
Shifts between gelatinous and crustacean plankton in a coastal upwelling region

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Abstract:

Variability in the dominance of copepods vs. gelatinous plankton was analysed using monthly time-series covering the last 55 years and related to changes in climatic, oceanographic, and fishery conditions in the upwelling region of Galicia (NW Spain). Seasonality was generally the main component of variability in all groups, both along the coast and in the nearby ocean, but no common long-term trend was found. Coastal copepods increased since the early 1990s, and gelatinous plankton increased in the ocean during the 1980s. Different trends were found for gelatinous plankton in two coastal sites, characterized by increases in either medusae or tunicates. In all series, multiyear periods of relative dominance of gelatinous vs. copepod plankton were evident. In general, copepod periods were observed in positive phases of the main modes of regional climatic variability. Conversely, gelatinous periods occurred during negative climatic phases. However, the low correlations between gelatinous plankton and climatic, oceanographic, or fishery variables suggest that local factors play a major role in their proliferations.

Keywords: climate ; Copepods ; Jellyfish ; planktivorous fish ; time-series ; tunicates ; upwelling

1. Introduction

Gelatinous plankton have always been intriguing organisms: first, because of their low organic matter content relative to their volume, and secondly, because of their noticeable, plague-like outbursts, often with negative effects on fish and humans (Purcell *et al.*, 2001; Parsons and Lalli, 2002; Boero *et al.*, 2008; Pitt and Purcell, 2009; Richardson *et al.*, 2009). In contrast, most other organisms characterizing present-day zooplankton

47 have a high ratio of organic matter to volume and are ascribed to the zoological subclass
48 Copepoda (Parsons and Lalli, 2002). Two main types of gelatinous plankton can be
49 found in almost all marine waters. The first group is formed by jellyfish, including
50 Hydrozoan and Scyphozoan medusae, Ctenophora, and Syphonophora. These
51 organisms are predators of other planktonic organisms (notably copepods) and even
52 fish, and their rapid proliferation relies on a complex cycle involving benthic stages
53 (polyps) and asexual reproduction. The second group is represented by tunicates,
54 including appendicularia, pyrosomes, doliolids, and salps. Pelagic tunicates filter-feed
55 on phytoplankton and bacteria, and, thus, are primary consumers in the foodweb. They
56 do not have a benthic stage as most jellyfish, but also have relatively complex
57 reproductive cycles with sexual and asexual phases. Tunicates form characteristic
58 colonies that can reach up to several metres in length, and while they do not have direct
59 harmful effects, like jellyfish, their large proliferations may significantly impact the
60 biochemical fluxes through the pelagic foodweb. For instance, they reduce the flow of
61 organic matter from primary producers to upper trophic levels, and their gelatinous
62 remains are degraded by microbes in the water column rather than exported to
63 sediments (Lebrato and Jones, 2011).

64 Both medusae and tunicates have adaptations to feed in environments where
65 food is scarce or, in the case of tunicates, of very small size with minimal energy
66 requirements. Tunicates have developed body forms and colony behaviour to overcome
67 their inability to perform large metabolic adjustments or migrations in the absence of
68 strong currents (Acuña, 2001). Medusae also have adopted forms and shapes facilitating
69 encounters with prey using minimal energy consumption (Acuña *et al.*, 2011). Large
70 proliferations of gelatinous plankton are always a noticeable event and lead to the
71 hypothesis of an increasing number of such proliferations as a result of climate and
72 global changes (Mills, 1995; Parsons and Lalli, 2002; Boero *et al.*, 2008; Richardson *et*
73 *al.*, 2009). Most of these studies focused on jellyfish, and their proliferations were
74 attributed to a variety of factors acting either separately or in combination (Richardson
75 *et al.*, 2009). Among the most cited were climatic conditions (Molinero *et al.*, 2005,
76 2008; Lavaniegos and Ohman, 2007; Lynam *et al.*, 2011), but also eutrophication
77 (Purcell *et al.*, 2001), invasion of species (Graham and Bayha, 2007), habitat
78 modifications (Pagés, 2001; Lo *et al.*, 2008), and overfishing (Bakun and Weeks, 2006;
79 Lynam *et al.*, 2011). However, recent reviews challenged the hypothesis of an overall
80 increase in gelatinous plankton related to global change and point out the importance of
81 trophic interactions to explain their proliferations (Richardson *et al.*, 2009; Lilley *et al.*,
82 2011; Condon *et al.*, 2012). One of the main limitations when addressing variability in
83 gelatinous plankton is the lack of long time-series of observations of the abundance,
84 biomass, and diversity of these organisms in different ecosystems. In contrast, there are
85 long series of other planktonic organisms, such as copepods (e.g. Mackas and
86 Beaugrand, 2010).

87 The objective of this study is to investigate the shifts between periods of relative
88 increase in copepods or gelatinous organisms in monthly series of plankton in the
89 upwelling influenced region of NW Spain over the last 55 years. Medusae and tunicates
90 were analysed both jointly and separately to ascertain if there are common or different
91 patterns of change related to their body adaptations. The plankton series were correlated
92 with climatic, oceanographic, and fishery series to determine the factors favouring
93 gelatinous organisms in this region.

94

95 **Methods**

96 **Zooplankton**

97 Monthly series of zooplankton abundance were obtained from two sources. Surface
98 waters (ca. 7 m depth) from the oceanic region surrounding the NW Iberian Peninsula
99 were sampled via Continuous Plankton Recorder (CPR, <http://www.sahfos.ac.uk/>). In
100 this study, pooled results for the standard zone F4 between 1958 and 2006 were used
101 (Figure 1). Abundance data for CPR series correspond to mean abundance values for
102 species recorded in the whole sample (eye count procedure in Richardson *et al.*, 2006)
103 and scaled to numbers m^{-3} by taking into account that individual CPR samples
104 correspond to approximately 3 m^3 . For gelatinous plankton, these series included the
105 categories “coelenterata tissue” (recorded as presence/absence) and Siphonophora to
106 form a medusae group for analysis. Data for CPR medusae were transformed to
107 frequency data when constructing monthly or annual series (Gibbons and Richardson,
108 2009). The CPR series were discontinued between 1987 and 1997 in the F4 zone.
109 Coastal zooplankton was sampled by project RADIALES
110 (<http://www.seriestemporales-ieo.com>) at Vigo and A Coruña between 1994 and 2006
111 (Figure 1). In this case, samples were collected using 50-cm diameter Juday–Bogorov
112 (A Coruña) or 40-cm diameter bongo plankton nets (Vigo) equipped with 200- μm mesh
113 size. Tows were double oblique from surface to near bottom (90 and 70 m in Vigo and
114 A Coruña, respectively). Samples were preserved in 2–4% sodium borate-buffered
115 formaldehyde. Abundance values were reported as number of individuals m^{-3} . For the
116 purpose of this study, the original coastal series were categorized in copepods (as
117 representative of crustacean zooplankton) and gelatinous plankton (medusae and
118 tunicates). Medusae included Hydrozoans and Scyphozoa, and tunicates included salps,
119 pyrosomes, doliolids, and appendicularia.

120 Because the sampling methods for any of the series were specifically designed
121 for collecting gelatinous plankton, the present data can only be considered as indicative
122 of periods of high abundance, when the probability of collecting these organisms is
123 high. Besides, the data from both the CPR and coastal series do not allow for a
124 computation of biomass, since individual species or size categories were not recorded.
125 Phases of relative increase in copepods or gelatinous plankton were revealed by
126 constructing a Relative Indicator Series index (RIS) as the difference between
127 detrended, normalized, and standardized abundance values of both groups, a procedure
128 initially conceived to describe alternating fish populations (Lluch-Cota *et al.*, 1997).

129

130 **Environmental variables**

131 Climatic forcing was represented by the North Atlantic Oscillation (NAO) distributed
132 by the NOAA Climate Prediction Center (<http://www.cpc.ncep.noaa.gov/>), obtained by
133 principal component analysis of standardized monthly means of geopotential height at
134 500 hPa in the region 20°N–90°N, which were computed from the reanalysis of series
135 of observations since January 1950 using an atmospheric model (Barnston and Livezey,
136 1987). Because of its known seasonal influence on European climate (Hurrell and
137 Dickson, 2004), NAO series were averaged for winter (December–March) and summer
138 (June–August) periods.

139 Large-scale variability in ocean temperature was represented by the Atlantic
140 Multidecadal Oscillation (AMO, Enfield *et al.*, 2001), a detrended series of anomalies
141 of mean surface temperature, obtained from the NOAA Earth System Research
142 Laboratory (ESRL, <http://www.esrl.noaa.gov/psd/data/timeseries/AMO/>).

143 Regional oceanographic settings were represented by sea surface temperature (SST)
 144 values and by the Ekman transport expressed as an upwelling index (UI). SST was
 145 obtained from data averaged in a 1° x 1° cell centred at 42°N 10°W from the
 146 International Comprehensive Ocean-Atmosphere Data Set (ICOADS,
 147 <http://dss.ucar.edu/datasets/>). Ekman transport was computed from geostrophic winds
 148 for a 2° x 2° cell centred at 43°N 11°W (Lavín *et al.*, 2000). In this study, we employed
 149 seasonal averages of both SST and UI for the upwelling (April–September) and
 150 downwelling (October–March) periods (<http://www.indicedeafloramiento.ieo.es>).

151

152 **Fisheries data**

153 The European sardine (*Sardina pilchardus*) was chosen as a representative planktivore
 154 and potential competitor for zooplankton prey with medusae. Series of sardine landings
 155 in the study region were obtained from annual catches in ICES Divisions VIIIc (S Bay
 156 of Biscay) and IXa (NW Spain and Portugal) as recorded in ICES (2011).

157

158 **Statistical analysis**

159 All series of observations were adjusted to a Box-Jenkins additive model representing
 160 the main sources of temporal variability (e.g. Nogueira *et al.*, 1998):

161

$$162 \quad x_t = \bar{x} + LT [x_t] + \sum CC [x_t] + R [x_t] \quad (1)$$

163

164 where the value of series x at time t (x_t) is decomposed in the mean of the series (\bar{x}), the
 165 lineal trend ($LT [x_t]$), the sum of cyclic components ($CC [x_t]$), and a random component
 166 ($R [x_t]$). The lineal trend was determined by linear regression, and the cyclic
 167 components by Fourier analysis. Significance of the cyclic terms was determined using
 168 the Anderson (A_c) criteria (Legendre and Legendre, 1998):

169

$$170 \quad A_c = -(2/n) \log_e(1 - \sqrt[m]{1 - \alpha}) \quad (2)$$

171

172 where n is the number of observations, m the period of the longest cycle, and α the
 173 significance level (0.05 in this case).

174

175 The random component was parameterized using an autoregressive model
 176 predicting values from previous observations in the series:

176

$$177 \quad R[x_t] = \phi_i(R[x_{t-1}]) + a_t \quad (3)$$

178

179 where ϕ_i are the autoregressive parameters and a_t the “prewhitened” residuals (i.e. a
 180 time-series of randomly distributed, independent observations of mean 0 and constant
 181 variance). Autoregressive parameters were estimated using the Yule-Walker equations
 182 (Wei, 1989). Significance of all deterministic terms in the series was determined at
 183 $p < 0.05$.

184

185 Zooplankton abundance values were log transformed ($\log [X+1]$) to minimize
 186 the weight of large values in the series (e.g. Head and Sameoto, 2007). The possible
 187 effect of environmental and fishery variables on plankton was investigated by
 188 crosscorrelation of prewhitened residuals of the series of annual mean values of paired
 189 plankton and environmental series. This procedure aimed at reducing the uncertainty
 190 caused by correlations due to parallel trends caused by an external forcing variable (e.g.
 warming).

191

192 **Results**

193 **Gelatinous vs. copepod abundance fluctuations**

194 The monthly series from the ocean showed a clear seasonal pattern for copepods, more
195 abundant in spring and autumn (Figure 2). In contrast, medusae and tunicates appeared
196 sporadically without a particular seasonal preference, but both had large interannual
197 variations. The decomposition of the series indicated a significant increase in tunicates
198 between 1958 and 1986, while no significant cycles or trends were found for other
199 groups or periods (Table 1). The coastal series (Figure 3) exhibited significant seasonal
200 variability in all groups (Table 1). Medusae displayed a significant increasing trend in
201 Vigo, but decreased in A Coruña. Copepods showed a significant increase in Vigo,
202 while tunicates did not have significant linear trends in any of the series.

203 The RIS index revealed the shift between periods of 4–7 years of marked
204 copepod dominance in the CPR series followed by generally short periods (< 3 years)
205 when gelatinous groups were relatively abundant (Figure 4a). The exception was the
206 decade of 1980 characterized by a large increase in tunicates. Unfortunately, the exact
207 duration of this phase of high abundance of gelatinous plankton cannot be determined
208 because of the discontinuation of the series until the late 1990s, but these groups
209 remained high until the early 2000s. In the coastal series, the length of the periods of
210 high gelatinous abundance was much shorter than for the ocean, as it did not exceeded 3
211 years in Vigo (Figure 4b) and was limited to one single year in A Coruña (Figure 4c).
212 Comparison of these abundance periods indicate a low temporal correspondence and,
213 consequently, large local variability in the presence of gelatinous plankton.

214 Averaging the series by years to remove the effect of seasonality and the
215 sporadic apparition of gelatinous plankton highlighted the importance of increasing
216 trends of tunicates in the late 1980s (accounting for 58% of the series variance), while
217 there was no significant trend in any of the groups of the CPR series after 1997. In
218 Vigo, the annual series showed significant increases in medusae (48% of variance) and
219 copepods (41%), while in A Coruña, none of the annual series showed significant trends
220 or cycles. The prewhitened residuals of these series showed significant correlations
221 between copepods and medusae in Vigo, and between copepods and tunicates in A
222 Coruña, but no correlations in the CPR series (Table 2). It must be noted that any of the
223 series showed significant correlations between medusae and tunicates.

224

225 **Environmental and fishery variability**

226 Positive anomalies of AMO characterized the first and last decades of the study period
227 considered, while negative anomalies dominated for a long central period (Figure 5a).
228 The decomposition of annually averaged AMO series indicated a weak autocorrelation
229 and interannual trend, but a marked significant cycle repeating maximum anomalies
230 after 48 years (Table 3). The period of negative AMO anomalies coincided with shorter
231 periods of positive NAO and, conversely, positive AMO with negative NAO (Figure
232 5b). Winter-averaged NAO values (NAO_{DM}) had a positive interannual trend (Table 3),
233 due mainly to the highly positive periods in the early 1990s. In contrast, summer NAO
234 (NAO_{JA}) did not show any significant deterministic component in our analysis (Table
235 3).

236 Sea surface temperature in the study area followed a temporal pattern very
237 similar to that of AMO, with positive anomalies in the 1960s and brief periods after
238 1990, while negative anomalies prevailed during the 1970s and 1980s (Figure 5c). Both

239 autumn–winter (SST_{OM}) and spring–summer (SST_{AS}) showed equivalent linear increase
240 rates of $0.02^{\circ}\text{C year}^{-1}$, and the latter also displayed a significant cycle of 46 years (Table
241 3). In turn, mean upwelling intensity during spring and summer (UI_{AS}) significantly
242 decreased (Table 3), due mostly to the high positive anomalies in the 1960s and early
243 1990s and the prevalence of negative anomalies during late 1970s and early 1980s and
244 2000s (Figure 5d). The duration of positive and negative phases of NAO and UI was
245 much shorter than those of AMO and SST (Figure 5).

246 The biomass of planktivorous fish, exemplified by sardine landings, decreased
247 throughout the study period (Figure 6). The decomposition of the series revealed a
248 significant linear decrease of ca. 900 tonnes (fresh weight) year^{-1} and several cycles at
249 19, 29, and 58 years.

250

251 **Relationships between plankton groups and environment or climate**

252 Only four relationships were significant after crosscorrelation analysis between the
253 prewhitened residuals of plankton and environmental series. Copepods in the ocean
254 were negatively correlated with NAO_{DM} , but after a lag of 2 years (Figure 7a) and
255 tunicates positively with AMO also after a lag of 2 years (Figure 7b). For the coastal
256 series, only in A Coruña was NAO_{JA} negatively correlated with tunicates at lag 0
257 (Figure 7c) and also with medusae, but in this case, at lag 2 year (Figure 7d). No
258 significant correlations were found between any of the plankton series and either SST,
259 upwelling, or sardine landings at lags from 0 to 7 years.

260

261 **Discussion**

262 **Phase shifts in plankton community composition**

263 Our analysis revealed a succession of periods of relatively high and low abundance of
264 gelatinous plankton in both oceanic and coastal waters near the NW Iberian Peninsula.
265 These periods generally span several years, particularly in oceanic waters. Although the
266 occurrence of blooms of gelatinous organism is not unusual in other areas, only few
267 studies report similar shifts in the plankton community composition (e.g. Molinero *et al.*,
268 2005, 2008; Boero *et al.*, 2008; Gibbons and Richardson, 2009; Schlüter *et al.*,
269 2010). The persistence of phases for several years, even taking into account that most
270 gelatinous organisms are recorded in low numbers in our series except during blooms,
271 suggest that the causes are major alterations of the ecosystem. Similar shifts were
272 reported in other marine communities for other regions, notably for planktivorous fish
273 (Lluch-Cota *et al.*, 1997; Chavez *et al.*, 2003; van der Lingen *et al.*, 2009), but also for
274 other ecosystem components (Beaugrand, 2004; Hátún *et al.*, 2009).

275 There is evidence that the phases of high relative abundance of gelatinous
276 plankton are not an artefact from the observations or the analysis. Even when the
277 plankton series employed in this study were not designed specifically to record
278 gelatinous plankton, the mean value of abundance observed and the significant
279 autocorrelation of the series in each group suggest that the anomalies indicate relatively
280 persistent changes in plankton composition (Table 1). The series for medusae, however,
281 may have been biased because of the small sample size relative to the mean size and
282 abundance of most jellyfish, particularly in the case of the CPR series, as the records
283 only represent surface samples collected through a very small opening of the sampler
284 (Richardson *et al.*, 2006). In this case, our conclusions are only indicative of the largest
285 potential changes in medusae, which would be recorded only if very abundant.

286 Tunicates, however, were better recorded because small individuals and parts of
287 the colonies remain in most plankton samples even if large colonies are removed as part
288 of the standard handling procedures, since most plankton observational programmes
289 focus on copepods (Mackas and Beaugrand, 2010). Still, direct comparison between the
290 abundance of plankton groups between CPR and coastal series is not feasible because of
291 the large differences in sampling methods. Similarities in trends and cycles among
292 series were compared instead, as in previous studies in this region (Bode *et al.*, 2009).
293 Shifts between different phases of marine communities often mirror similar shifts in
294 large-scale environmental factors, as illustrated by fluctuations in sardine (*Sardinops*
295 *sagax*) and anchovy (*Engraulis ringens*) populations and climatic conditions in the
296 Pacific (Chavez *et al.*, 2003). Decadal phases are characteristic of oscillating systems
297 with gradual variations affecting several components. This is characteristic of climate-
298 driven changes, as exemplified by the main climate modes as the NAO (Hurrell and
299 Dickson, 2004), and by large spatial-scale properties of the ocean, as the AMO (Enfield
300 *et al.*, 2001). Significant autocorrelation and multiannual cycles are the key components
301 of the phase periods of these series, as found in our analysis (Tables 1 and 3). However,
302 only long series can adequately detect multidecadal phases, as the CPR series, while
303 shorter phases result in coastal plankton because of the smaller length of the series. Our
304 results also show the maximum in medusae frequency in the late 1960s reported in the
305 pooled series of CPR for all North Atlantic regions, but they did not reflect the later
306 increase in late 1980s, mainly related to the regime shift in the North Sea (Gibbons and
307 Richardson, 2009). Instead, the F4 series showed a marked increase in tunicates during
308 the late 1980s, thus suggesting latitudinal differences in the shift of plankton
309 communities. A similar conclusion was reached when comparing other CPR series for
310 both phytoplankton and zooplankton species or groups (Richardson and Schoeman,
311 2004).

312

313 **Environmental vs. ecological factors explaining gelatinous plankton anomalies**

314 Phase shifts in planktonic communities involving anomalies in the proportion of
315 copepods and gelatinous plankton have been related to both large-scale (climatic) and
316 small-scale (local) variability for jellyfish (Molinero *et al.*, 2005, 2008) and tunicates
317 (Lavaniegos and Ohman, 2007). Local variability would explain gelatinous blooms of
318 short duration in periods when copepods dominated, while in some phases, the
319 interaction of local variability with climate changes would cause the persistence of
320 periods of high gelatinous plankton abundance relative to that of copepods for several
321 years. In our study, the phases of high and low gelatinous plankton abundance occurred
322 at different times for each series. This would imply a major effect of local variability,
323 particularly in the coastal series that were collected only a few kilometres apart. The
324 small number of significant correlations between plankton and climatic series found in
325 our study, often with lags of several years, would support the lower importance of
326 climate relative to local factors in the structure of plankton communities in this region.
327 Other studies also noted the generally weaker relationships between plankton and NAO
328 index values for southern compared to northern areas in the Northeast Atlantic (e.g.
329 Planque *et al.*, 2003; Bode *et al.*, 2009), and this was attributed to the opposite
330 responses of oceanographic variables to climate forcing between adjacent regions. For
331 instance, winter NAO greatly influences wind regimes and upwelling patterns in the
332 North Sea (Beaugrand, 2004) and North African upwelling (Pérez *et al.*, 2010), but in

333 Galicia, the summer NAO was instead related to phytoplankton biomass and upwelling
334 intensity.

335 In addition, the two gelatinous groups considered had different variability
336 patterns. Besides, there was no significant correlation between these groups for any of
337 the series analysed (Table 2). One first explanation of this variability may be their
338 clearly different trophic position: predators (medusae) or primary consumers (tunicates).
339 Medusae are likely to be sensitive to multiple interactions in the foodweb because they
340 prey on copepods competing with fish and are also sensitive to local environmental
341 factors, such as temperature (Molinero *et al.*, 2005, 2008; Gibbons and Richardson,
342 2009; Richardson *et al.*, 2009). This would imply both top-down and bottom-up
343 controls; therefore, medusae would operate as “wasp-waist” organisms in the foodweb
344 in a similar way as planktivorous fishes (Cury *et al.*, 2000). Tunicates, in turn, while
345 also favoured by local factors, such as warming (e.g. Lavaniegos and Ohman, 2007),
346 may be less sensitive to top-down controls. Their high efficiency when feeding on the
347 scarce and small cells of picophytoplankton and bacteria (Acuña, 2001), such as those
348 found in oligotrophic waters, suggest that bottom-up factors would be the major cause
349 of their proliferation. In the study region, pelagic tunicates (as exemplified by
350 appendicularia) display a seasonal species succession related to temperature at the
351 vertical chlorophyll maximum (Acuña and Anadón, 1992). This was interpreted as the
352 interaction of temperature, a metabolic constrain, with phytoplankton productivity,
353 which selected the species dominating in each season. Bottom-up mechanisms would
354 control tunicate abundance because these organisms have a limited capability of
355 regulating metabolism (Gorsky *et al.*, 1987) and do not perform systematic vertical
356 migrations (Palma, 1986). Top-down effects on tunicates are less likely, as only few
357 consumers are specialized in feeding on these organisms (Harbison, 1998). Therefore,
358 and despite the similarities in the body adaptations in both tunicates (Acuña, 2001) and
359 medusae (Acuña *et al.*, 2011) leading to feeding advantages in oligotrophic water, there
360 is no evidence that both groups are selected by the same large-scale climatic or
361 oceanographic conditions.

362 Tunicates were only partly related to climate. The large increase observed in the
363 oceanic CPR series in the early 1980s was weakly correlated with AMO, but with after
364 2 years lag. In the series of A Coruña, high tunicate abundance was related to negative
365 anomalies in summer NAO conditions, the latter related to reduced upwelling and,
366 therefore, new production in this region (Pérez *et al.*, 2010). However, our analysis did
367 not detect significant direct relationships with general upwelling intensity or SST in the
368 area, further supporting the hypothesis that the effects of the environment on plankton
369 composition were more important at local than at regional scales. Positive correlations
370 between gelatinous groups and copepods varied locally, but all groups, except medusae
371 in the first part of the CPR series, showed significant increasing trends in at least some
372 of the series. These increases coincided with similar positive trends in SST and reduced
373 upwelling, which would imply reduced levels of new production (Pérez *et al.*, 2010).
374 However, *in situ* measurements indicate a significant increase in primary production
375 (Bode *et al.*, 2011) and changes in the composition of phytoplankton towards higher
376 abundance of small cells at coastal sites (Huete-Ortega *et al.*, 2010). The observed
377 changes suggest an increased prevalence of microbial foodwebs, which would favour
378 gelatinous plankton, as shown for jellyfish in the northwest Mediterranean (Molinero *et*
379 *al.*, 2005, 2008).

380 In contrast to tunicates, medusae series were only related to climate in A
381 Coruña; only in Vigo were they significantly correlated (but positively) with copepods
382 (Table 2). This result differs from those reported for the nearby Irish Sea, where
383 jellyfish increases after the 1990s were related to climate and overfishing (Lynam *et al.*,
384 2011), which suggests that factors other than climate are more influential in their
385 abundance patterns in Galician waters. Other studies also revealed a weak relationship
386 between jellyfish and climate for most areas in the Northeast Atlantic (Gibbons and
387 Richardson, 2009). Release of competition with planktivorous fishes has been invoked
388 to explain medusae outbursts in the Benguela Upwelling (Bakun and Weeks, 2006), but
389 in our study area, there was no clear relationship between decreasing sardine
390 populations and a consistent increase in medusae. However, the increase in both
391 copepods and medusae in Vigo in recent years may be the first sign of a local change in
392 plankton structure caused by the decrease in planktivorous fish. A negative correlation
393 between copepods and medusae would be expected in the future if sardine populations
394 continue decreasing, as reflected in the fishery data (ICES, 2011). Direct introduction of
395 medusae, as described for other seas (e.g. Richardson *et al.*, 2009) has not been
396 performed in our study area, although the accidental introduction by ballast water
397 cannot be discarded because of the intense shipping activity in this region.
398 Eutrophication was also invoked as a factor favouring jellyfish dominance (Mills, 1995;
399 Purcell *et al.*, 2001), but there are no signs of eutrophication in coastal Galician waters
400 in recent years (Nogueira *et al.*, 1998; Pérez *et al.*, 2010; Bode *et al.*, 2011). Finally, the
401 increasing availability of solid substrates in coastal waters (e.g. by oil rigs, new harbour
402 developments, aquaculture facilities) may facilitate reproduction by providing new
403 habitats for the benthic phase (polyps) of medusae (Pagés, 2001; Lo *et al.*, 2008).
404 Cnidarian polyps were not reported in significant numbers as part of the rich epifauna
405 associated with mussel (*Mytilus edulis*) rafts used extensively in Galicia (Lopez-Jamar
406 *et al.*, 1984), but there are no data on the presence of polyps in other man-made
407 structures.

408 Our analysis showed that gelatinous organisms, although always present in
409 Galician waters, showed mostly short time-scale outbursts that may lead to multiannual
410 periods of increased dominance. These periods were not obviously related to large-scale
411 climatic or oceanographic fluctuations; instead, the series analysed were indicative of
412 large local variability. Interaction between environmental and trophic factors at local
413 scales is likely the cause of occasional dominance of gelatinous plankton in this
414 upwelling ecosystem, characteristically adapted to frequent environmental disturbance.
415 The different temporal variability pattern displayed by tunicates and medusae may be
416 explained by their different trophic position, affecting their sensitivity to bottom-up vs.
417 top-down control. Although, specific effects of direct anthropogenic influence on the
418 abundance of gelatinous organisms in this region cannot be discarded, our results are in
419 line with current reviews of gelatinous plankton variability in different environments,
420 stressing the importance of local interactions while questioning the validity of general
421 effects of large-scale climate fluctuations (Haddock, 2008; Richardson *et al.*, 2009;
422 Lilley *et al.*, 2011; Condon *et al.*, 2012).

423

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434

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579 **Table 1.** Results of decomposition of monthly time-series of the abundance of plankton groups (X) according to the model: $X = \bar{X} + bt + a$
580 $+ \sum A_i \cos [(2 \pi t / T_i) + \theta_i] + \phi_{it} + \varepsilon_t$. Only significant variance components were considered ($p < 0.05$). \bar{X} : mean, **b**: linear trend, **a**: intercept,
581 T_i : period (months), A_i : amplitude, θ_i : phase, **L**: lag (months), ϕ_i : autocorrelation coefficient, % v_t , % v_p , % v_a and % v_{total} : percent variance
582 accounted by linear regression, periodic components, autocorrelation or all model terms, respectively. ε_t : prewhitened residuals.
583

Series/period	Group	\bar{X}	b	a	% v_t	T_i	A_i	θ_i	% v_p	L	ϕ_i	% v_a	% v_{total}
F4-CPR	Medusae	0.003	-0.0002	0.35	1.95	---	---	---	---	---	---	---	1.95
1958–1986	Tunicates	0.54	0.0310	-61.18	18.80	348	0.25	6.10	5.73	---	---	---	24.53
	Copepods	2.08	---	---	---	12	0.53	3.10	41.90	1	-0.17	1.67	51.12
						6	0.23	2.47	7.56				
F4-CPR	Medusae	0.002	0.0009	-1.87	3.47	---	---	---	---	---	---	---	3.47
1997–2006	Tunicates	0.75	---	---	---	---	---	---	---	1	-0.21	4.42	4.42
	Copepods	1.96	---	---	12	0.56	3.02	32.82	---	---	---	---	32.82
Vigo	Medusae	1.473	0.0589	-117.83	4.93	11	0.54	4.06	15.56	1	-0.23	3.26	44.18
						10	0.48	1.10	12.30				
						12	0.46	4.24	11.39				
1994–2006	Tunicates	0.33	-----	-----	-----	-----	-----	-----	---	1	-0.37	13.48	13.48
	Copepods	2.91	0.04	-89.5	10.56	11	0.26	4.75	12.59	1	-0.29	6.61	29.75
A Coruña	Medusae	0.881	-0.0345	68.95	4.46	10	0.33	5.15	9.01	1	-0.62	30.43	52.24
						11	0.32	0.19	8.33				
						11	0.37	0.22	12.37	1	-0.23	4.02	26.99
1989–2006	Tunicates	1.20	---	---	---	11	0.37	0.22	12.37	1	-0.23	4.02	26.99
						10	0.34	0.22	10.59				
						10	0.25	5.05	18.20	1	-0.34	9.53	27.73
	Copepods	3.03	-----	-----	-----	10	0.25	5.05	18.20	1	-0.34	9.53	27.73

584

585 **Table 2.** Pearson correlations between prewhitened residuals of the series of mean
 586 annual values of abundance of zooplankton groups. *: $p < 0.05$, ***: $p < 0.001$.
 587

Series	Copepods vs. Medusae		Copepods vs. tunicates		Medusae vs. tunicates
F4-CPR	0.205		0.205		0.091
Vigo	0.796	***	0.408	*	0.574
A Coruña	0.166		0.636	**	-0.140

588

589 **Table 3.** Results of decomposition of annually averaged time-series of climatic and oceanographic variables. Parameter values and model
590 as in Table 1. Only significant ($p < 0.05$) components were listed. AMO: Atlantic Multidecadal Oscillation. NAO_{DM} and NAO_{JA}: North
591 Atlantic Oscillation averaged from December to March and from June to August, respectively. SST_{OM} and SST_{AS}: sea surface temperature
592 averaged from October to March and from April to September, respectively. UI_{AS}: Upwelling Index averaged from April to September.
593 The period considered for all series was 1960–2007.
594

Series/period	\bar{x}	b	a	% v_t	T_i	A_i	θ_i	% v_p	L	ϕ_i	% v_a	% v_{total}
AMO	-0.03	0.01	-12.25	20.47	48	0.16	0.15	45.72	1	-0.35	3.65	69.84
NAO _{DM}	0.07	0.03	-50.86	33.28	---	---	---	---	1	-0.36	9.58	42.86
NAO _{JA}	0.06	---	---	---	---	---	---	---	---	---	---	---
SST _{OM}	14.73	0.02	-35.66	39.51	---	---	---	---	---	---	---	39.51
SST _{AS}	16.53	0.02	-37.79	32.11	46	0.28	0.20	33.09	---	---	---	65.20
UI _{AS}	286.34	-6.05	12 016.03	21.70	---	---	---	---	---	---	---	21.70

595

596 **Figure captions**

597

598 **Figure 1.** Map of study area with location of coastal time-series stations (stars) and
599 CPR standard area F4.

600

601 **Figure 2.** Variability of the abundance of medusae (a), tunicates (b), and copepods (c)
602 in F4-CPR time-series. Abundance scale units are relative frequency (medusae) or
603 number m^{-3} (tunicates and copepods).

604

605 **Figure 3.** Variability of the abundance ($n m^{-3}$) of medusae (a, b), tunicates (c, d), and
606 copepods (e, f) in the coastal time-series of Vigo and A Coruña.

607

608 **Figure 4.** Shifts between phases of relative dominance of copepods (red) or gelatinous
609 plankton (blue) in the F4-CPR (a), Vigo (b), and A Coruña (c) monthly time-series. RIS
610 values were computed as the difference between copepod and gelatinous plankton
611 abundance series after detrending and standardization. Final RIS series were smoothed
612 with a running mean of 12 months.

613

614 **Figure 5.** Shifts between phases of relative high (red) or low (blue) values in the
615 Atlantic Multidecadal Oscillation (AMO, a), North Atlantic Oscillation (NAO, b), sea
616 surface temperature (SST, c), and Upwelling Index (UI, c) monthly time-series. The
617 series were detrended, standardized, and smoothed with a running mean of 12 months.

618

619 **Figure 6.** Decrease in annual biomass of sardine landings ($\times 10^3$ tonnes fresh weight) in
620 the study region (ICES Divisions VIIIc and IXa). The line shows the linear trend
621 ($p < 0.001$).

622

623 **Figure 7.** Crosscorrelation between mean annual values of plankton group abundance
624 and selected climatic series. (a) NAO_{DM} : winter North Atlantic Oscillation averaged
625 between December and March. (b) AMO: Atlantic Multidecadal Oscillation. (c and d)
626 NAO_{JA} : summer North Atlantic Oscillation averaged between June and August. The
627 dotted lines indicate the 95% confidence interval.

628

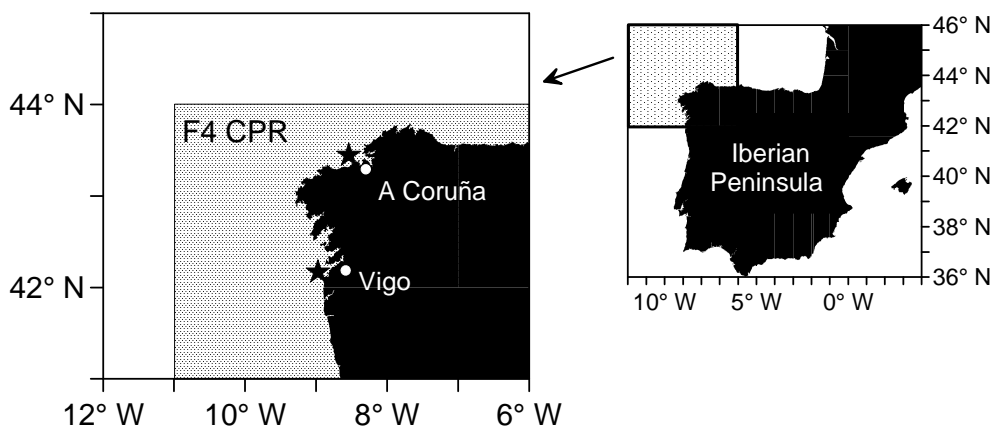


Fig. 1. Map of study area with location of coastal time-series stations (stars) and CPR standard area F4.

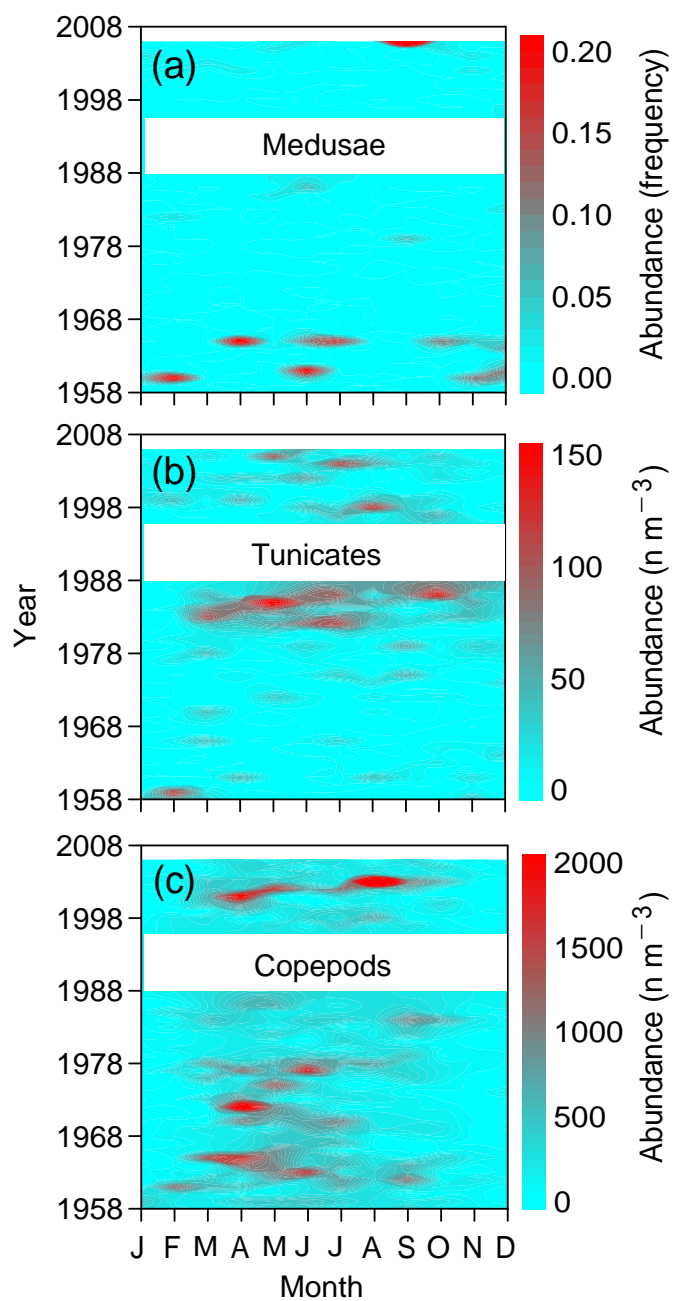


Fig. 2. Variability of the abundance of medusae (a), tunicates (b) and copepods (c) in F4-CPR time series. Abundance scale units are relative frequency (medusae) or number m^{-3} (tunicates and copepods).

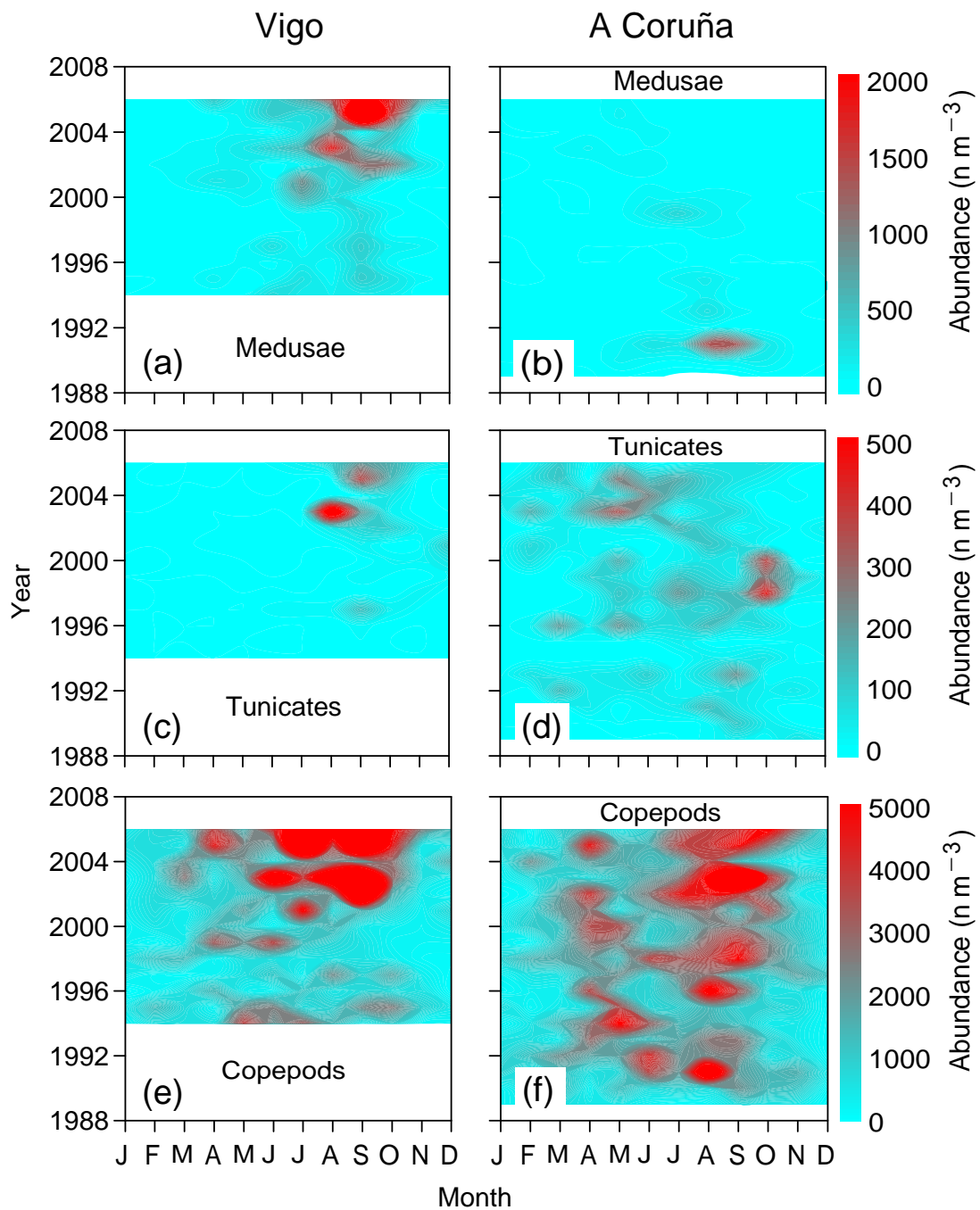


Fig. 3. Variability of the abundance (n m^{-3}) of medusae (a, b), tunicates (c, d) and copepods (e, f) in the coastal time series of Vigo and A Coruña. Abundance scale units are number m^{-3} in all cases.

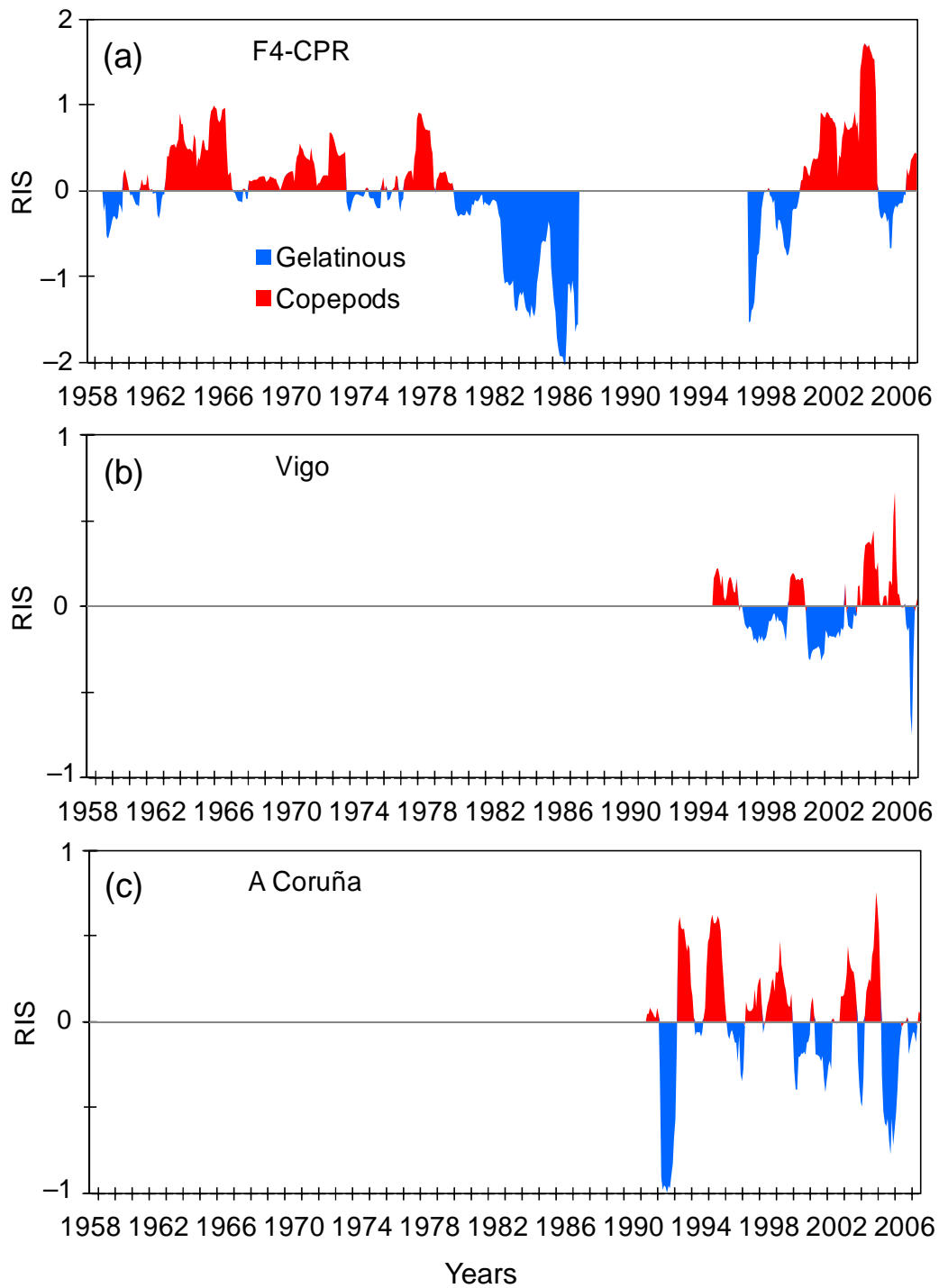


Fig. 4. Shifts between phases of relative dominance of copepods (red) or gelatinous plankton (blue) in the F4-CPR (a), Vigo (b) and A Coruña (c) monthly time-series. RIS values were computed as the difference between copepod and gelatinous plankton abundance series after detrending and standardisation. Final RIS series were smoothed with a running mean of 12 months

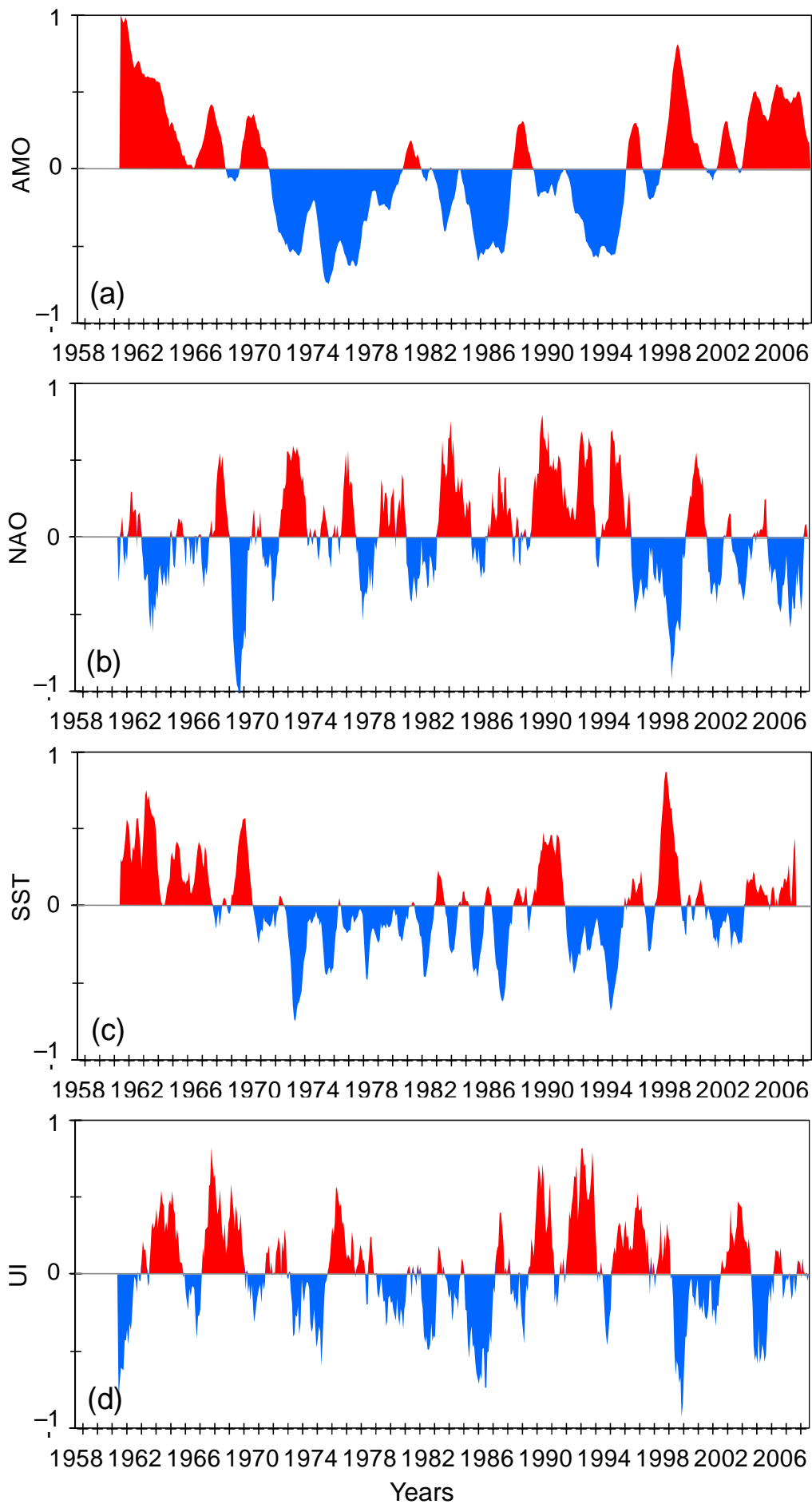


Fig. 5. Shifts between phases of relative high (red) or low (blue) values in the Atlantic Multidecadal Oscillation (AMO, a), North Atlantic Oscillation (NAO, b), Sea Surface Temperature (SST, c) and Upwelling Index (UI, c) monthly time-series. The series were detrended, standardised and smoothed with a running mean of 12 months.

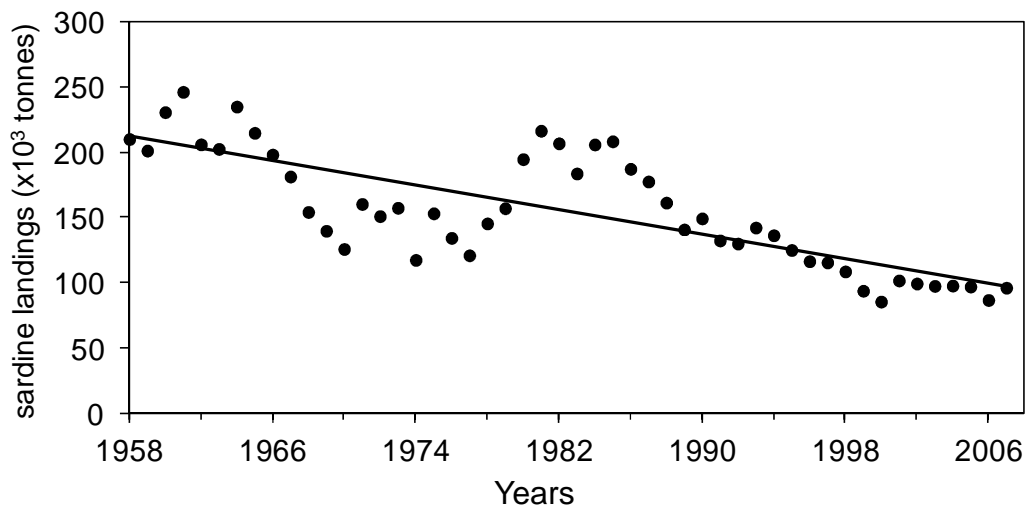


Fig. 6. Decrease in annual biomass of sardine landings ($\times 10^3$ tons fresh weight) in the study region (ICES areas VIIIc and IXa). The line shows the linear trend ($P < 0.001$).

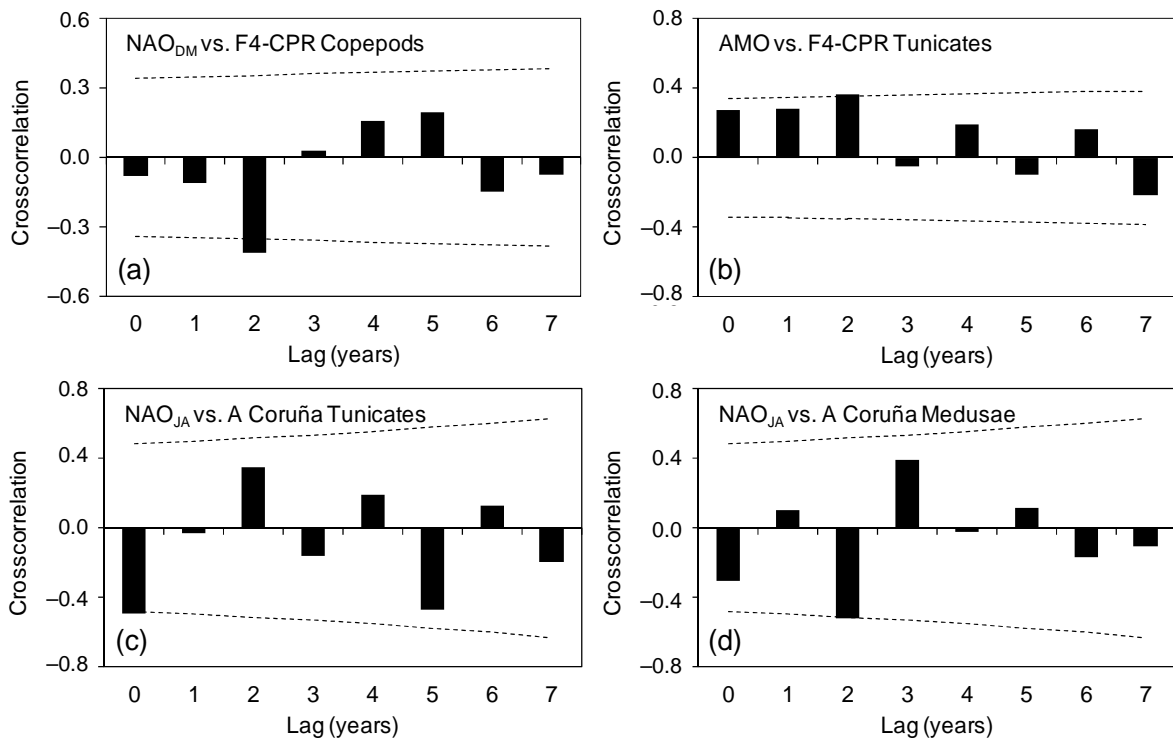


Fig. 7. Crosscorrelation between mean annual values of plankton group abundance and selected climatic series. a) NAO_{DM}: winter North Atlantic Oscillation averaged between March and December. b) AMO: Atlantic Multidecadal Oscillation. c and d) NAO_{JA}: summer North Atlantic Oscillation averaged between June and August. The dotted lines indicate the 95% confidence interval.