



Shifts between gelatinous and crustacean plankton in a coastal upwelling region

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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.

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 outbreaks, 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 have a high ratio of organic matter to volume and are ascribed to the zoological subclass Copepoda (Parsons and Lalli, 2002). Two main types of gelatinous plankton can be found in almost all marine waters. The first group is formed by jellyfish, including Hydrozoan and Scyphozoan medusae, Ctenophora, and Siphonophora. These organisms are predators of other planktonic organisms (notably copepods) and even fish, and their rapid proliferation relies on a complex cycle involving benthic stages (polyps) and asexual reproduction. The second group is represented by tunicates, including appendicularia, pyrosomes, doliolids, and salps. Pelagic tunicates filter-feed on phytoplankton and bacteria, and, thus, are primary consumers in the foodweb. They do not have a benthic phase as

most jellyfish, but also have relatively complex reproductive cycles with sexual and asexual phases. Tunicates form characteristic colonies that can reach up to several metres in length, and while they do not have direct harmful effects, like jellyfish, their large proliferations may significantly impact the biochemical fluxes through the pelagic foodweb. For instance, they reduce the flow of organic matter from primary producers to upper trophic levels, and their gelatinous remains are degraded by microbes in the water column rather than exported to sediments (Lebrato and Jones, 2011).

Both medusae and tunicates have adaptations to feed in environments where food is scarce or, in the case of tunicates, of very small size with minimal energy requirements. Tunicates have developed body forms and colony behaviour to overcome their inability to perform large metabolic adjustments or migrations in the absence of strong currents (Acuña, 2001). Medusae also have adopted forms and shapes facilitating encounters with prey using minimal energy consumption (Acuña *et al.*, 2011). Large proliferations of gelatinous plankton are always a noticeable event and lead to the hypothesis of an increasing number of

such proliferations as a result of climate and global changes (Mills, 1995; Parsons and Lalli, 2002; Boero *et al.*, 2008; Richardson *et al.*, 2009). Most of these studies focused on jellyfish, and their proliferations were attributed to a variety of factors acting either separately or in combination (Richardson *et al.*, 2009). Among the most cited were climatic conditions (Molinero *et al.*, 2005, 2008; Lavaniegos and Ohman, 2007; Lynam *et al.*, 2011), but also eutrophication (Purcell *et al.*, 2001), invasion of species (Graham and Bayha, 2007), habitat modifications (Pagés, 2001; Lo *et al.*, 2008), and overfishing (Bakun and Weeks, 2006; Lynam *et al.*, 2011). However, recent reviews challenged the hypothesis of an overall increase in gelatinous plankton related to global change and point out the importance of trophic interactions to explain their proliferations (Richardson *et al.*, 2009; Lilley *et al.*, 2011; Condon *et al.*, 2012). One of the main limitations when addressing variability in gelatinous plankton is the lack of long time-series of observations of the abundance, biomass, and diversity of these organisms in different ecosystems. In contrast, there are long series of other planktonic organisms, such as copepods (e.g. Mackas and Beaugrand, 2010).

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

Material and methods

Zooplankton

Monthly series of zooplankton abundance were obtained from two sources. Surface waters (ca. 7 m depth) from the oceanic region surrounding the NW Iberian Peninsula were sampled via Continuous Plankton Recorder (CPR, <http://www.sahfos.ac.uk/>). In this study, pooled results for the standard zone F4 between 1958 and 2006 were used (Figure 1). Abundance data for CPR series correspond to mean abundance values for species recorded in the whole sample (eye count procedure in Richardson *et al.*, 2006) and scaled to numbers m^{-3} by taking into account that individual CPR samples correspond to $\sim 3 m^3$. For gelatinous plankton, these series included the categories “coelenterata tissue” (recorded as presence/absence) and Siphonophora to form a medusae group for analysis. Data for CPR medusae were transformed to frequency data when constructing monthly or annual series (Gibbons and Richardson, 2009). The CPR series

were discontinued between 1987 and 1997 in the F4 zone. Coastal zooplankton was sampled by project RADIALES (<http://www.seriestemporales-ieo.com>) at Vigo and A Coruña between 1994 and 2006 (Figure 1). In this case, samples were collected using 50-cm diameter Juday–Bogorov (A Coruña) or 40-cm diameter bongo plankton nets (Vigo) equipped with 200- μm mesh size. Tows were double oblique from surface to near bottom (90 and 70 m in Vigo and A Coruña, respectively). Samples were preserved in 2–4% sodium borate-buffered formaldehyde. Abundance values were reported as number of individuals m^{-3} . To this study, the original coastal series were categorized in copepods (as representative of crustacean zooplankton) and gelatinous plankton (medusae and tunicates). Medusae included Hydrozoans and Scyphozoa, and tunicates included salps, pyrosomes, doliolids, and appendicularia.

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

Environmental variables

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

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

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

Fisheries data

The European sardine (*Sardina pilchardus*) was chosen as a representative planktivore and potential competitor for zooplankton prey with medusae. Series of sardine landings in the study region were obtained from annual catches in ICES Divisions

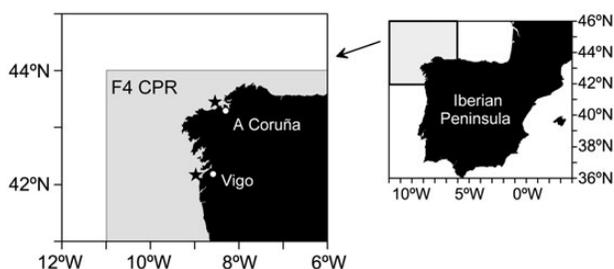


Figure 1. Map of study area with location of coastal time-series stations (stars) and CPR standard area F4.

VIIIc (S Bay of Biscay) and IXa (NW Spain and Portugal) as recorded in ICES (2011).

Statistical analysis

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

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

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

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

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

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

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

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

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

Results

Gelatinous vs. copepod abundance fluctuations

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

The RIS index revealed the shift between periods of 4–7 years of marked copepod dominance in the CPR series followed by generally short periods (<3 years) when gelatinous groups were

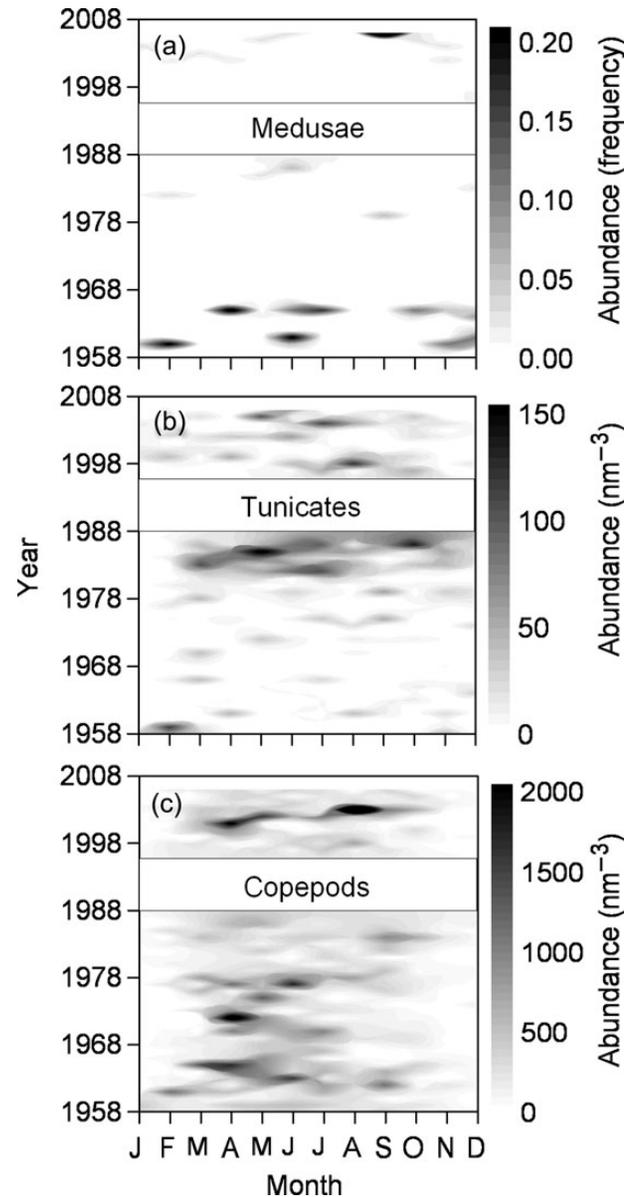


Figure 2. Variability of the abundance of medusae (a), tunicates (b), and copepods (c) in F4-CPR time-series. Abundance scale units are relative frequency (medusae) or number m^{-3} (tunicates and copepods).

relatively abundant (Figure 4a). The exception was the decade of 1980 characterized by a large increase in tunicates. Unfortunately, the exact duration of this phase of high abundance of gelatinous plankton cannot be determined because of the discontinuation of the series until the late 1990s, but these groups remained high until the early 2000s. In the coastal series, the length of the periods of high gelatinous abundance was much shorter than for the ocean, as it did not exceed 3 years in Vigo (Figure 4b) and was limited to one single year in A Coruña (Figure 4c). Comparison of these abundance periods indicate a low temporal correspondence and, consequently, large local variability in the presence of gelatinous plankton.

Averaging the series by years to remove the effect of seasonality and the sporadic apparition of gelatinous plankton highlighted the

Table 1. Results of decomposition of monthly time-series of the abundance of plankton groups (X) according to the model: $X = \bar{x} + bt + a + \sum A_i \cos[2\pi t/T_i + \theta_i] + \phi_{it} + \varepsilon_t$.

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
F4-CPR	Medusae	0.002	0.0009	-1.87	3.47	-	-	-	-	-	-	-	3.47
	Tunicates	0.75	-	-	-	-	-	-	-	1	-0.21	4.42	4.42
1997-2006	Copepods	1.96	-	-	12	0.56	3.02	32.82	-	-	-	-	32.82
	Medusae	1.473	0.0589	-117.83	4.93	11	0.54	4.06	15.56	1	-0.23	3.26	44.18
Vigo						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
1989-2006						11	0.32	0.19	8.33				
						11	0.37	0.22	12.37	1	-0.23	4.02	26.99
						10	0.34	0.22	10.59				
Copepods						10	0.25	5.05	18.20	1	-0.34	9.53	27.73

Only significant variance components were considered ($p < 0.05$). \bar{x} : mean, b : linear trend, a : intercept, T_i : period (months), A_i : amplitude, θ_i : phase, L : lag (months), ϕ_i : autocorrelation coefficient, $\%v_t$, $\%v_p$, $\%v_a$, and $\%v_{total}$: per cent variance accounted by linear regression, periodic components, autocorrelation, or all model terms, respectively. ε_t : prewhitened residuals.

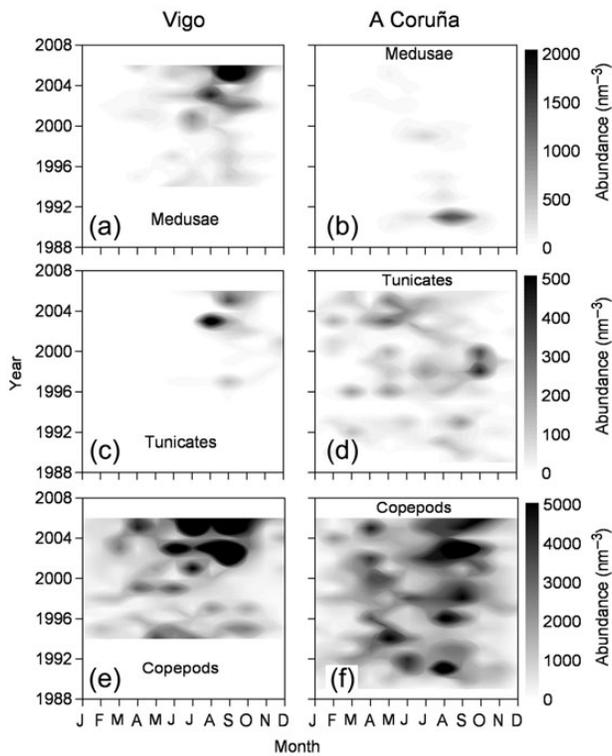


Figure 3. Variability of the abundance ($n\ m^{-3}$) of medusae (a, b), tunicates (c, d), and copepods (e, f) in the coastal time-series of Vigo and A Coruña.

importance of increasing trends of tunicates in the late 1980s (accounting for 58% of the series variance), while there was no significant trend in any of the groups of the CPR series after 1997. In Vigo, the annual series showed significant increases in medusae

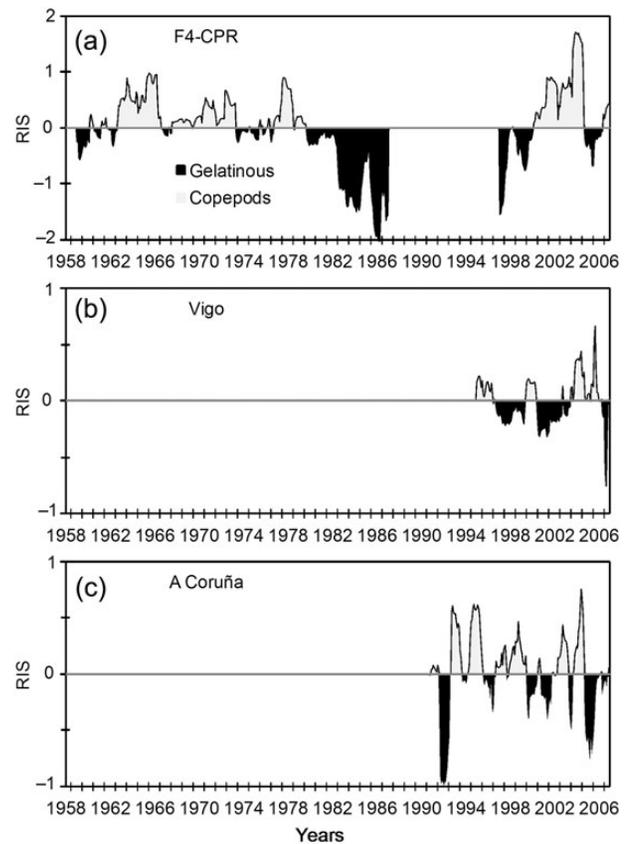


Figure 4. Shifts between phases of relative dominance of copepods (grey) or gelatinous plankton (black) in the F4-CPR (a), Vigo (b), and A Coruña (c) monthly time-series. RIS values were computed as the difference between copepod and gelatinous plankton abundance series after detrending and standardization.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

Table 2. Pearson correlations between prewhitened residuals of the series of mean annual values of abundance of zooplankton groups.

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

* $p < 0.05$, *** $p < 0.001$.

(48% of variance) and copepods (41%), while in A Coruña, none of the annual series showed significant trends or cycles. The prewhitened residuals of these series showed significant correlations between copepods and medusae in Vigo, and between copepods and tunicates in A Coruña, but no correlations in the CPR series (Table 2). It must be noted that any of the series showed significant correlations between medusae and tunicates.

Environmental and fishery variability

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

SST in the study area followed a temporal pattern very similar to that of AMO, with positive anomalies in the 1960s and brief periods after 1990, while negative anomalies prevailed during the 1970s and 1980s (Figure 5c). Both autumn–winter (SST_{DM}) and spring–summer (SST_{AS}) showed equivalent linear increase rates of $0.02^{\circ}\text{C year}^{-1}$, and the latter also displayed a significant cycle of 46 years (Table 3). In turn, mean upwelling intensity during spring and summer (UI_{AS}) significantly decreased (Table 3), due mostly to the high positive anomalies in the 1960s and early 1990s and the prevalence of negative anomalies during late 1970s and early 1980s and 2000s (Figure 5d). The duration of positive and negative phases of NAO and UI was much shorter than those of AMO and SST (Figure 5).

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

Relationships between plankton groups and environment or climate

Only four relationships were significant after cross-correlation analysis between the prewhitened residuals of plankton and environmental series. Copepods in the ocean were negatively correlated with NAO_{DM} , but after a lag of 2 years (Figure 7a), and tunicates positively with AMO also after a lag of 2 years (Figure 7b). For the coastal series, only in A Coruña was NAO_{JA} negatively correlated with tunicates at lag 0 (Figure 7c) and also with medusae, but in

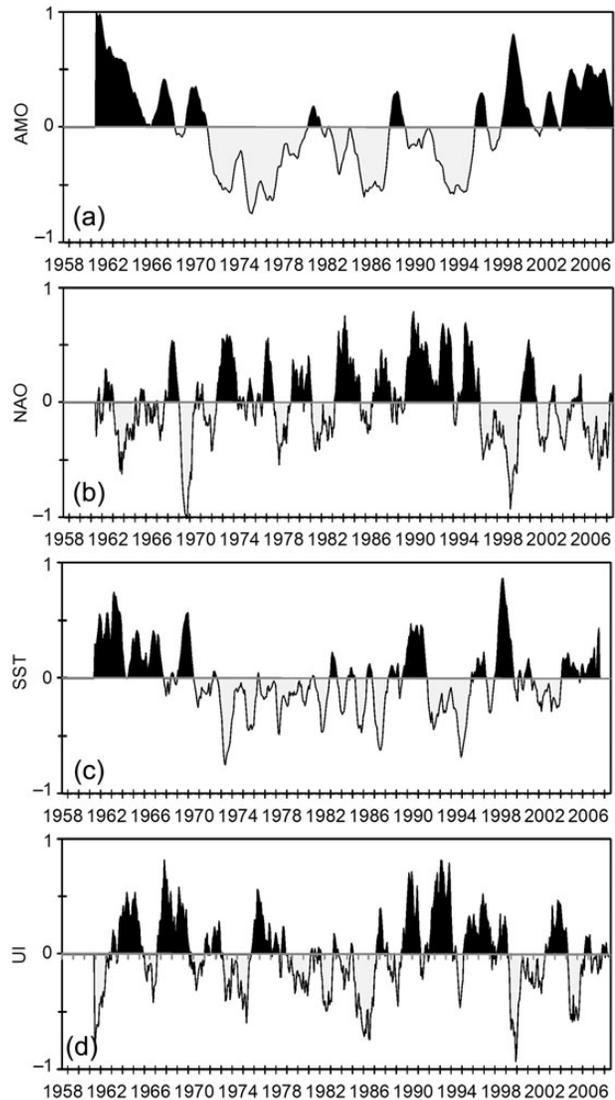


Figure 5. Shifts between phases of relative high (black) or low (grey) values in the AMO (a), NAO (b), SST (c), and UI (c) monthly time-series. The series were detrended, standardized, and smoothed with a running mean of 12 months.

this case, at lag of 2 years (Figure 7d). No significant correlations were found between any of the plankton series and SST, upwelling, or sardine landings at lags from 0 to 7 years.

Discussion

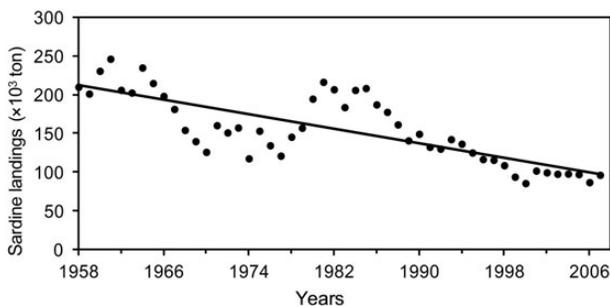
Phase shifts in plankton community composition

Our analysis revealed a succession of periods of relatively high and low abundance of gelatinous plankton in both oceanic and coastal waters near the NW Iberian Peninsula. These periods generally span several years, particularly in oceanic waters. Although the occurrence of blooms of gelatinous organisms is not unusual in other areas, only few studies report similar shifts in the plankton community composition (e.g. Molinero *et al.*, 2005, 2008; Boero *et al.*, 2008; Gibbons and Richardson, 2009; Schlüter *et al.*, 2010). The persistence of phases for several years, even taking into account that most gelatinous organisms are recorded in

Table 3. Results of decomposition of annually averaged time-series of climatic and oceanographic variables.

Series/period	\bar{x}	b	a	$\%v_{\epsilon}$	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

Parameter values and model as in Table 1. Only significant ($p < 0.05$) components were listed. AMO, Atlantic Multidecadal Oscillation; NAO_{DM} and NAO_{JA}, North Atlantic Oscillation averaged from December to March and from June to August, respectively; SST_{OM} and SST_{AS}, sea surface temperature averaged from October to March and from April to September, respectively; UI_{AS}, Upwelling Index averaged from April to September. The period considered for all series was 1960–2007.

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

small numbers in our series except during blooms, suggest that the causes are major alterations of the ecosystem. Similar shifts were reported in other marine communities for other regions, notably for planktivorous fish (Lluch-Cota *et al.*, 1997; Chavez *et al.*, 2003; van der Lingen *et al.*, 2009), but also for other ecosystem components (Beaugrand, 2004; Hátún *et al.*, 2009).

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

Tunicates, however, were better recorded because small individuals and parts of the colonies remain in most plankton samples even if large colonies are removed as part of the standard handling procedures, since most plankton observational programmes focus on copepods (Mackas and Beaugrand, 2010). Still, direct comparison between the abundance of plankton groups between CPR and coastal series is not feasible because of the large differences in sampling methods. Similarities in trends and cycles among series were compared instead, as in previous studies in this region (Bode *et al.*, 2009).

Shifts between different phases of marine communities often mirror similar shifts in large-scale environmental factors, as

illustrated by fluctuations in sardine (*Sardinops sagax*) and anchovy (*Engraulis ringens*) populations and climatic conditions in the Pacific (Chavez *et al.*, 2003). Decadal phases are characteristic of oscillating systems with gradual variations affecting several components. This is characteristic of climate-driven changes, as exemplified by the main climate modes as the NAO (Hurrell and Dickson, 2004), and by large spatial-scale properties of the ocean, such as the AMO (Enfield *et al.*, 2001). Significant autocorrelation and multiannual cycles are the key components of the phase periods of these series, as found in our analysis (Tables 1 and 3). However, only long series can adequately detect multidecadal phases, such as the CPR series, while shorter phases result in coastal plankton because of the smaller length of the series. Our results also show the maximum in medusae frequency in the late 1960s reported in the pooled series of CPR for all North Atlantic regions, but they did not reflect the later increase in late 1980s, mainly related to the regime shift in the North Sea (Gibbons and Richardson, 2009). Instead, the F4 series showed a marked increase in tunicates during the late 1980s, thus suggesting latitudinal differences in the shift of plankton communities. A similar conclusion was reached when comparing other CPR series for both phytoplankton and zooplankton species or groups (Richardson and Schoeman, 2004).

Environmental vs. ecological factors explaining gelatinous plankton anomalies

Phase shifts in planktonic communities involving anomalies in the proportion of copepods and gelatinous plankton have been related to both large-scale (climatic) and small-scale (local) variability for jellyfish (Molinero *et al.*, 2005, 2008) and tunicates (Lavaniegos and Ohman, 2007). Local variability would explain gelatinous blooms of short duration in periods when copepods dominated, while in some phases, the interaction of local variability with climate changes would cause the persistence of periods of high gelatinous plankton abundance relative to that of copepods for several years. In our study, the phases of high and low gelatinous plankton abundance occurred at different times for each series. This would imply a major effect of local variability, particularly in the coastal series that were collected only a few kilometres apart. The small number of significant correlations between plankton and climatic series found in our study, often with lags of several years, would support the lower importance of climate relative to local factors in the structure of plankton communities in this region. Other studies also noted the generally weaker relationships between plankton and NAO index values for southern compared with northern areas in the Northeast Atlantic (e.g. Planque *et al.*, 2003; Bode *et al.*, 2009), and this was attributed to the

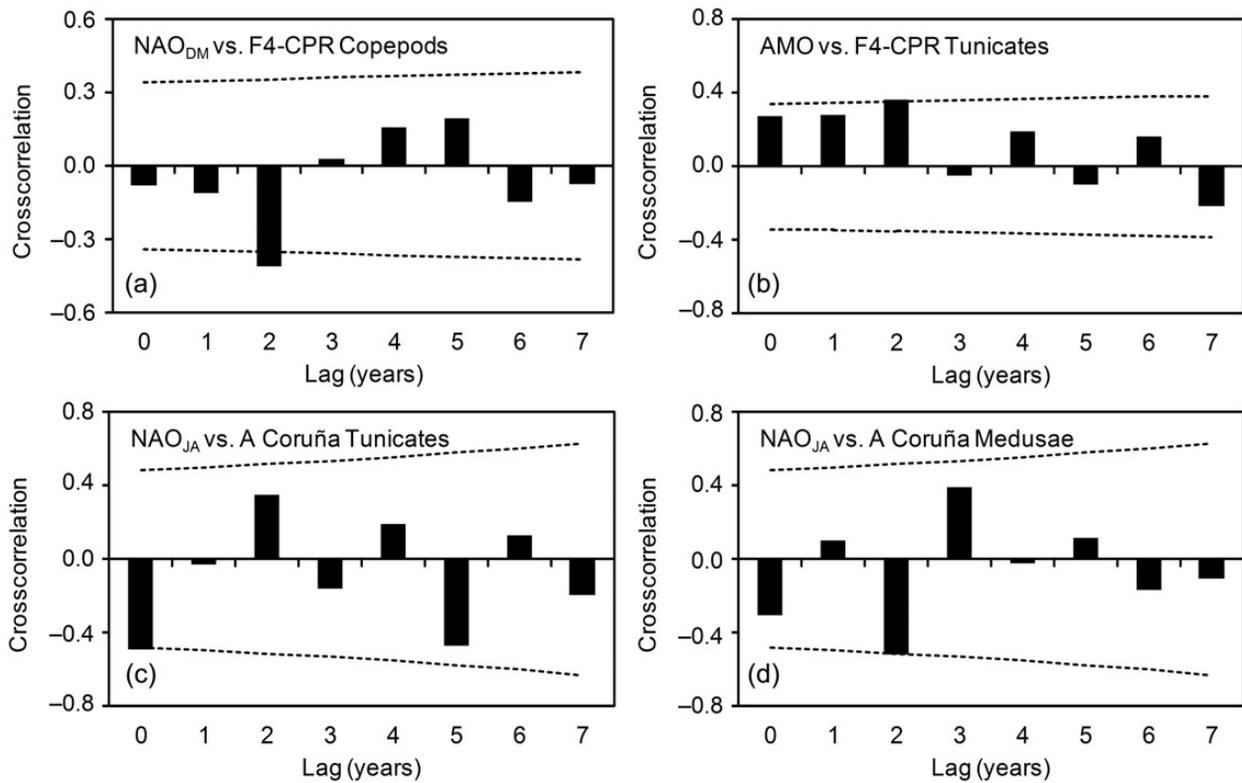


Figure 7. Cross-correlation between mean annual values of plankton group abundance and selected climatic series. (a) NAO_{DM}: winter NOA averaged between December and March. (b) AMO: Atlantic Multidecadal Oscillation. (c and d) NAO_{JA}: summer NOA averaged between June and August. The dotted lines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

opposite responses of oceanographic variables to climate forcing between adjacent regions. For instance, winter NAO greatly influences wind regimes and upwelling patterns in the North Sea (Beaugrand, 2004) and North African upwelling (Pérez *et al.*, 2010), but in Galicia, the summer NAO was instead related to phytoplankton biomass and upwelling intensity.

In addition, the two gelatinous groups considered had different variability patterns. Besides, there was no significant correlation between these groups for any of the series analysed (Table 2). One first explanation of this variability may be their clearly different trophic position: predators (medusae) or primary consumers (tunicates). Medusae are likely to be sensitive to multiple interactions in the foodweb because they prey on copepods competing with fish and are also sensitive to local environmental factors, such as temperature (Molinero *et al.*, 2005, 2008; Gibbons and Richardson, 2009; Richardson *et al.*, 2009). This would imply both top-down and bottom-up controls; therefore, medusae would operate as “wasp-waist” organisms in the foodweb in a similar way as planktivorous fish (Cury *et al.*, 2000). Tunicates, in turn, while also favoured by local factors, such as warming (e.g. Lavaniegas and Ohman, 2007), may be less sensitive to top-down controls. Their high efficiency when feeding on the scarce and small cells of picophytoplankton and bacteria (Acuña, 2001), such as those found in oligotrophic waters, suggest that bottom-up factors would be the major cause of their proliferation. In the study region, pelagic tunicates (as exemplified by appendicularia) display a seasonal species succession related to temperature at the vertical chlorophyll maximum (Acuña and Anadón, 1992). This was interpreted as the interaction of

temperature, a metabolic constraint, with phytoplankton productivity, which selected the species dominating in each season. Bottom-up mechanisms would control tunicate abundance because these organisms have a limited capability of regulating metabolism (Gorsky *et al.*, 1987) and do not perform systematic vertical migrations (Palma, 1986). Top-down effects on tunicates are less likely, as only few consumers are specialized in feeding on these organisms (Harbison, 1998). Therefore, and despite the similarities in the body adaptations in both tunicates (Acuña, 2001) and medusae (Acuña *et al.*, 2011) leading to feeding advantages in oligotrophic water, there is no evidence that both groups are selected by the same large-scale climatic or oceanographic conditions.

Tunicates were only partly related to climate. The large increase observed in the oceanic CPR series in the early 1980s was weakly correlated with AMO, but with after 2 years lag. In the series of A Coruña, high tunicate abundance was related to negative anomalies in summer NAO conditions, the latter related to reduced upwelling and, therefore, new production in this region (Pérez *et al.*, 2010). However, our analysis did not detect significant direct relationships with general upwelling intensity or SST in the area, further supporting the hypothesis that the effects of the environment on plankton composition were more important at local than at regional scales. Positive correlations between gelatinous groups and copepods varied locally, but all groups, except medusae in the first part of the CPR series, showed significant increasing trends in at least some of the series. These increases coincided with similar positive trends in SST and reduced upwelling, which would imply reduced levels of new production (Pérez *et al.*, 2010). However, *in situ* measurements indicate a significant

increase in primary production (Bode *et al.*, 2011) and changes in the composition of phytoplankton towards higher abundance of small cells at coastal sites (Huete-Ortega *et al.*, 2010). The observed changes suggest an increased prevalence of microbial foodwebs, which would favour gelatinous plankton, as shown for jellyfish in the northwest Mediterranean (Molinero *et al.*, 2005, 2008).

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

Our analysis showed that gelatinous organisms, although always present in Galician waters, showed mostly short time-scale outbursts that may lead to multiannual periods of increased dominance. These periods were not obviously related to large-scale climatic or oceanographic fluctuations; instead, the series analysed were indicative of large local variability. Interaction between environmental and trophic factors at local scales is likely the cause of occasional dominance of gelatinous plankton in this upwelling ecosystem, characteristically adapted to frequent environmental disturbance. The different temporal variability pattern displayed by tunicates and medusae may be explained by their different trophic position, affecting their sensitivity to bottom-up vs. top-down control. Although, specific effects of direct anthropogenic influence on the abundance of gelatinous organisms in this region cannot be discarded, our results are in line with current reviews of gelatinous plankton variability in different environments, stressing the importance of local interactions while questioning the validity of general effects of large-scale

climate fluctuations (Haddock, 2008; Richardson *et al.*, 2009; Lilley *et al.*, 2011; Condon *et al.*, 2012).

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