances and covariances  
240 (unconstrained). For both species, the correlations of observation errors were fitted  
241 to all possible model structures in the time series, including 1 up to 3 common trends.

242 Owing to pronounced differences in environmental conditions (SST,  
243 productivity regimes), oceanographic properties and hydrography between the  
244 western and eastern Mediterranean basins (Lascaratos et al., 1999), two separate  
245 DFA-analyses were conducted grouping GSAs according to their location. GSAs 1-16  
246 are positioned in the western Mediterranean, while GSAs 17-23 are located in the  
247 eastern basin. In this analysis, we included time series of 13-20 years length from 15  
248 different GSAs. For comparison, abundance data were scaled between 0 and 1.



249 The Akaike information criterion (AIC) was used as a measure of goodness-of-  
250 fit, the best model having the lowest AIC (Chen and Lee, 2013; Zuur et al., 2003). All  
251 analyses were done in R (version 3.2.1; <http://www.r-project.org/>) using the  
252 Multivariate Autoregressive State-Space (MARSS) package (Holmes et al., 2012).

253

### 254 2.2.3 General Linear Models

255 General Linear Models (GLM) were applied to investigate the influence of  
256 environmental drivers on the abundance of the two objective species. Sea surface  
257 temperature (SST) and chlorophyll-a concentration (Chla) were used as putative  
258 drivers owing to their significant effects on cephalopod populations (Keller et al.,  
259 2014; Pierce et al., 2008; Puerta et al., 2016b). Chla and SST data resulted from  
260 MODIS-Aqua and NPP-VIIRS sensors measurements already processed with regional  
261 ocean colour algorithms (resolution 1 km, daily data) and were downloaded from the  
262 MyOcean database (<http://marine.copernicus.eu/web/69-interactive-catalogue.php>).  
263 The availability of satellite data restricted this analysis to the time series of 1998-  
264 2012 from 15 GSA's. Available survey years per GSA reach from a minimum of 9 to a  
265 maximum of 15 years.

266 Cephalopod abundances (response variable) were modelled using the  
267 following explanatory variables: SST, Chla, year and GSA. Year and GSA were  
268 considered factors. Mean seasonal Chla and SST were averaged separately for each  
269 GSA for all years. Chla concentration was used as a proxy for food availability and was  
270 modelled using seasonal means of: i) the spring (March-May) before the survey, and  
271 ii) the preceding winter (December-February). This way we account for different time  
272 lags (time required for energy transfer between trophic levels), and also for the fact  
273 that food availability will influence ecological and metabolic processes differently  
274 across ontogeny. For this reason, the same two seasons were used to calculate mean  
275 seasonal SST. Covariates (Chla, SST) and seasons (winter, spring) of year were chosen  
276 as they proofed to be good descriptors of the key oceanographic processes  
277 determining spring productivity in the Mediterranean (Lloret et al., 2001; Quetglas et  
278 al., 2011).

279 Two different models, designed for different purposes, were constructed for  
280 each species. The first one (non-standardized model) included the log of the catch per

281 unit effort (CPUE) as response variable and attempts to detect proportional  
282 (temporal and spatial) effects between CPUE and environmental covariates:

283  $\text{Log (CPUE)} \sim \text{YEAR} + \text{GSA} + \text{Chla\_Winter} + \text{Chla\_Spring} + \text{SST\_Winter} + \text{SST\_Spring}.$   
284

285 The second model (standardized model) was based on standardized data for  
286 CPUE, SST and Chla (data scaled between 0 and 1). This model is specifically designed  
287 to look at the influence of the covariates on the inter-annual variability once spatial  
288 gradients are removed, taking into account the interactions between SST/Chla and  
289 the GSAs to analyse regional-specific differences of environmental influences. This  
290 model therefore detects possible drivers for synchronic behaviour of spatially distant  
291 populations:

292  $\text{CPUE (standardized)} \sim \text{YEAR} + \text{GSA} + \text{Chla\_Winter} + \text{Chla\_Spring} + \text{SST\_Winter} +$   
293  $\text{SST\_Spring} + \text{Chla\_Winter:GSA} + \text{Chla\_Spring:GSA} + \text{SST\_Winter:GSA} + \text{SST\_Spring:GSA}.$

294  
295 All GLM analyses were carried out with R (version 3.2.1, packages *mgcv* and  
296 *MuMIn*) assuming Gaussian error distribution and using the identity link function.  
297 Models were selected according to their sample-size corrected Akaike Information  
298 Criterion (AICc), with the model resulting in the lowest value being considered the  
299 best fit (Burnham and Anderson, 2004). The variance inflation factor (VIF) was  
300 calculated for the best model to confirm the absence of correlation amongst  
301 covariates. Model residuals were checked and confirmed the assumptions of variance  
302 homogeneity and normal distribution of residuals.

303

### 304 **3. Results**

305

#### 306 3.1 Abundance data

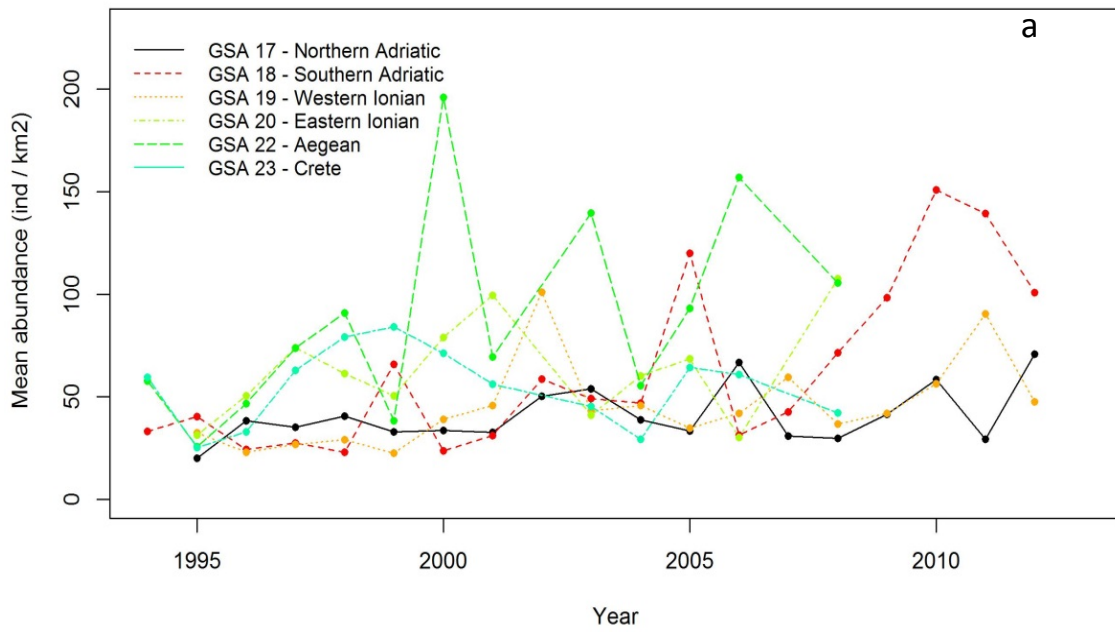
307 CPUEs of *Octopus vulgaris* normally do not exceed 400 individuals/km<sup>2</sup>, with  
308 the exceptions of the Alboran and the Balearic Sea, where the highest catches  
309 occurred (Fig 2 a + b). Except in the Adriatic (GSA 17, 18) and south of Sicily (GSA 16),  
310 CPUEs show a – often remarkable - increase in the year 2011. Catches were generally  
311 higher in the western basin. The opposite is true for *Illex coindetii* abundances, which  
312 are generally lower in the west, where only the Tyrrhenian and Ligurian Sea (GSA 9,  
313 10) reached catches similar to the eastern basin (Fig 2 c + d). CPUEs were highest in  
314 the waters around Crete (GSA 23), while lowest in the Gulf of Lions (GSA 7) and

315 around the Balearic Islands and Corsica (GSA 5, 8). The high squid abundance in  
 316 Northern Spain in 2000 was based on various high catches and is no outlier.

317

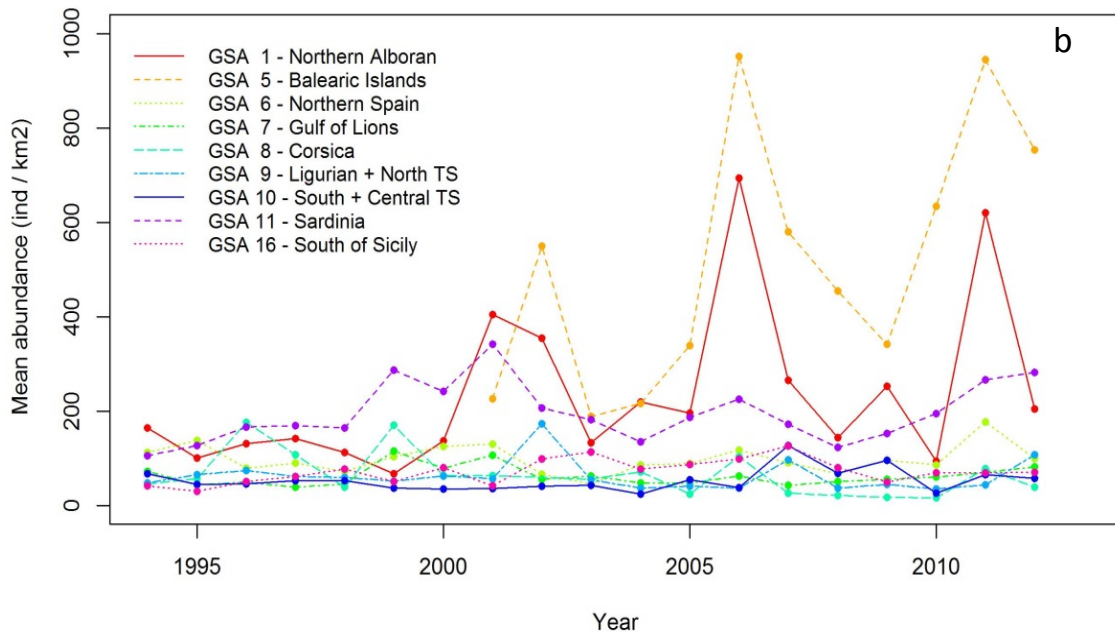
**Eastern basin**

318



**Western basin**

327



339

### Eastern basin

340

341

342

343

344

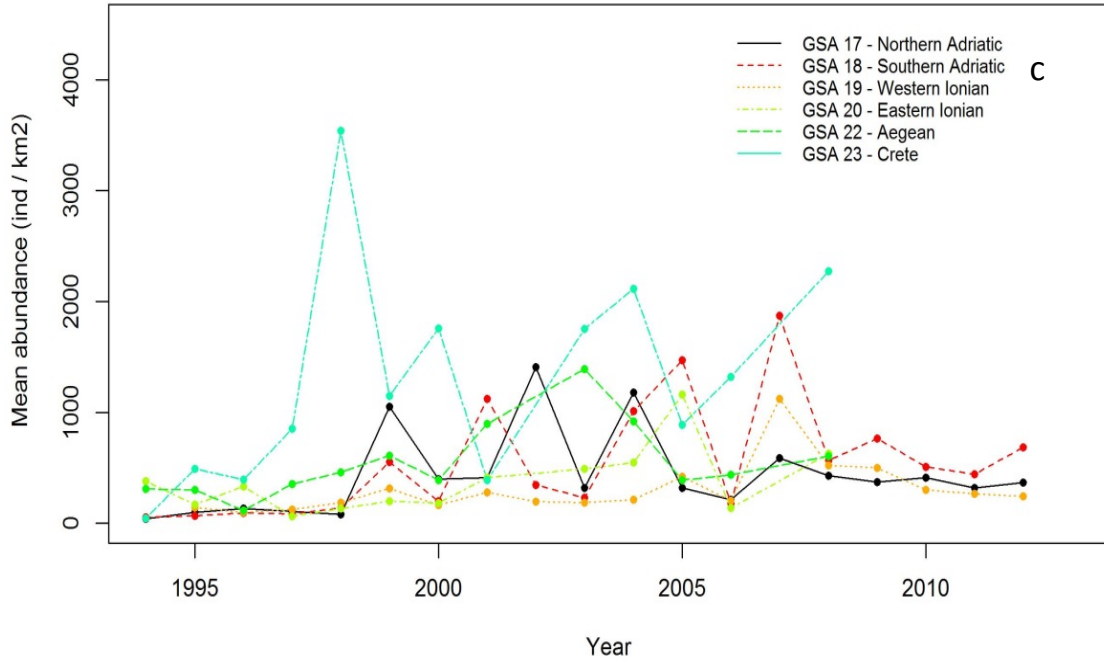
345

346

347

348

349



346

347

348

349

### Western basin

350

351

352

353

354

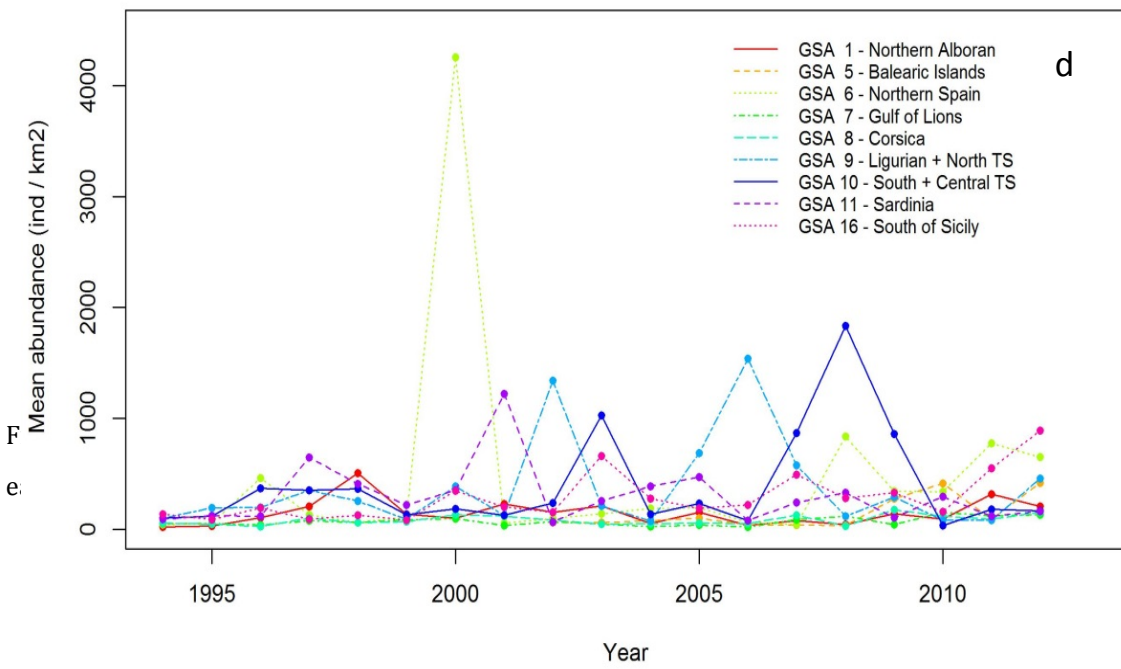
355

356

357

358

359



355

356

357

358

359

### 3.2 Decorrelation analysis

361

362

363

364

As expected, correlations between locations decreased with distance, describing a significant non-linear fit ( $p < 0.05$ ) for both species (Fig 3). The decorrelation scale was higher for squid ( $385 \pm 43$  km) than for octopus ( $193 \pm 36$  km). For comparison, the maximum distance between locations was around 2620 km.

365

366

367

368

369

370

371

372

373

374

375

376

377

378

379

380

381

382

383

384

385

386

387

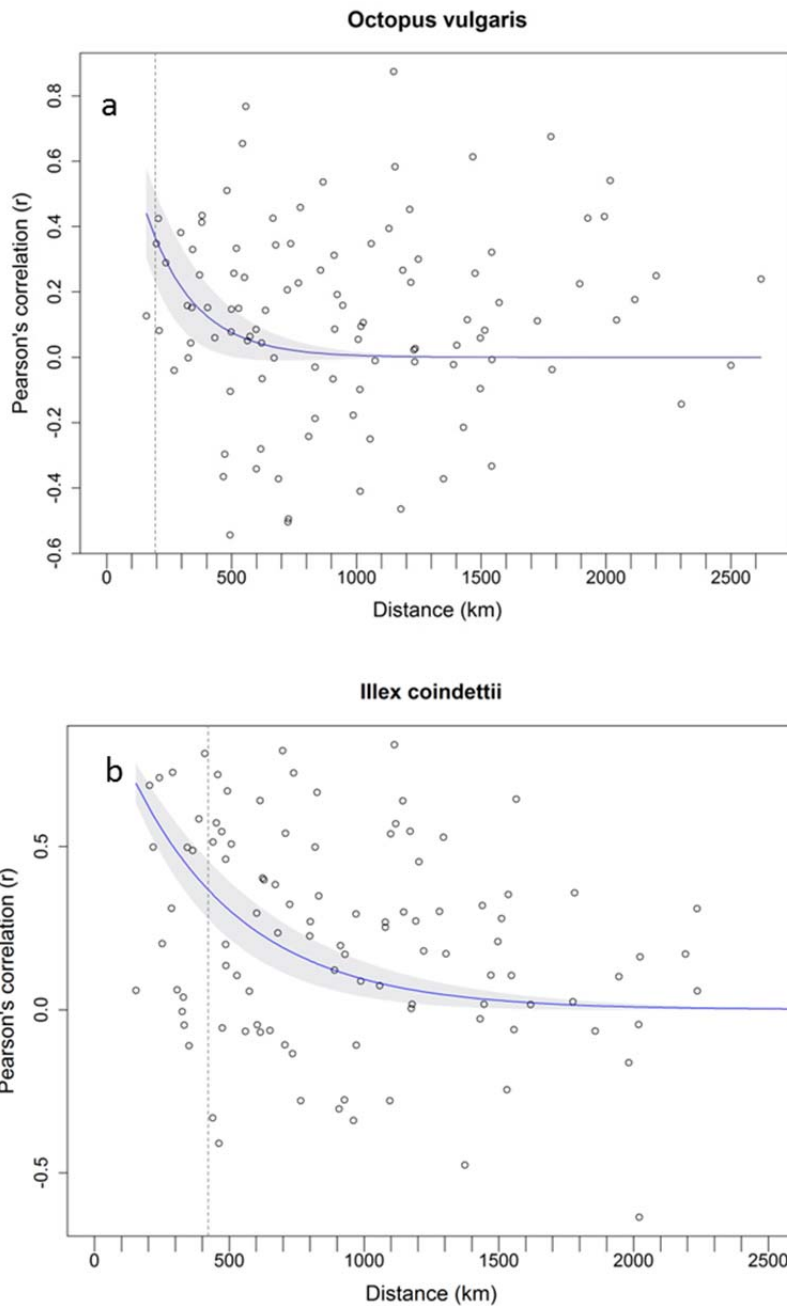
388

389

390

391

392



383 Figure 3: Correlograms of CPUEs of *Octopus vulgaris* (a) and *Illex coindettii* (b) showing the Pearson's  
384 correlation coefficients between all pairs of time series versus their distances. Model fits (least-square  
385 estimates, blue lines) and confidence intervals (in grey) are shown. Vertical lines indicate the spatial  
386 decorrelation scale.

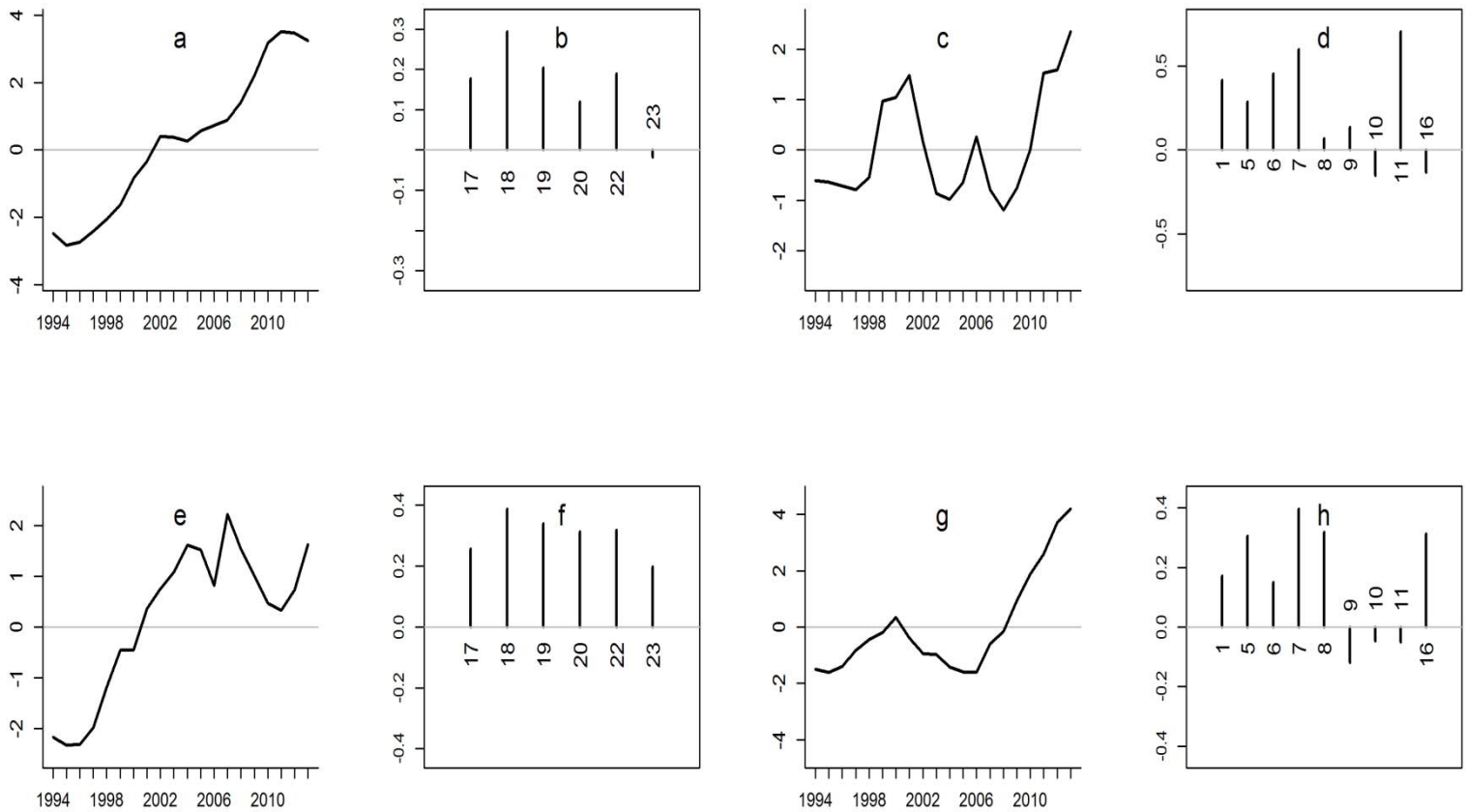
387

### 388 3.3 Dynamic Factor Analysis

389 For both species and in both basins, the best DFA model had a single common  
390 trend and observation errors with equal variances and no covariance (Table A1). All  
391 trends exhibit higher values in 2012 than at the start of the time series in 1994 (Fig  
392 4). Furthermore, all trends show a step increase in CPUEs during the last few years.

393 The common abundance trend for octopus shows a steady rise in the eastern  
 394 basin and fluctuates in the western basin, increasing continuously only from 2008  
 395 onwards. The factor loadings reveal that octopus abundances follow the common  
 396 rising trend in all areas except the waters around Crete (GSA 23, Fig 4 b) in the  
 397 eastern basin and the Tyrrhenian Sea and south of Sicily (GSAs 10 and 16, Fig 4 d) in  
 398 the western basin.

399 Although squid abundances showed a general increasing trend with time on  
 400 both basins (Fig 4 e+g), the western one was truncated with a decrease during 2000-  
 401 2006 (Fig 4 g). In the eastern basin, factor loadings of all areas were positive with no  
 402 opposite trends (Fig 4 f). Factor loadings for the western basin show that the  
 403 Tyrrhenian and the Ligurian Sea (GSAs 9 and 10) and the waters of Sardinia (GSA 11)  
 404 follow abundance trends opposite to the common trend (Fig 4 h).



419

420 Figure 4: Common trends and factor loadings resulting from the Dynamic Factor Analysis of CPUE time series of *Octopus vulgaris* (above) and *Illex coindetii* (below) in the eastern (left) and western (right)  
 421 basin during 1994-2013. GSAs are denoted by their numbers and located as seen in Figure 1. All y-axis  
 422 are unitless.  
 423

424  
 425

426 3.4 General Linear Models

427 The best model predicting the non-standardized CPUEs of octopus was  
 428 obtained including the factor GSA only (Table 1). In the standardized model, both Chla  
 429 content of the spring concurrent with the surveys and the SST of the previous winter  
 430 were retained in the best model (Fig 5 a + b). Both parameters negatively affected the  
 431 inter-annual octopus abundances, independently of the region.

432  
 433 Table 1: Results of both non-standardized and standardized Generalized Linear Models for *Octopus*  
 434 *vulgaris* and *Illex coindetii*. The five best models for each case are shown (best model in bold; significant  
 435 variables marked by an asterisk for  $p < 0.05$  and by + for  $p < 0.1$ ). For each model, the covariates, the degrees  
 436 of freedom (df), and the corrected Akaike Information Criterion (AICc) are given. Covariates: Year of  
 437 sampling (factor, year), GSA (factor, gsa\_f), mean chlorophyll a concentration in spring or winter  
 438 (Chl\_Spring, Chl\_Winter, in  $\text{mg}\cdot\text{m}^{-3}$ ) and mean SST in spring or winter (SST\_Spring, SST\_Winter, in  $^{\circ}\text{C}$ ).

439  
 440

Octopus non-standardized model	df	AICc	Octopus standardized model	df	AICc
<b>gsa_f</b>	16	413.81	<b>Chl_Spring * + SST_Winter</b>	4	75.84
gsa_f + Chl_Spring	17	414.23	Chl_Spring	3	77.03
gsa_f + year_f + Chl_Spring + SST_Spring	32	415.02	Chl_Spring + SST_Spring + SSTWinter	5	77.06
gsa_f + year_f + SST_Spring	31	415.31	Chl_Spring + SST_Spring	4	78.09
gsa_f + Chl_Spring + SST_Winter	18	415.93	Chl_Spring + Chl_Winter	4	78.42

Illex non-standardized model	df	AICc	Illex standardized model	df	AICc
<b>gsa_f + SSTSpring* + Chl_Winter<sup>+</sup></b>	18	502.01	<b>Chl_Winter</b>	3	68.80
gsa_f + Chl_Winter	17	504.00	Chl_Winter + SST_Spring	4	69.60
gsa_f	16	504.68	Chl_Winter + SST_Winter	4	70.22
gsa_f + SST_Winter + Chl_Winter	18	505.62	SST_Winter	3	70.32
gsa_f + Chl_Spring + Chl_Winter	18	506.24	SST_Spring	3	70.57

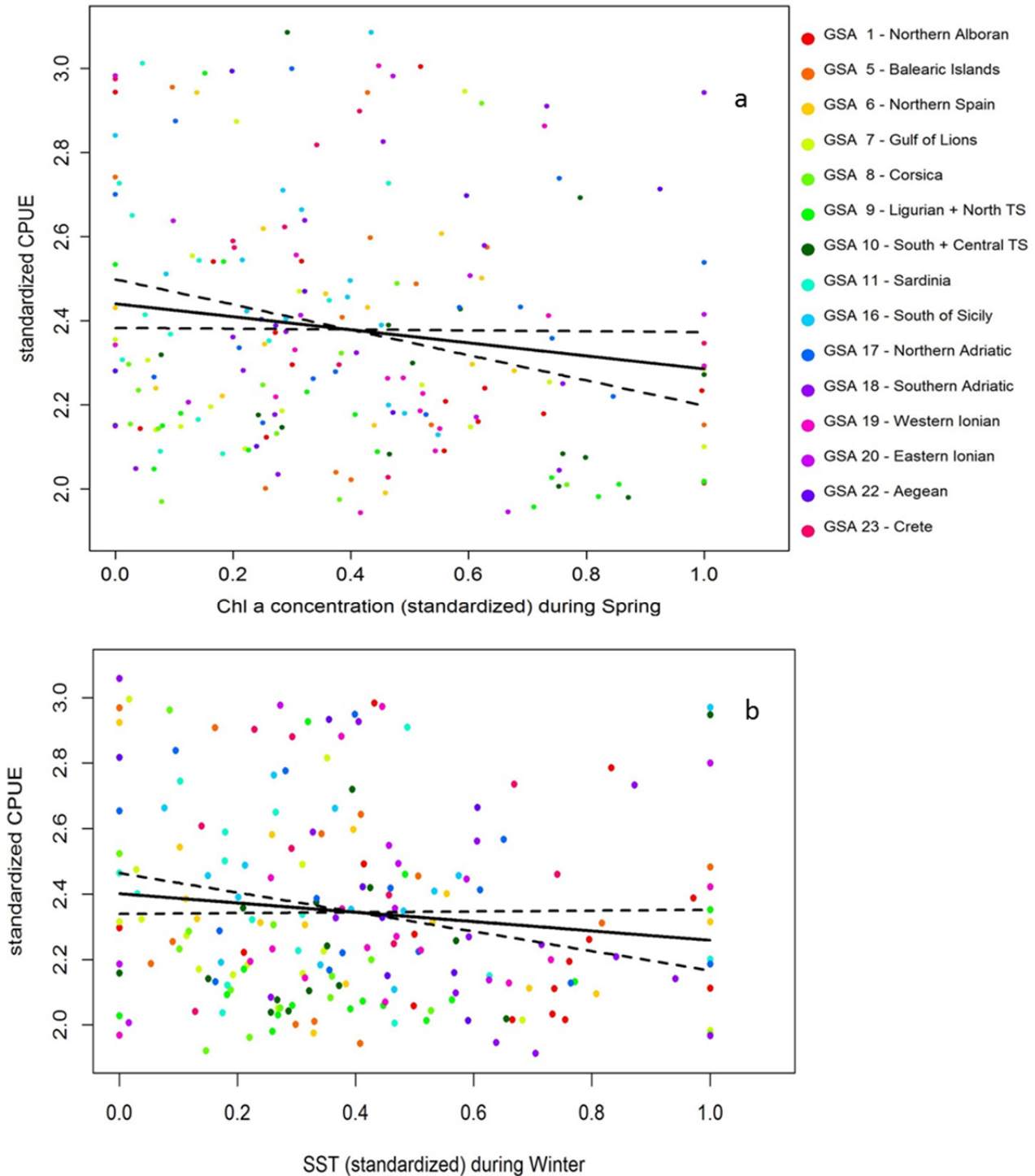
441  
 442 The best fit for squid in the non-standardized model was obtained including  
 443 the GSA as factor, the Chla content of the preceding winter and the SST during spring  
 444 (Table 1). The coloured residuals evidenced that the negative effect of Chla on CPUEs  
 445 was due to a geographic gradient in productivity (Fig 6 a). The SST had a slightly  
 446 positive effect on squid CPUEs (Fig 6 b). The model of standardized CPUEs revealed  
 447 that the Chla of the preceding winter negatively affects inter-annual squid  
 448 abundances, independently of the mean CPUE per area (Fig 6 c).

449

450 In general, both the standardized and non-standardized models gave  
 451 consistent results, being Chla the most important explanatory variable (Table 1).  
 452 However, the season with the best predicting power differed between species: spring

453 for octopus but previous winter for squid. While Chla correlated negatively with  
 454 CPUEs, the correlation between CPUEs and SST varied with species and was negative  
 455 for octopus, but positive for squid. The factor GSA improved the un-standardized  
 456 models only, while the factor year resulted irrelevant.

457

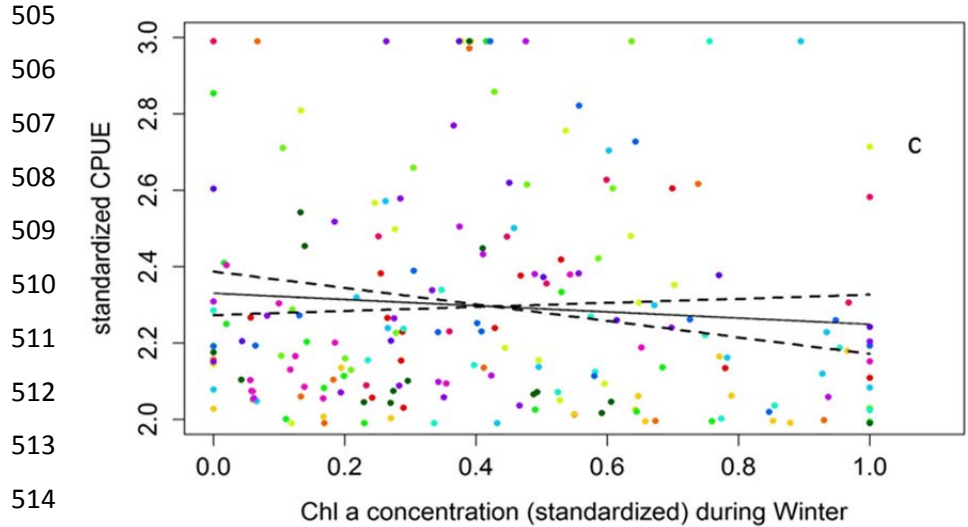
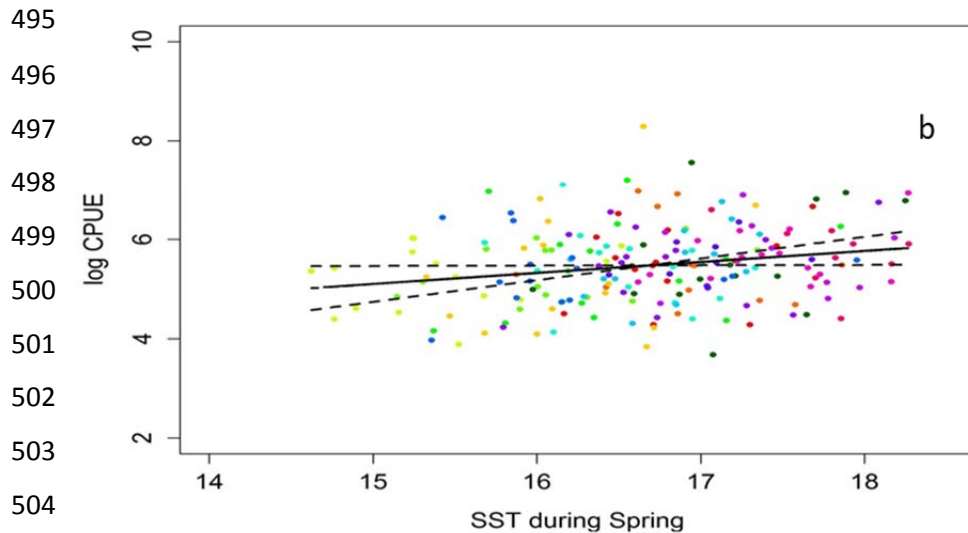
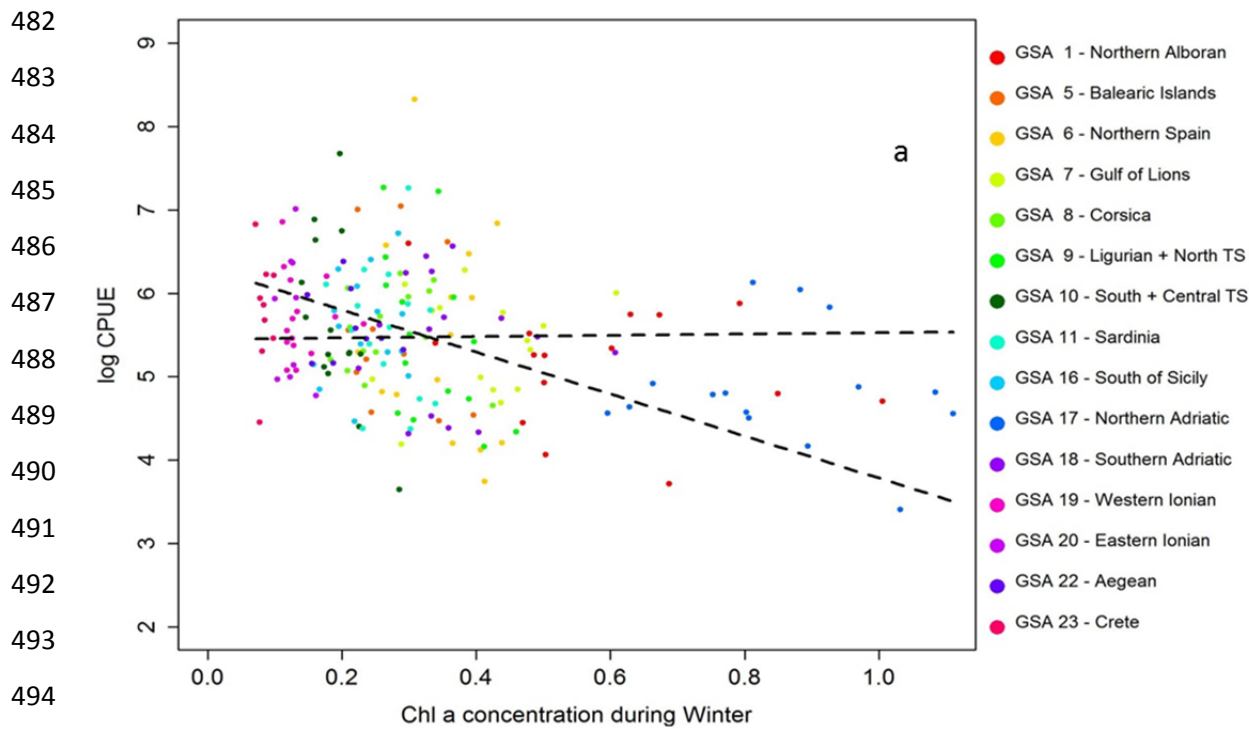


477

478 Figure 5: Model predictions and confidence intervals (dashed lines) of the effect of Chla content (a) and  
 479 SST (b) on *Octopus vulgaris* CPUEs (GLM results of the standardized best model). Partial residuals  
 480 colours are coded by GSA. TS = Tyrrhenian Sea.

481





516 Figure 6: Model predictions and confidence intervals (dashed lines) of the effect of Chla content and  
517 SST on *Illex coindetii* CPUEs (GLM results): unstandardized (a+b) and standardized best model (c).  
518 Partial residuals colours are coded by GSA. TS = Tyrrhenian Sea.

519

#### 520 **4. Discussion**

521

522 The strength and nature of the synchrony among populations affects the  
523 abundances, resilience and recovery of connected populations, with important  
524 implications for their management. In this study, large-scale population dynamics of  
525 two cephalopod species with contrasting life histories were analyzed combining three  
526 different methods. In the decorrelation analysis, higher correlation coefficients mean  
527 higher connectivity and therefore higher synchrony between locations. Similar  
528 dynamics have been revealed within smaller distances for octopus (*Octopus vulgaris*)  
529 than for squid (*Illex coindetii*), related to the fact that the latter is an oceanic species  
530 with higher mobility and a wider home range (Roper et al., 2010). This characteristic  
531 should lead to closer connections even between more distant populations of the  
532 squid. This neritic species also lives in deeper waters in the Mediterranean (Roper et  
533 al., 2010) and therefore most likely experiences a more homogeneous environment  
534 than the coastal, shallow water octopus. Our results are in accordance with a previous  
535 work at smaller spatial scale, where the correlation scale of *I. coindetii* was bigger  
536 than that of *O. vulgaris* both around the Balearic Islands and off the Mediterranean  
537 coast of the Iberian Peninsula (Puerta et al., 2016b).

538 Results of the DFA revealed that populations of both species followed the  
539 modelled common trends in most areas in the western basin and in all (squid) or  
540 nearly all (octopus) areas in the eastern basin. Synchronic population fluctuations can  
541 be due to different mechanisms such as (Gouhier et al., 2010; Liebhold et al., 2004): i)  
542 predator-prey interaction; ii) dispersal of individuals between populations; or iii)  
543 large-scale climatic events or environmental influences affecting various populations  
544 in the same way. The first one is very improbable due to the nature of cephalopods as  
545 rather unselective and adaptable predators (Coll et al., 2013; Rodhouse and  
546 Nigmatullin, 1996) and the different interannual prey dynamics in such a  
547 heterogeneous system as the Mediterranean. Connectivity via dispersal should lead to  
548 more similar abundance time series in neighbouring areas, but our results of the  
549 decorrelation analysis do not support a direct linkage over many hundreds of  
550 kilometres either. Therefore, the rising abundances are more likely due to large-scale  
551 climatic phenomena or synchronous environmental influences.

552 Supporting the last hypothesis, our results revealed a negative influence of  
553 chlorophyll *a* content (Chla) on the abundances of both cephalopod species, a result  
554 that has already been reported on a smaller scale in the Western Mediterranean for *I.*  
555 *coindetii* (Puerta et al., 2015). Those authors argue that small pelagic fishes, which  
556 make up an important part of the Mediterranean food chain (Coll et al., 2006), are  
557 effective competitors for food with early and juvenile stages of squid species like *I.*  
558 *coindetii*. Higher Chla contents will usually foster the survival and growth of small  
559 fish, enhancing food competition and, thus, reduce cephalopod survival and  
560 abundance. The mechanism does not seem to differ among different areas, as the GSA  
561 was only statistically significant in the non-standardized models. However, the crucial  
562 time of the systems productivity varies between the two species, being spring for the  
563 octopus but winter for the squid.

564 Apart from productivity, rising temperatures would cause declining  
565 abundances in octopus (standardized model), but warmer areas do not necessarily  
566 have fewer octopus, as other factors apparently play a more crucial role in  
567 determining abundances / distribution. The mechanism for the negative temperature  
568 effect could be a stronger and more durable stratification of water masses during  
569 summer, causing less nutrient mixing and therefore lower phytoplankton and  
570 zooplankton growth rates. Warmer temperatures induced a reduction of zooplankton  
571 abundance together with a change in community composition and structure in the  
572 study area (Fernández de Puelles et al., 2008), which might negatively affect their  
573 predators. The common octopus preys directly on zooplankton during its paralarval  
574 stage (Roura et al., 2010) but it is also indirectly linked to zooplankton abundance via  
575 the food web, as it mainly consumes small mollusks and crustaceans (Quetglas et al.,  
576 1998; Roura et al., 2010). For squid, the temperature effect is different, as sea surface  
577 temperature (SST) only affects their abundances in the non-standardized model,  
578 where warmer areas show higher abundances. Warmer ecosystems support higher  
579 metabolic rates, higher food intake and growth (Segawa and Nomoto, 2002; Semmens  
580 et al., 2004) and can therefore foster higher squid abundances. Small inter-annual  
581 temperature changes (standardized model), on the other hand, do not affect squid  
582 abundance, probably due to its high mobility and the fact that the adult's habitat  
583 temperature will be little influenced by small changes of surface temperatures.

584 Our study reveals, for the first time, a common increasing trend in the  
585 population abundance of two cephalopod species throughout the entire

586 Mediterranean over the last 20 years, which is in accordance with the worldwide  
587 global trend reported recently (Doubleday et al., 2016). While the GLM results show  
588 the importance of Chla and SST on the abundance of both species, the similar trends  
589 in all the 15 survey areas of very different temperature and productivity regimes  
590 suggests that additional forces, acting at regional scale, are at play. The rising  
591 abundances are likely to be due to the constant, high fishing effort in this sea over  
592 decades (Colloca et al., 2013; Vasilakopoulos et al., 2014), reducing (directly or  
593 indirectly) the abundance of key cephalopod competitors and predators like bony  
594 fish, sharks and whales. Various studies have already observed changes in food webs,  
595 where the missing predators have been replaced by lower-level species (Frank et al.,  
596 2005; Myers and Worm, 2003; Pauly et al., 1998). While depletion of their predators  
597 releases the predation pressure on cephalopods (Caddy and Rodhouse, 1998),  
598 (over)fishing of species with similar habitat and resource needs will release  
599 competition pressure and open new ecological niches. Cephalopods are fast-growing,  
600 opportunistic and adaptable species with short generation times. They are generalist  
601 predators, which enables them to take advantage of changing trophic relations and  
602 rapid colonisation of new habitats (Jackson and O'Dor, 2001; Rodhouse et al., 2014).  
603 Therefore, ecosystem changes due to fishing exploitation could explain some of the  
604 observed rising catches of cephalopod species around the world (Caddy and  
605 Rodhouse, 1998; Vecchione et al., 2009), even though opinions differ on the  
606 importance and implication of other factors such as changed fishing tactics, new  
607 techniques and gears, license issues and environmental influences (Balguerías, 2000).  
608 While the direct impact of the commercial fishery on stocks is evident, amount and  
609 composition of bycatch may play an indirect role by supplying additional food to  
610 scavengers like crustaceans, an important prey of cephalopods (Oro et al., 2013).  
611 Crustaceans often survived being discarded, and the commercial fishery may  
612 therefore indirectly cause an increase in cephalopod abundances in two different  
613 ways (Balguerías, 2000).

614         Climate change, or the synchronic effects of climate and harvesting, might also  
615 explain the proliferation of cephalopods (Doubleday et al., 2016). Apart from the  
616 discussed effect of rising temperatures, it causes further ecosystem changes (e.g.  
617 acidification, distribution shifts, altered productivity regimes, enhanced stratification)  
618 which may lead to competitive advantages for this taxa (Hoving et al., 2013).  
619 However, on a physiological and morphological basis, the effects of climate change

620 will likely be negative at least at the early life stage, leading to a complex response of  
621 still uncertain direction (Pecl and Jackson, 2008). In terms of primary production, the  
622 two Mediterranean basins are likely to be affected by climate change in different ways  
623 (Macias et al., 2015): while the eastern basin will probably experience an increase in  
624 Chla due to vertical density changes caused by a combination of warming and  
625 salinization, the western basin is expected to have decreasing Chla concentrations.  
626 According to our results this would lead to increasing cephalopod abundances in this  
627 basin, while their abundance would decrease in the eastern basin.

628         On smaller spatial scales, also oceanographic features can cause synchronic  
629 population dynamics. Specific local conditions may explain the rather stable octopus  
630 abundance in the Tyrrhenian and Ligurian waters (including all waters around  
631 Corsica), where eddies might retain paralarvae, causing a separate population  
632 dynamic in these waters. In the Ligurian Sea, this mechanism of retention has already  
633 been proposed to be of relevance for hake larvae (Abella et al., 2008). Furthermore,  
634 these waters are characterised by resident Atlantic waters, which are more saline  
635 than Spanish and French coastal and off-shore waters (Reglero et al., 2012). Other  
636 local scale processes leading to separate population dynamics are river run-offs,  
637 which have been suggested to foster the abundances of certain cephalopod species  
638 including *O. vulgaris* and *I. coindetii* (Lloret et al., 2001; Puerta et al., 2016b, 2014).  
639 Our results for octopus agree with these findings, since the two western areas that do  
640 not follow the general trend of rising abundances are not influenced by major river  
641 inputs (Tyrrhenian Sea, Sicily).

642         Up to now, all available studies investigating the influence of environmental  
643 and climatic effects on cephalopod populations from the Mediterranean Sea were  
644 carried out at local scales (Keller et al., 2014; Lloret et al., 2001; Puerta et al., 2016b,  
645 2014; Quetglas et al., 2013). However, analysis at broader spatial scales are needed,  
646 especially in the framework of the regionalisation process envisaged under the new  
647 CFP (Article 18 of the [EU Regulation N° 1380/2013](#)). In this sense, our study, which  
648 encompassed the whole Mediterranean basin, constitutes an important step forward  
649 with clear relevance for fisheries management in the area. Our results and those from  
650 previous works seem to be at odds with the regionalisation objectives. Cephalopods  
651 from the western basin displayed complex population structures and dynamics even  
652 at local scales (Puerta et al., 2014) and were correlated only within a radius of a few  
653 hundred kilometres (Puerta et al., 2016b; this work). Nevertheless, the situation may

654 differ between basins because populations from the eastern basin were more  
655 strongly connected than those from the western basin. In spite of the population  
656 complexities, our work also revealed common trends of rising abundances during the  
657 last 20 years, which agree with the global proliferation of cephalopods (Doubleday et  
658 al., 2016).

659

660 Funding: This work was supported by a PhD grant of the Spanish Institute of Oceanography to S.K.

661 Data collection was performed under the Data Collection Framework (cofunded by the EU and the

662 national governments involved in the study).

## 663 **References**

664 A.A.V.V., 2016. MEDITS-Handbook. Version n. 8. MEDITS Work. Gr. 177 pp.

665 Abella, A., Fiorentino, F., Mannini, A., Orsi Relini, L., 2008. Exploring relationships  
666 between recruitment of European hake (*Merluccius merluccius* L. 1758) and  
667 environmental factors in the Ligurian Sea and the Strait of Sicily (Central  
668 Mediterranean). J. Mar. Syst. 71, 279–293.

669 Balguerías, E., 2000. The origin of the Saharan Bank cephalopod fishery. ICES J. Mar.  
670 Sci. 57, 15–23.

671 Batchelder, H.P., Mackas, D.L., O'Brien, T.D., 2012. Spatial–temporal scales of  
672 synchrony in marine zooplankton biomass and abundance patterns: A world-  
673 wide comparison. Prog. Oceanogr. 97–100, 15–30.

674 Bertrand, J.A., Gil de Sola, L., Papaconstantinou, C., Relini, G., Souplet, A., 2002. The  
675 general specifications of the MEDITS surveys. Sci. Mar. 66, 9–17.

676 Burnham, K.P., Anderson, D.R., 2004. Multimodel Inference: Understanding AIC and  
677 BIC in Model Selection. Sociol. Methods Res. 33, 261–304.

678 Caddy, J.F., Rodhouse, P.G., 1998. Cephalopod and groundfish landings: evidence for  
679 ecological change in global fisheries? Rev. Fish Biol. Fish. 8, 431–444.

680 Chen, C., 2010. Abundance trends of two neon flying squid (*Ommastrephes bartramii*)  
681 stocks in the North Pacific. ICES J. Mar. Sci. 1336–1345.

682 Chen, C.-S., Lee, B.-W., 2013. Trends in trawl-targeted species landings off northern  
683 Taiwan and effects of fishing and environmental factors. Fish. Sci. 79, 163–176.

684 Chen, X., Chen, Y., Tian, S., Liu, B., Qian, W., 2008. An assessment of the west winter-  
685 spring cohort of neon flying squid (*Ommastrephes bartramii*) in the Northwest  
686 Pacific Ocean. Fish. Res. 92, 221–230.

687 Coll, M., Navarro, J., Olson, R.J., Christensen, V., 2013. Assessing the trophic position  
688 and ecological role of squids in marine ecosystems by means of food-web  
689 models. Deep Sea Res. Part II Top. Stud. Oceanogr. 95, 21–36.

690 Coll, M., Palomera, I., Tudela, S., Sardà, F., 2006. Trophic flows, ecosystem structure  
691 and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. J.  
692 Mar. Syst. 59, 63–96.

693 Colloca, F., Cardinale, M., Maynou, F., Giannoulaki, M., Scarcella, G., Jenko, K., Bellido,  
694 J.M., Fiorentino, F., 2013. Rebuilding Mediterranean fisheries: a new paradigm for

- 695 ecological sustainability. *Fish Fish.* 14, 89–109.
- 696 Colloca, F., Garofalo, G., Bitetto, I., Facchini, M.T., Grati, F., Martiradonna, A.,  
697 Mastrantonio, G., Nikolioudakis, N., Ordinas, F., Scarcella, G., Tserpes, G., Tugores,  
698 M.P., Valavanis, V., Carlucci, R., Fiorentino, F., Follesa, M.C., Iglesias, M., Knittweis,  
699 L., Lefkaditou, E., Lembo, G., Manfredi, C., Massutí, E., Pace, M.L., Papadopoulou,  
700 N., Sartor, P., Smith, C.J., Spedicato, M.T., 2015. The seascape of demersal fish  
701 nursery areas in the North Mediterranean Sea, a first step towards the  
702 implementation of spatial planning for trawl fisheries. *PLoS One* 10, e0119590.
- 703 D’Ortenzio, F., Ribera d’Alcalà, M., 2009. On the trophic regimes of the Mediterranean  
704 Sea : a satellite analysis. *Biogeosciences* 6, 139–148.
- 705 Descamps, S., Strøm, H., Steen, H., 2013. Decline of an arctic top predator: synchrony  
706 in colony size fluctuations, risk of extinction and the subpolar gyre. *Oecologia*  
707 173, 1271–1282.
- 708 Doubleday, Z.A., Thomas, A.A., Arkhipkin, A., Pierce, G.J., Semmens, J., Steer, M.,  
709 Leporati, S.C., Lourenço, S., Quetglas, A., Sauer, W., Bronwyn, M., 2016. Global  
710 proliferation of cephalopods. *Curr. Biol. Mag.* 26, 1–3.
- 711 Doyle, R.W., Poore, R. V., 1974. Nutrient competition and division synchrony in  
712 phytoplankton. *J. Exp. Mar. Bio. Ecol.* 14, 201–210.
- 713 Druon, J., Fromentin, J., Aulanier, F., Heikkonen, J., 2011. Potential feeding and  
714 spawning habitats of Atlantic bluefin tuna in the Mediterranean Sea. *Mar. Ecol.*  
715 *Prog. Ser.* 439, 223–240.
- 716 Druon, J., Panigada, S., David, L., Gannier, A., Mayol, P., Arcangeli, A., Cañadas, A., Laran,  
717 S., Di Méglia, N., Gauffier, P., 2012. Potential feeding habitat of fin whales in the  
718 western Mediterranean Sea: an environmental niche model. *Mar. Ecol. Prog. Ser.*  
719 464, 289–306.
- 720 Druon, J.-N., Fiorentino, F., Murenu, M., Knittweis, L., Colloca, F., Osio, C., Mérigot, B.,  
721 Garofalo, G., Mannini, A., Jadaud, A., Sbrana, M., Scarcella, G., Tserpes, G.,  
722 Peristeraki, P., Carlucci, R., Heikkonen, J., 2015. Modelling of European hake  
723 nurseries in the Mediterranean Sea: An ecological niche approach. *Prog.*  
724 *Oceanogr.* 130, 188–204.
- 725 Druon, J.-N., Fromentin, J.-M., Hanke, A.R., Arrizabalaga, H., Damalas, D., Tičina, V.,  
726 Quílez-Badia, G., Ramirez, K., Arregui, I., Tserpes, G., Reglero, P., Deflorio, M.,  
727 Oray, I., Saadet Karakulak, F., Megalofonou, P., Ceyhan, T., Grubišić, L., MacKenzie,  
728 B.R., Lamkin, J., Afonso, P., Addis, P., 2016. Habitat suitability of the Atlantic  
729 bluefin tuna by size class: An ecological niche approach. *Prog. Oceanogr.* 142, 30–  
730 46.
- 731 Erzini, K., 2005. Trends in NE Atlantic landings (southern Portugal): identifying the  
732 relative importance of fisheries and environmental variables. *Fish. Oceanogr.* 14,  
733 195–209.
- 734 Fernández de Puelles, M.L., López-Urrutia, Á., Morillas, A., Molinero, J.C., 2008.  
735 Seasonal variability of copepod abundance in the Balearic region (Western  
736 Mediterranean) as an indicator of basin scale hydrological changes.  
737 *Hydrobiologia* 617, 3–16.
- 738 Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly  
739 cod-dominated ecosystem. *Science* 308, 1621–3.
- 740 Gouhier, T.C., Guichard, F., Menge, B. a, 2010. Ecological processes can synchronize  
741 marine population dynamics over continental scales. *Proc. Natl. Acad. Sci. U. S. A.*

- 742 107, 8281–6.
- 743 Hidalgo, M., Rueda, L., Molinero, J.C., Guijarro, B., Massutí, E., 2015. Spatial and  
744 temporal variation of seasonal synchrony in the deep-sea shrimp *Aristeus*  
745 *antennatus* in the Western Mediterranean. *J. Mar. Syst.* 148, 131–141.
- 746 Holmes, E.E., Ward, E.J., Wills, K., 2012. MARSS: Multivariate Autoregressive State-  
747 space Models for Analyzing Time-series Data. *R J.* 4, 11–19.
- 748 Hoving, H.-J.T., Gilly, W.F., Markaida, U., Benoit-Bird, K.J., -Brown, Z.W., Daniel, P.,  
749 Field, J.C., Parassenti, L., Liu, B., Campos, B., 2013. Extreme plasticity in life-  
750 history strategy allows a migratory predator (jumbo squid) to cope with a  
751 changing climate. *Glob. Chang. Biol.* 19, 2089–103.
- 752 Jackson, G.D., O’Dor, R.K., 2001. Time, space and the ecophysiology of squid growth,  
753 life in the fast lane. *Vie Milieu* 51, 205–215.
- 754 Keller, S., Valls, M., Hidalgo, M., Quetglas, A., 2014. Influence of environmental  
755 parameters on the life-history and population dynamics of cuttlefish *Sepia*  
756 *officinalis* in the western Mediterranean. *Estuar. Coast. Shelf Sci.* 145, 31–40.
- 757 Kelly, J., Frank, K., Leggett, W., 2009. Degraded recruitment synchrony in Northwest  
758 Atlantic cod stocks. *Mar. Ecol. Prog. Ser.* 393, 131–146.
- 759 Koeller, P., Fuentes-Yaco, C., Platt, T., Sathyendranath, S., Richards, a, Ouellet, P., Orr,  
760 D., Skúladóttir, U., Wieland, K., Savard, L., Aschan, M., 2009. Basin-scale coherence  
761 in phenology of shrimps and phytoplankton in the North Atlantic Ocean. *Science*  
762 324, 791–3.
- 763 Lascaratos, A., Roether, W., Nittis, K., Klein, B., 1999. Recent changes in deep water  
764 formation and spreading in the eastern Mediterranean Sea: a review. *Prog.*  
765 *Oceanogr.* 44, 5–36.
- 766 Liebhold, A., Koenig, W.D., Bjørnstad, O.N., 2004. Spatial Synchrony in Population  
767 Dynamics. *Annu. Rev. Ecol. Evol. Syst.* 35, 467–490.
- 768 Lloret, J., Lleonart, J., Sole, I., Fromentin, J.M., 2001. Fluctuations of landings and  
769 environmental conditions in the north-western Mediterranean Sea. *Fish.*  
770 *Oceanogr.* 10, 33–50.
- 771 Macias, D.M., Garcia-Gorriz, E., Stips, A., 2015. Productivity changes in the  
772 Mediterranean Sea for the twenty-first century in response to changes in the  
773 regional atmospheric forcing. *Front. Mar. Sci.* 2, 1–13.
- 774 Millot, C., 2005. Circulation in the Mediterranean Sea: evidences, debates and  
775 unanswered questions. *Sci. Mar.* 69, 5–21.
- 776 Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish  
777 communities. *Lett. to Nat.* 423, 280–283.
- 778 Navarro, J., Cardador, L., Fernández, Á.M., Bellido, J.M., Coll, M., 2016. Differences in  
779 the relative roles of environment, prey availability and human activity in the  
780 spatial distribution of two marine mesopredators living in highly exploited  
781 ecosystems. *J. Biogeogr.* 43, 440–450.
- 782 Nieblas, A.-E., Drushka, K., Reygondeau, G., Rossi, V., Demarcq, H., Dubroca, L.,  
783 Bonhommeau, S., 2014. Defining Mediterranean and Black Sea biogeochemical  
784 subprovinces and synthetic ocean indicators using mesoscale oceanographic  
785 features. *PLoS One* 9, 1–13.
- 786 Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., Martínez-Abraín, A., 2013. Ecological  
787 and evolutionary implications of food subsidies from humans. *Ecol. Lett.* 16,



- 788 1501–14.
- 789 Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F.J., 1998. Fishing Down  
790 Marine Food Webs. *Science* (80-. ). 279, 860–863.
- 791 Pecl, G.T., Jackson, G.D., 2008. The potential impacts of climate change on inshore  
792 squid: biology, ecology and fisheries. *Rev. Fish Biol. Fish.* 18, 373–385.
- 793 Pierce, G.J., Allcock, L., Bruno, I., Jereb, P., Lefkaditou, E., Malham, S., Moreno, A.,  
794 Pereira, J., Piatkowski, U., Rasero, M., Sánchez, P., Santos, M.B., Santurtún, M.,  
795 Seixas, S., Sobrino, I., Villanueva, R., 2010. Cephalopod biology and fisheries in  
796 Europe. *ICES Coop. Res. Rep.* 303, 175.
- 797 Pierce, G.J., Valavanis, V.D., Guerra, A., Jereb, P., Orsi-Relini, L., Bellido, J.M., Katara, I.,  
798 Piatkowski, U., Pereira, J., Balguerías, E., Sobrino, I., Lefkaditou, E., Wang, J.,  
799 Santurtun, M., Boyle, P.R., Hastie, L.C., MacLeod, C.D., Smith, J.M., Viana, M.,  
800 González, A.F., Zuur, A.F., 2008. A review of cephalopod–environment  
801 interactions in European Seas. *Hydrobiologia* 612, 49–70.
- 802 Puerta, P., Hidalgo, M., González, M., Esteban, A., Quetglas, A., 2014. Role of hydro-  
803 climatic and demographic processes on the spatio-temporal distribution of  
804 cephalopods in the western Mediterranean. *Mar. Ecol. Prog. Ser.* 514, 105–118.
- 805 Puerta, P., Hunsicker, M.E., Hidalgo, M., Reglero, P., Ciannelli, L., Quetglas, A., Esteban,  
806 A., 2016a. Community–environment interactions explain octopus-catshark  
807 spatial overlap. *ICES J. Mar. Sci.* 73, 1901–1911.
- 808 Puerta, P., Hunsicker, M.E., Quetglas, A., Álvarez-Berastegui, D., Esteban, A., González,  
809 M., Hidalgo, M., 2015. Spatially Explicit Modeling Reveals Cephalopod  
810 Distributions Match Contrasting Trophic Pathways in the Western  
811 Mediterranean Sea. *PLoS One* 10, e0133439.
- 812 Puerta, P., Quetglas, A., Hidalgo, M., 2016b. Seasonal variability of cephalopod  
813 populations: a spatio-temporal approach in the Western Mediterranean Sea. *Fish.*  
814 *Oceanogr.* 25, 373–389.
- 815 Quetglas, A., Alemany, F., Carbonell, A., Merella, P., Sanchez, P., 1998. Biology and  
816 fishery of *Octopus vulgaris* Cuvier, 1797, caught by trawlers in Mallorca (Balearic  
817 Sea, Western Mediterranean). *Fish. Res.* 36, 237–249.
- 818 Quetglas, A., Carbonell, A., Sanchez, P., 2000. Demersal continental shelf and upper  
819 slope cephalopod assemblages from the balearic sea (north-western  
820 Mediterranean). *Biological aspects of some deep-sea species. Estuar. Coast. Shelf*  
821 *Sci.* 50, 739–749.
- 822 Quetglas, A., Ordines, F., Hidalgo, M., Monserrat, S., Ruiz, S., Amores, A., Moranta, J.,  
823 Massuti, E., 2013. Synchronous combined effects of fishing and climate within a  
824 demersal community. *Ices J. Mar. Sci.* 70, 319–328.
- 825 Quetglas, A., Ordines, F., Valls, M., 2011. What drives seasonal fluctuations of body  
826 condition in a semelparous income breeder octopus? *Acta Oecologica* 37, 476–  
827 483.
- 828 Reglero, P., Ciannelli, L., Alvarez-Berastegui, D., Balbín, R., López-Jurado, J., Alemany,  
829 F., 2012. Geographically and environmentally driven spawning distributions of  
830 tuna species in the western Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 463, 273–  
831 284.
- 832 Rodhouse, P.G., Nigmatullin, C.M., 1996. Role as consumers. *The Role of Cephalopods*  
833 *in the World’s Oceans. Philos. Trans. R. Soc. London. Ser. B.* 351, 1003–1022.

- 834 Rodhouse, P.G.K., Pierce, G.J., Nichols, O.C., Sauer, W.H.H., Arkhipkin, A.I.,  
835 Laptikhovskiy, V. V., Lipiński, M.R., Ramos, J.E., Gras, M., Kidokoro, H., Sadayasu,  
836 K., Pereira, J., Lefkaditou, E., Pita, C., Gasalla, M., Haimovici, M., Sakai, M., Downey,  
837 N., 2014. Advances in Cephalopod Science: Biology, Ecology, Cultivation and  
838 Fisheries, in: Vidal, E. (Ed.), Advances in Marine Biology, Advances in Marine  
839 Biology. Academic Press, pp. 99–233.
- 840 Roper, C.F.E., Nigmatullin, C., Jereb, P., 2010. Family Ommastrephidae, in: Jereb, P.,  
841 Roper, C.F.E. (Eds.), Cephalopods of the World. An Annotated and Illustrated  
842 Catalogue of Species Known to Date. Volume 2. Myopsid and Oegopsid Squids.  
843 FAO Species Catalogue for Fishery Purposes. No. 4, Rome, p. 269–347.
- 844 Rossi, V., Ser-giacomi, E., López, C., Hernández-garcía, E., 2014. Hydrodynamic  
845 provinces and oceanic connectivity from a transport network help designing  
846 marine reserves. Geophys. Res. Lett. 2883–2891.
- 847 Roura, Á., González, Á.F., Pascual, S., Guerra, Á., 2010. A molecular approach to  
848 identifying the prey of cephalopod paralarvae. ICES J. Mar. Sci. 67, 1408–1412.
- 849 Sartor, P., Belcari, P., Carboell, A., Gonzalez, M., Quetglas, A., Sánchez, P., 1998. The  
850 importance of cephalopods to trawl fisheries in the western Mediterranean.  
851 South African J. Mar. Sci. 20, 67–72.
- 852 Saville, A., 1977. Survey methods of appraising fishery resources. Food Agric. Organ.  
853 United Nations 76 pp.
- 854 Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L. A,  
855 Webster, M.S., 2010. Population diversity and the portfolio effect in an exploited  
856 species. Nature 465, 609–12.
- 857 Segawa, S., Nomoto, A., 2002. Laboratory growth, feeding, oxygen consumption and  
858 ammonia excretion of *Octopus ocellatus*. Bull. Mar. Sci. 71, 801–813.
- 859 Semmens, J.M., Pecl, G.T., Villanueva, R., Jouffre, D., Sobrino, I., Wood, J.B., Rigby, P.R.,  
860 2004. Understanding octopus growth: patterns, variability and physiology. Mar.  
861 Freshw. Res. 55, 367–377.
- 862 Souplet, A., 1996. Définition des estimateurs, in: Bertrand, J.A. (Ed.), Campagne  
863 Internationale de Chalutage Démersal En Méditerranée (Medit 95). p. Etude  
864 94/047 IFREMER/CE, 94/011 IEO/CE, 94/057 SIB.
- 865 Vasilakopoulos, P., Maravelias, C.D., Tserpes, G., 2014. The alarming decline of  
866 Mediterranean fish stocks. Curr. Biol. 24, 1643–8.
- 867 Vecchione, M., Allcock, L., Piatkowski, U., Jorgensen, E., Barratt, I., 2009. Persistent  
868 Elevated Abundance of Octopods in an Overfished Antarctic Area. Smithson.  
869 Poles Contrib. to Int. Polar Year Sci. 197–203.
- 870 Woillez, M., Poulard, J., Rivoirard, J., Petitgas, P., Bez, N., 2007. Indices for capturing  
871 spatial patterns and their evolution in time, with application to European hake  
872 (*Merluccius merluccius*) in the Bay of Biscay. ICES J. Mar. Sci. 64, 537–550.
- 873 Zuur, A.F., Pierce, G.J., 2004. Common trends in northeast Atlantic squid time series. J.  
874 Sea Res. 52, 57–72.
- 875 Zuur, A.F., Tuck, I.D., Bailey, N., 2003. Dynamic factor analysis to estimate common  
876 trends in fisheries time series. Fish. Res. 55, 542–552.
- 877
- 878

880 Table A1: DFA results for *Octopus vulgaris* and *Illex coindetii* from the eastern and the western  
 881 Mediterranean basin. Shown are the twelve best models for each case (best model in bold). For each  
 882 model, the model number, the error matrix structure (R), the number of common trends (m), and the  
 883 corrected AIC (AICc) are given.

Octopus eastern Mediterranean					
MODEL	R	m	logLik	K	AICc
<b>1</b>	<b>diagonal and equal</b>	<b>1</b>	<b>-125.41</b>	<b>7</b>	<b>266.099</b>
7	equalvarcov	1	-126.78	8	271.225
4	diagonal and unequal	1	-123.83	12	275.458
2	diagonal and equal	2	-125.62	12	279.05
8	equalvarcov	2	-125.53	13	281.556
5	diagonal and unequal	2	-123.81	17	289.564
3	diagonal and equal	3	-125.63	16	290.243
9	equalvarcov	3	-125.55	17	293.05
10	unconstrained	1	-112.5	27	301.564
6	diagonal and unequal	3	-123.81	21	302.274
11	unconstrained	2	-113.54	32	325.139
12	unconstrained	3	-114.24	36	346.404

Octopus western Mediterranean					
MODEL	R	m	logLik	K	AICc
<b>1</b>	<b>diagonal and equal</b>	<b>1</b>	<b>-227.48</b>	<b>10</b>	<b>476.359</b>
7	equalvarcov	1	-226.40	11	476.481
4	diagonal and unequal	1	-218.10	18	476.765
8	equalvarcov	2	-219.39	19	481.871
2	diagonal and equal	2	-220.73	18	482.011
5	diagonal and unequal	2	-211.48	26	484.845
9	equalvarcov	3	-214.39	26	490.662
3	diagonal and equal	3	-217.19	25	493.469
6	diagonal and unequal	3	-206.90	33	496.416
10	unconstrained	1	-191.86	54	543.827
11	unconstrained	2	-183.29	62	564.282
12	unconstrained	3	-181.69	69	598.959

Illex eastern Mediterranean					
MODEL	R	m	logLik	K	AICc
<b>1</b>	<b>diagonal and equal</b>	<b>1</b>	<b>-127.16</b>	<b>7</b>	<b>269.569</b>
7	equalvarcov	1	-126.14	8	269.922
4	diagonal and unequal	1	-123.81	12	275.338
2	diagonal and equal	2	-125.41	12	278.541

8	equalvarcov	2	-124.7	13	279.785
5	diagonal and unequal	2	-120.02	17	281.789
3	diagonal and equal	3	-125.95	16	290.69
9	equalvarcov	3	-124.99	17	291.737
10	unconstrained	1	-109.05	27	294.022
6	diagonal and unequal	3	-120.8	21	295.921
11	unconstrained	2	-108.82	32	314.638
12	unconstrained	3	-108.39	36	333.179

Illex western Mediterranean					
MODEL	R	m	logLik	K	AICc
<b>1</b>	<b>diagonal and equal</b>	<b>1</b>	<b>-221.65</b>	<b>10</b>	<b>464.702</b>
7	equalvarcov	1	-221.65	11	466.989
4	diagonal and unequal	1	-217.23	18	475.06
2	diagonal and equal	2	-219.36	18	479.318
8	equalvarcov	2	-219.34	19	481.808
5	diagonal and unequal	2	-215.62	26	493.197
3	diagonal and equal	3	-219.36	25	497.882
9	equalvarcov	3	-219.34	26	500.63
6	diagonal and unequal	3	-215.62	33	513.985
10	unconstrained	1	-201.96	54	564.487
11	unconstrained	2	-199.79	62	597.983
12	unconstrained	3	-198.04	69	632.654

884

885

886

887

888

889

890

891

892

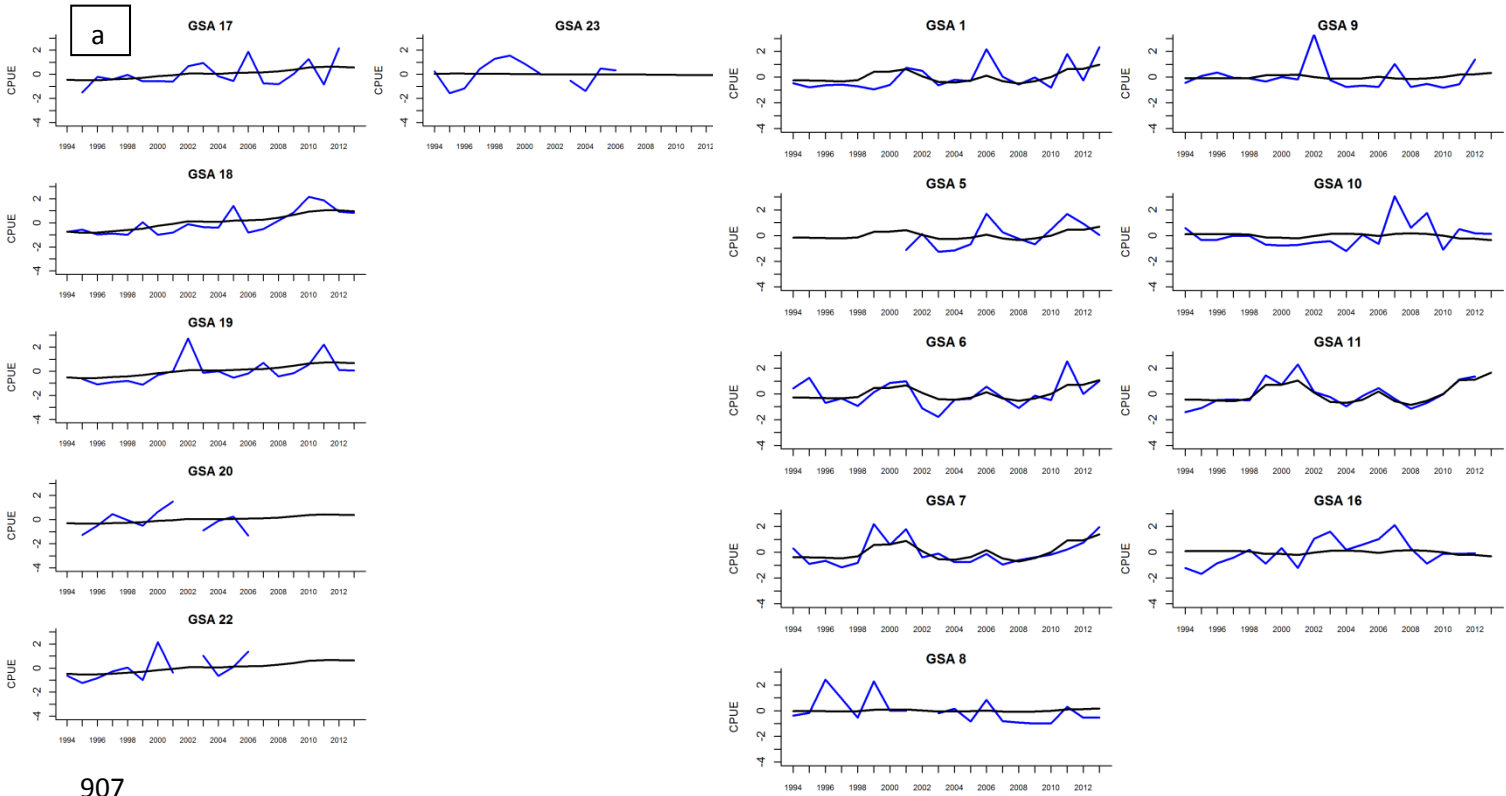
893

894

895

896

*Octopus vulgaris*



907

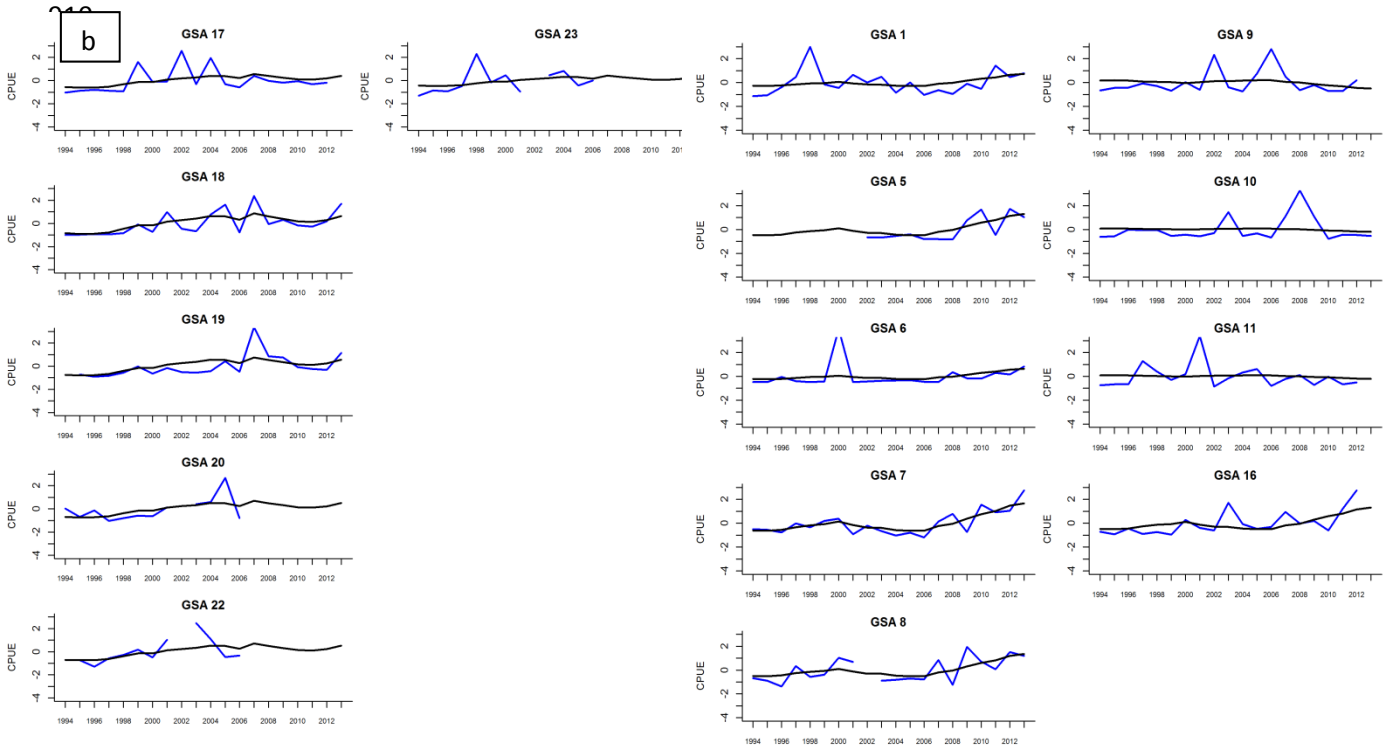
Eastern basin

Western basin

908

909

*Illex coindetii*



920 Eastern basin

Western basin

921 Figure A1: Model fits (blue lines) of the best models obtained by DFA on standardized CPUE time series  
922 for a) *Octopus vulgaris* and b) *Illex coindetii*; GSAs are separated into eastern (left) and western (right)  
923 basin.

924

925

- Synchronies in population dynamics of Mediterranean cephalopod species are revealed
- A general increasing trend in cephalopod abundances is found
- Temperature and productivity affect population dynamics on a regional scale
- Populations are more closely connected in the Eastern than in the Western basin
- Results are relevant for current European management regulations