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Pteropod time series from the North Western Mediterranean (1967–2003): impacts of pH and climate variability

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ABSTRACT: Environmental changes resulting from anthropogenic CO_2 emissions occur at global and local levels and have potentially harmful effects, particularly for calcifying taxa in the marine environment. A time series of pteropod abundance covering the period 1967–2003 was isolated from the Point B (northwestern Ligurian Sea) zooplankton time series. Inter- and intra-annual changes in the abundance of 3 families (Limacinidae, Cavoliniidae and Creseidae) were compared with the copepod time series to identify any differential effects driven by ocean acidification and temperature. pH values were hind-cast from total alkalinity estimated from local temperature and salinity measurements, and atmospheric CO_2 taken from the Mauna Loa time series. Although surface waters were supersaturated with respect to aragonite throughout the study period, it is estimated that pH declined by 0.05 units. All pteropod groups displayed a trend of increasing abundance, suggesting that any deleterious effect of declining pH_T in the range of 0.05 units has not caused sufficient reductions in fitness as to decrease local abundances between 1967–2003. Pteropod populations are influenced by inter-annual changes in summer temperatures. Spectral analysis identified a ~14 yr periodic oscillation in sea surface temperature. Similarly timed oscillations in abundance are present for all pteropod families but not for copepods, indicating a possible influence of the North Atlantic quasi-decadal mode on pteropod populations. While laboratory studies have shown pteropods to be sensitive to changes in pH, this analysis suggests that local and regional scale drivers have had a greater effect on pteropod populations in the northwestern Mediterranean Sea in recent decades. It should be noted that pH changes in laboratory studies exceed 0.05 pH units and that the saturation state with respect to aragonite (Ω_{ar}) is usually much lower than that of the Mediterranean.

KEY WORDS: Time series · Pteropod · Ocean acidification · Mediterranean · Global change

INTRODUCTION

Anthropogenic activities such as the burning of fossil fuels, cement production and deforestation are causing an increase in atmospheric concentrations of CO_2 at rates that are potentially unparalleled in the past 300 million years (Hönisch et al. 2012). Atmospheric CO_2 acts as a greenhouse gas, causing global warming. Ocean heat content has risen by 0.40×10^{22} J yr^{-1} (±0.05; Levitus et al. 2009) and accounts for 80% of total increase in heat content of the earth system (Levitus et al. 2005). The increasing sea surface temperatures (SSTs) lower the solubility of oxygen, and cause stronger stratification and subsequent de-oxygenation (Keeling et al. 2010).

Approximately one fourth of atmospheric CO_2 is absorbed by the world's oceans, leading to a lowering of pH and a reduction in carbonate ion concentration ($[CO_3^{2-}]$) (Caldeira & Wickett 2003). The reduction in $[CO_3^{2-}]$ caused by ocean acidification has potentially negative effects for calcifying organisms, as it decreases the calcium carbonate saturation state (Ω). Ω is mainly controlled by $[CO_3^{2-}]$, as the residence time of Ca^{2+} is ~1 Myr (Broecker & Peng 1982) and hence, $[Ca^{2+}]$ remains constant over the short time scales considered here:

$$\Omega = \frac{[Ca^{2+}][CO_3^{2-}]}{K_{sp}} \quad (1)$$

K_{sp} is the equilibrium constant for $CaCO_3$. In a system of pure Ca^{2+} and CO_3^{2-}, if Ω is <1, the mineral phase is undersaturated and dissolution will occur. Conversely, if Ω is >1, the mineral phase is supersaturated and precipitation will occur. Three different polymorphs of $CaCO_3$ are precipitated by marine calcifiers: high Mg calcite, low Mg calcite and aragonite. Aragonite is ~50% more soluble than low Mg calcite (Mucci 1983). Consequently, calcifying organisms have been observed to exhibit the strongest negative responses to ocean acidification (Kroeker et al. 2013). The effects of decreased pH can also interact with other stressors, such as elevated temperatures, often increasing organism sensitivity (Kroeker et al. 2013).

Some areas have been identified as being more vulnerable to the effects of climate change than others (Giorgi 2006). Due to its semi-enclosed nature and the short residence time of water masses, the Mediterranean Sea is sensitive to external forcing, making it a 'hotspot' for climate change effects (The MerMex Group 2011). This sensitivity means that the region has the potential to provide an early warning for global ocean changes (Duarte et al. 1999). Time series and satellite data evidence a steady increase in SSTs at a rate of 0.03–0.167°C yr^{-1} since the year 1900 (Nykjaer 2009, Vargas-Yáñez et al. 2010). By the year 2100, mean temperatures in the western Mediterranean are projected to rise by ~2–2.5°C, pushing average summer maxima to >28°C (Lazzari et al. 2013). The Mediterranean acts as a small to medium sink for CO_2, absorbing ~0.24 Gt C yr^{-1} (D'Ortenzio et al. 2008). Its rate of acidification is also relatively fast compared to the open oceans: −0.14 to −0.05 pH units yr^{-1}, with higher acidification in the western basin (Touratier & Goyet 2009, 2011). Model simulations predict a further decrease in the pH of Mediterranean surface waters of 0.3 to 0.4 units by the end of the 21st century (Geri et al. 2014).

Due to their short generation time, sensitivity to temperature, and lack of commercial exploitation, zooplankton populations have been suggested as good indicators of climate variability (Perry et al. 2004). Unfortunately, time series and experimental works on zooplankton are still rare, and it is difficult to distinguish between natural variability and anthropogenic forcing. Different zooplankton groups have varying sensitivities and comparing them in long time series gives some insight into community responses to various forcings such as temperature and acidity.

Copepods are one of the most important components of marine zooplankton as they play a pivotal role in the structure and functioning of marine planktonic food webs and in nutrient cycling. As non-calcifying organisms, they are not directly affected by changes in Ω, and are predicted to be less vulnerable to pH perturbations than many other groups (Fitzer et al. 2012). Several short-term laboratory studies have assessed copepod response to acute ocean acidification (Kurihara et al. 2004, Mayor et al. 2007, Kurihara & Ishimatsu 2008, Zhang et al. 2011, Fitzer et al. 2012, Li & Gao 2012, Mayor et al. 2012, Weydmann et al. 2012, Zervoudaki et al. 2013). Results indicate a variety of sub-lethal effects, including decreased egg production, lower hatching success and a negative effect on excretion rates. The copepod time series was chosen for comparison with the pteropod time series as they are locally abundant and their population fluctuations have been relatively well studied (Banse 1995). They have also been shown to be sensitive to warming in the North Atlantic (Beaugrand et al. 2002), although evidence of the same effect has not been found in the Mediterranean Sea, where decadal cycles appear to predominate. Garcia-Comas et al. (2011) linked fluctuations in zooplankton abundances at Point B in the Bay of Villefranche-sur-Mer to the NAO (North Atlantic Oscillation) cycles and to a 'bottom up' control on populations, driven by more intense spring blooms following cold and dry winter conditions.

Thecosome pteropods are cosmopolitan holoplanktonic opisthobranchs representing a major group of aragonite-producing pelagic calcifiers that contribute between 20 to 42% of the global carbonate budget (Bednaršek et al. 2012a). They are not as well studied as copepods, despite a strong sensitivity to acidification that make them a possible sentinel organism. Experimental evidence and field studies show decreased calcification rate, increased mortality and shell dissolution, and retarded larval development under lower pH, suggesting that pteropods may be particularly sensitive to the effects of climate

change (Comeau et al. 2009, Lischka et al. 2011, Bednaršek et al. 2012b, 2014, Lischka & Riebesell 2012). Studies on metabolic rate have also revealed that CO_2 acts in concert with other environmental stressors, influencing swimming speed and oxygen consumption of several pteropod species (Comeau et al. 2010b, Maas et al. 2012, Manno et al. 2012). To date, experimental work on pteropods is limited to short-term (< 30 d) studies due to difficulties in maintaining laboratory cultures (Howes et al. 2014). As pteropods play important roles in both the trophic system and biogeochemical cycling (Lalli & Gilmer 1989), it is important that the longer-term effects of climate change on pteropod populations are better understood.

Several time series of pteropod abundances exist for other ocean basins (Ohman et al. 2009, Mackas & Galbraith 2011, Beare et al. 2013, Beaugrand et al. 2013, Loeb & Santora 2013). Studies indicate a potential influence of SST on abundances. Significant declines in the abundance of *Limacina* spp. were observed in the North Atlantic and off the coast of Vancouver Island (Mackas & Galbraith 2011, Beaugrand et al. 2013), with authors suggesting a possible poleward migration in response to increasing SST. Beare et al. (2013) found evidence for a decline in thecosome pteropod abundance in the North Sea, concurrent with a decreasing trend in pH, although the 2 time series were not significantly correlated to imply that pH was the driving factor behind the decline in thecosomes. The authors concluded that a combination of biological, climatic and chemical drivers likely caused the decline. Until now, long-term changes in pteropod populations have never been investigated in the Mediterranean Sea. Here we assess the changes in pteropod abundance at Point B in relation to declining pH, and attempt to identify the physical factors controlling inter-annual changes in their abundance. The copepod group was analysed to provide contrast using a group not directly affected by a decrease in calcium carbonate saturation state.

MATERIALS AND METHODS

Sampling site

Point B (43° 41.10′ N, 7° 18.94′ E) is located at the mouth of the Bay of Villefranche-sur-Mer (Fig. 1). The site has a depth of ~80 m and is situated on a narrow continental shelf; a few kilometres offshore, the slope increases down to ~2000 m depth, giving this
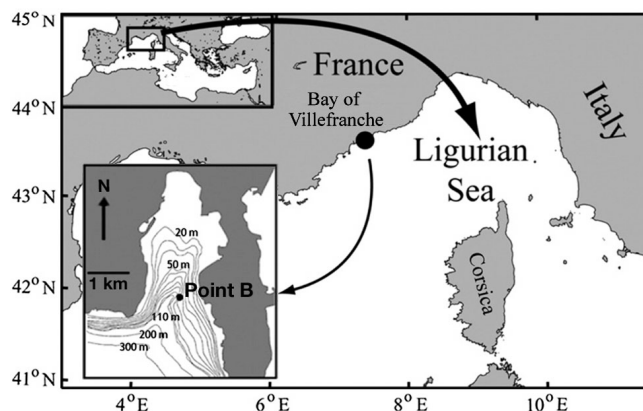

Fig. 1. Location of Point B in the Ligurian Sea

coastal site the characteristics of an open ocean area. The NAO has a significant influence on the area (Molinero et al. 2005). The site experiences strong seasonality, with chl *a* maxima during the spring months (Berline et al. 2012). The conditions during winter have been shown to strongly influence the productivity of the following year (Buecher et al. 1997, Garcia-Comas et al. 2011).

Environmental variables

Environmental variables were provided by the long-term hydrological time series run at Point B, which is now operated as part of the Service d'Observation en Milieu Littoral (SOMLIT/CNRS-INSU). Sampling is undertaken at depths of 0, 10, 20, 30, 50 and 75 m on a weekly basis. Temperature (T) and salinity (S) have been continually measured throughout the study period (1967–2003). Further information on environmental sampling methods is available at the SOMLIT web site (http://somlit.epoc.u-bordeaux1.fr/fr/). T and S were averaged over the full depth profile for the calculation of annual anomalies. Values for 20 and 50 m depths were also used to assess differences above and below the thermocline. Wind speeds were provided by Météo France.

During the years 2007–2012, water for the determination of total inorganic carbon (C_T) and total alkalinity (A_T) was collected using 10 l Niskin bottles, transferred to combusted glass bottles, overfilled, and poisoned with $HgCl_2$ as recommended by Dickson et al. (2007). C_T and A_T were determined colorimetrically and potentiometrically, respectively (Edmond 1970, DOE 1994).

Sea water density (kg m^{-3}) was calculated from T, S and pressure (P), using the UNESCO formula implemented in the R package OCE (Fofonoff & Millard Jr.

1983, Kelley 2013). A_T was calculated from monthly averages of T and S using a variation of the equations provided by Lee et al. (2006), where A_T is in µmol kg^{-1} and a, b, c, d and e are constants:

$$A_T = a + b \times S + c \times S^2 + d \times T + e \times T^2 \qquad (2)$$

The most parsimonious model was determined from Eq. (1) using Akaike's information criterion on sub-sampled (1 per 10 wk, to reduce autocorrelation of the time series) alkalinity measurements taken from 2007–2012. The temperature variables were dropped as they did not affect the goodness of fit of the model to the measured data. The coefficients a, b and c were derived using all the weekly measurements of alkalinity taken from 2007–2012. Finally, the calculation of A_T was extended for the years 1967–2006.

The partial pressure of CO_2 (pCO_{2sw}) was estimated from T and the concentration of CO_2 in the atmosphere (CO_{2atm}, ppm) using Lefevre & Taylor (2002):

$$pCO_{2sw} = a \times T + b \times pCO_{2atm} + c \qquad (3)$$

There are no measurements of CO_{2atm} in the Mediterranean region covering the entire study period (1967–2003). The Mauna Loa (19°53′ N, 155°57′ W, Hawaii) atmospheric CO_2 time series was used, as this is the only station in the northern hemisphere that has data for the entire study period. To account for geographical differences, the data were compared to the CO_{2atm} time series from the Italian station, Monte Cimone (44°18′ N, 10°7′ E), which operated from 1979–1995. Seasonal differences were minimised by lagging the Mauna Loa data by 2 mo and adjusting the Mauna Loa seasonal maxima and minima to obtain the best fit with the data from Monte Cimone. The coefficients were determined using a linear model for 1 m depth based on pCO_{2sw} values computed from weekly measurements of C_T and A_T made by SOMLIT from January 2007 to March 2012.

Using the estimations of A_T and pCO_{2sw} alongside the measured values of T, S and P, it was possible to calculate seawater pH using the R package Seacarb (Lavigne & Gattuso 2013). Weekly measurements of pH_T at Point B began in 2007. These measurements (2007–2012) were used to assess the goodness of fit of the calculated data.

Zooplankton time series

Daily zooplankton sampling (Monday to Friday) has been performed at Point B from 1968–2003, using the Juday Bogorov net (330 µm mesh size and 50 cm opening diameter, vertical haul from 0–75 m performed at midday), which has a mesh size appropriate for catching the full range of pteropod species present in the area. The daily samples from each week were pooled into one beaker to form a weekly sample, thereby overcoming issues with localised patchiness. The pooled weekly samples were preserved in formalin (2.5%) buffered with borax (sodium borate) until saturation. The preserved weekly samples were sorted using the Zooscan digital imaging system (www.obs-vlfr.fr/LOV/ZooPart/ZooScan/; Gorsky et al. 2010). Each sample was split and analysed in 2 size fractions to avoid biased representation of large, rare organisms (Garcia-Comas et al. 2011). Zooplankton analysis with the Zooscan works in 4 steps: (1) digitalisation of the sample, (2) image analysis and morphological feature extraction, (3) automatic recognition using a training set, and (4) validation by an expert. During the regular observations undertaken at the Observatory of Villefranche, step 3 sorted all images into broad categories (20 on a standard basis, with an average correct classification of 0.6 and a contamination [non-pteropods sorted into pteropod folder] of 0.23 for the 2 morphotypes of pteropods identified at this step) (see Table 2 in Gorsky et al. 2010). The automatic sorting was then validated, and further classified into more detailed categories (typically 45 groups) during step 4. During this last step, the pteropods were visually sorted into the 3 morphotypes: Cavoliniidae, Limacinidae and Creseidae (including *Creseis* spp. and *Styliola subula*). Limacinidae are clearly distinguishable from gastropod veligers based on body and shell shape, size and sampling season; however, any ambiguous images were discounted from the analysis, which may account for the low abundances of Limacinidae. Copepod abundance was also analysed to provide a common zooplankton group for comparison with the pteropods.

Analyses

Monthly averages of environmental and zooplankton data were used, with missing data being linearly interpolated. For each times series of both environmental and zooplankton data, <30 observations were missing from the 432 monthly averaged observations. Zooplankton time series were log-transformed ($\log_{10}$[abundance + 1]) in order to better describe periods outside of the bloom when abundances were very low. CUMSUM (cumulative sum of differences

from the mean) analysis was used to identify turning points in abundance above or below the mean of the series (Ibanez et al. 1993). To assess the environmental forcing on zooplankton abundances, 2 principal component analyses (PCA) of seasonal anomalies (normalised by SD from the annual mean) were performed using the R package FactoMineR (Lê et al. 2008) on environmental data (with biological data added as supplementary variables) and on zooplankton abundances. Seasons were defined following Vandromme et al. (2011): winter = Jan–Mar, spring = Apr–Jun, summer = Jul–Sept, autumn = Oct–Dec. Seawater densities were not included in the PCA because they were computed from T and S, and the strong correlation among these variables could artificially alter PCA results. CUMSUM analysis was used to highlight the turning point values above or below the mean of the series, for PC1 of biological and environmental variables (Ibanez et al. 1993). The year 1981 was excluded from the analysis, as there were 7 consecutive months when data was missing.

Singular spectrum analysis (SSA; Allen & Smith 1996) was performed using the R package RSSA (Korobeynikov 2010) on normalised monthly means to search for statistically significant periodic components in the environmental and zooplankton time series. SSA is well suited for use with short and/or noisy time series, identifying trends, oscillations and noise within the dataset. To minimise noise to signal ratio, as large a window as possible was used, while remaining under half of the length of the time series (Allen & Smith 1996). Trends were analysed using SSA of non-log-transformed data, as transformation can cause inaccurate estimation of trends. The window size used for the analysis presented herein was 200 mo. As this is a relatively large window in comparison to the total length of the series, results were checked for robustness by comparison with analyses undertaken using a smaller window (150 mo), which obtained similar results. All statistical analyses were undertaken using R 3.0.1 (R Core Team 2008).

RESULTS

The results from the model prediction of pCO_{2sw} values were accurate when compared to 'real' values calculated from A_T and C_T measured at Point B, producing an r^2 of 0.89. The extreme high values that occurred in September 2009 were not replicated by the model (Fig. 2A); it is likely that these values were related to local events that were not possible to replicate with Mauna Loa pCO_{2atm} data. Comparison of
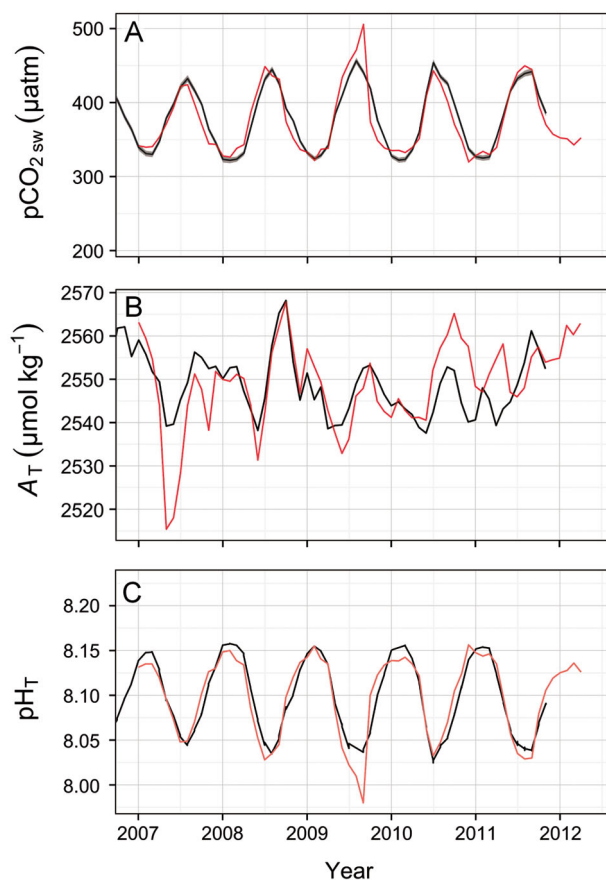

Fig. 2. (A) Estimation of monthly means of pCO_{2sw} calculated from the Mauna Loa pCO_{2atm} time series and the SOMLIT temperature time series (black) and monthly means calculated from A_T (total alkalinity) and C_T (dissolved inorganic carbon) measured by the SOMLIT from 2007 to 2012 (red). (B) Estimation of monthly means of A_T values calculated from the SOMLIT salinity time series (black) and measured monthly means from 2007 to 2012 (red). (C) Estimation of monthly means of pH_T values based on calculations of A_T, pCO_{2sw} and the measured values of salinity and temperature (black) and measured monthly means from 2007 to 2012 (red)

estimated A_T with measured values from 2007–2012 using linear regression produced an r^2 of 0.39. The overall trend of fluctuations in A_T was well predicted; however, the model did not replicate the periods of short-term high variability in A_T that are evident in the measured values (Fig. 2B). This lack of resolution may be the cause of the relatively low r^2 value. Comparison of calculated surface pH_T values to measured values (2007–2012) using linear regression produced an r^2 of 0.49; as the model failed to accurately predict the extreme low observations, these observations corresponded to a peak in pCO_{2sw} during 2009 that was not predicted by the pCO_{2sw} model. However, the high values were well predicted and the overall
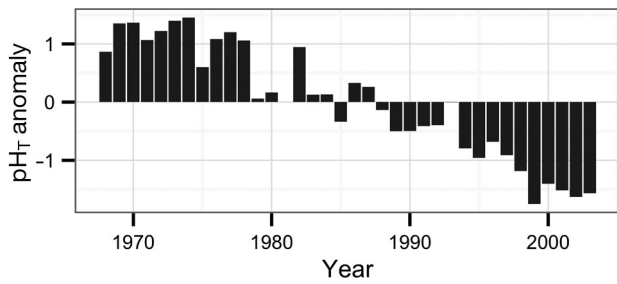
Fig. 3. Standardised annual anomalies of calculated pH_T

trend and seasonal oscillations fit well with the real data (Fig. 2C). The surface pH_T hind-cast shows a decreasing trend, with a decrease in annual mean pH of 0.05 pH_T units over the study period (1967–2003), or 0.014 units per decade. Standardised anomalies of annual means of predicted pH_T values (Fig. 3) reflect the steady downward trend, with values being mostly above average up to 1982 and mostly below average from 1983–2003.

SST showed strong seasonal patterns (Fig. 4A) and ranged from winter minima of 12.4–14.7°C and summer maxima of 21.4–27.1°C. Alternating periods were observed, with temperature below the average until 1982, after which a warm period began, lasting until 1990 (Fig. 4D). Between 1990 and 1995, temperatures were again below average, but increased after 1995 and remained above average for the rest of

study period. Aside from the periodic oscillations, there was no significant increase or decrease in the long-term SST trend between 1967 and 2003. Salinity was less seasonally influenced than temperature (Fig. 4B). It ranged between 36.46 and 38.52, with the lowest values observed in spring and winter. Inter-annual variations in winter salinity also alternated between periods of low (before 1981, 1988–1998) and high salinity (1981–1987, after 1998) (Fig. 4E). Winter density at Point B was slightly below average for the first 3 yr of the series, and tended to oscillate in short, 3 to 5 yr cycles of high and low density (Fig. 4F). The variations from the mean were typically small, except for 2 yr in the 1980s (1981 and 1982). From 1996 onwards, values were all below average, except for the years 2000 and 2003. Seasonal variations showed lower densities in the summer during the early 1970s and the late 1990s to early 2000s (Fig. 4C). Higher densities were observed in the winter during the 1980s and early 1990s.

Within the pteropod family groups, Creseidae comprised *Creseis clava*, *C. virgula* and *Styliola subula.* Cavoliniidae was exclusively *Cavolinia inflexa*, and the group Limacinidae comprised *Heliconoides inflatus* and *Limacina retroversa.* The dominant species in the 3 groups were *Creseis clava*, *Cavolinia inflexa* and *H. inflatus*, respectively. Creseidae constituted the majority of the pteropod species sampled at Point
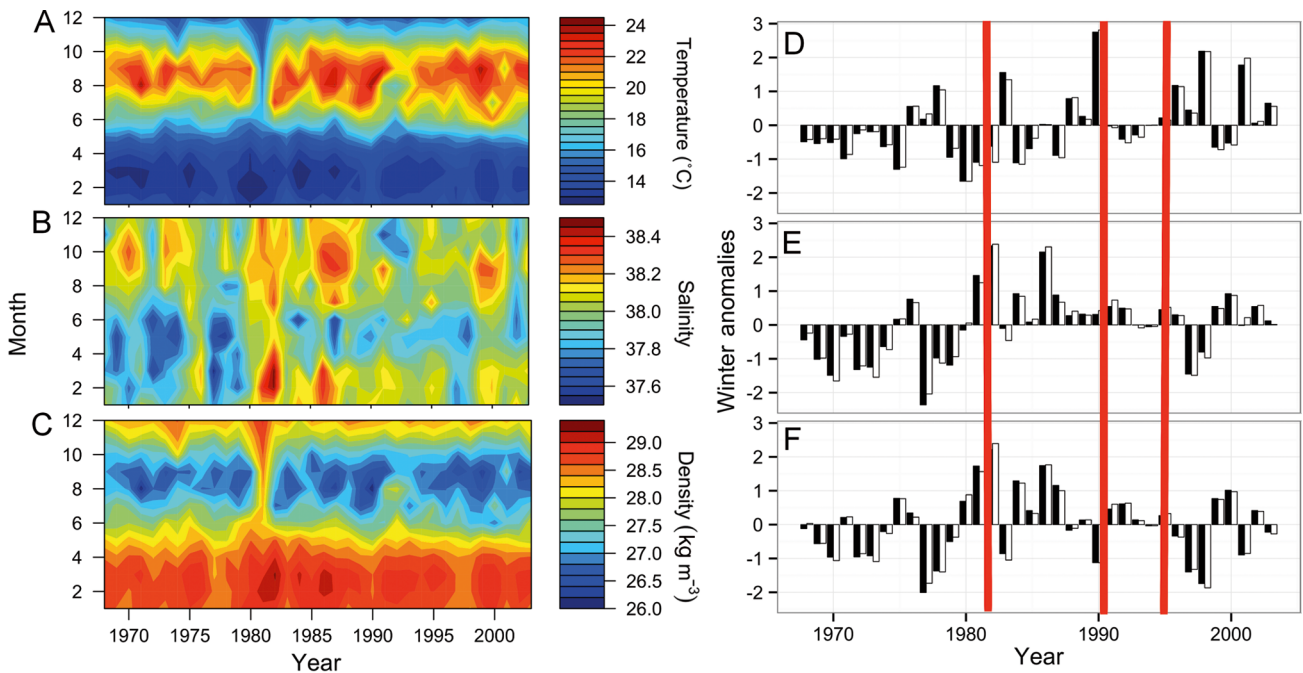

Fig. 4. Seasonal and inter-annual variability of (A) temperature, (B) salinity and (C) density at 20 m depth, and standardised winter (Jan–Mar) anomalies of (D) temperature, (E) salinity and (F) density at 20 (white bars) and 50 (black bars) m depths. Red lines: turning points in abundance of the zooplankton time series
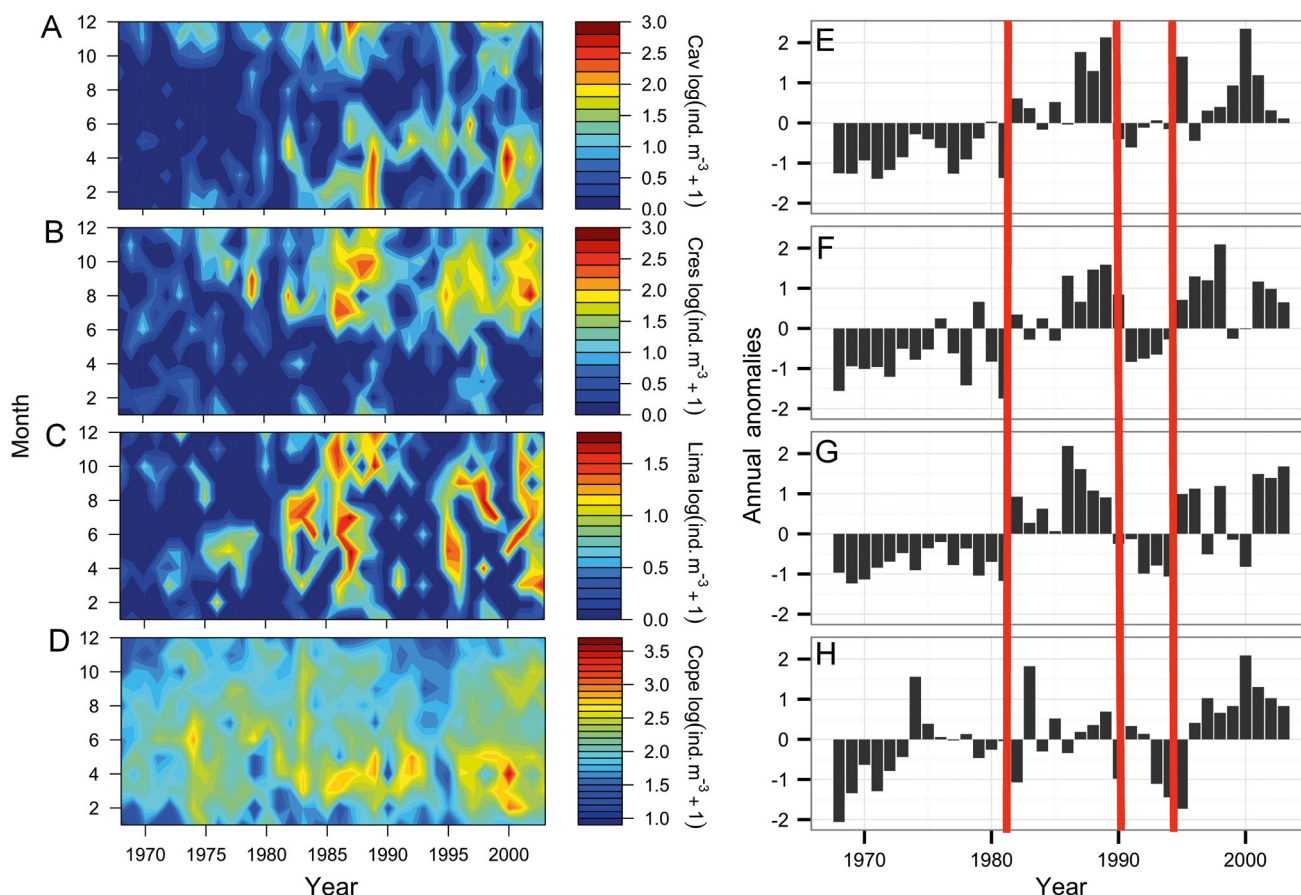
Fig. 5. Seasonal and inter-annual variability of (A) Cavoliniidae (Cav), (B) Creseidae (Cres), (C) Limacinidae (Lima) and (D) copepod (Cope) abundances (log ind. m^{-3}), and standardised annual anomalies of the abundances of (E) Cavoliniidae, (F) Creseidae, (G) Limacinidae and (H) copepods at Point B. Red lines separate alternating periods of high and low abundances

B (mean: 15.7 ind. m^{-3}; Fig. 5). Cavoliniidae had a mean abundance of 13.8 ind. m^{-3}. *Limacina* spp. were the least abundant (mean: 5.5 ind. m^{-3}, maxima: 60.8 ind. m^{-3}). Inter-annual abundances of all pteropod species alternated between low and high abundances on an approximately decadal timescale, with periods of high abundance during the mid to late 1980s and the early 2000s (Fig. 5E–G). Cavoliniidae exhibited no obvious changes in the timing of seasonal blooms (Fig. 5A); however, Creseidae bloomed during summer and early winter, with blooms occurring earlier in the year as the series progressed (Fig. 5B). Limacinid species tended to exhibit high abundances twice a year, with one bloom in spring and another in early autumn; during periods of low abundance, this pattern was less pronounced (Fig. 5C). Pteropod veligers were not observed for any of the groups, although juvenile stages were abundant.

Copepod abundances fluctuated inter-annually, with slightly lower abundances until the mid 1970s (Fig. 5H). This alternating trend has been previously

linked to inter-annual alternations between dry and wet years (Buecher et al. 1997), and was suggested by Garcia-Comas et al. (2011) to drive a nutrient enrichment process whereby dry conditions in the previous winter produce more intense convection (higher salinity, more heat loss from the sea surface and colder winter temperature, despite higher annual temperature). This loads more nutrients to the upper water layers, thereby favouring phytoplankton growth in the following spring. The enhanced spring bloom leads to a more abundant zooplankton community, exerting a 'bottom-up' control on their abundances (Garcia-Comas et al. 2011).

The first and second principal components (PC) of environmental variables explained 46 and 32% of the variance in the dataset, respectively. Temperature and salinity have strong positive loadings on PC1, while pH$_T$ and wind speed have strong negative loadings (Fig. 6A). Salinity is positively, and SST negatively, correlated with PC2. All pteropod groups are positively placed with respect to PC1, while cope-

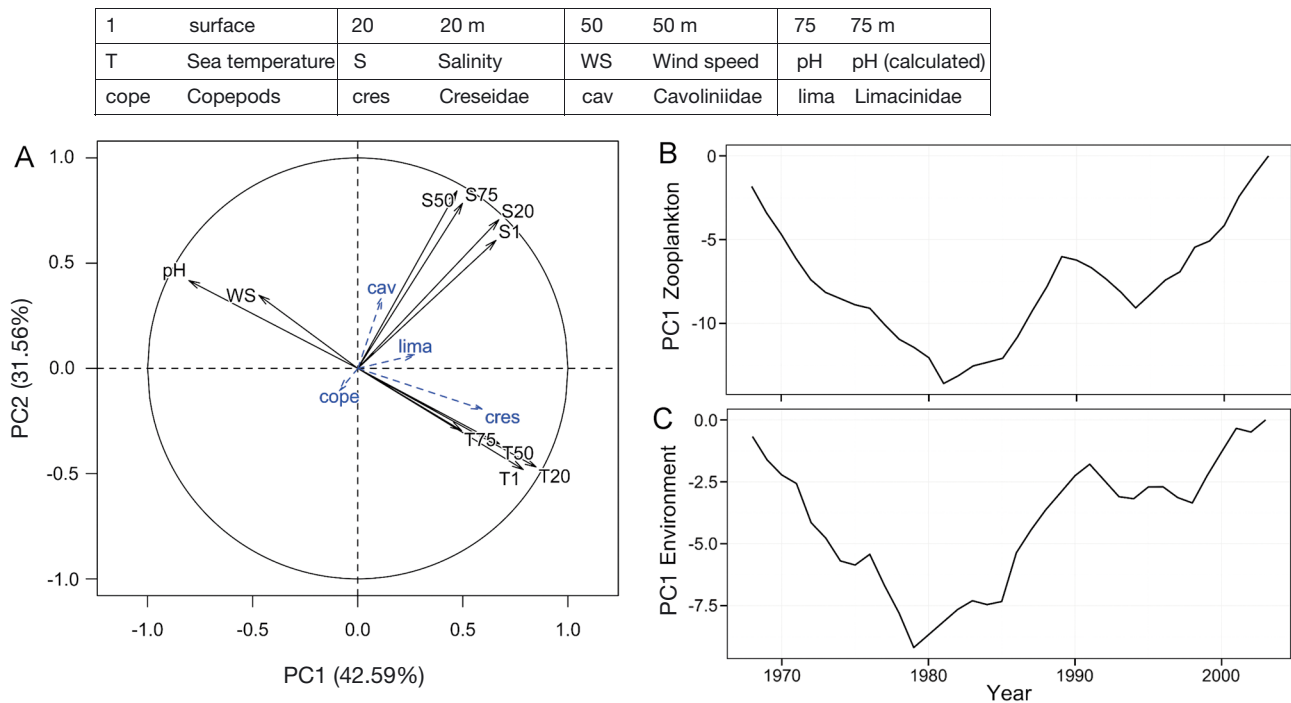| 1 | surface | 20 | 20 m | 50 | 50 m | 75 | 75 m |
| T | Sea temperature | S | Salinity | WS | Wind speed | pH | pH (calculated) |
| cope | Copepods | cres | Creseidae | cav | Cavoliniidae | lima | Limacinidae |

Fig. 6. (A) Principal component analysis of environmental variables at Point B (1968–2003), with biological data as supplementary variables, and CUMSUM (cumulative sum of differences from the mean) of the first principal components of the PCA of (B) zooplankton abundances and (C) environmental variables

pods are negatively correlated with PC1. Both Cavoliniidae and Limacinidae are positively correlated with PC2, while Creseidae are negatively placed with respect to PC2. Creseidae abundances are strongly positively associated with surface temperatures, while Cavoliniidae abundances correlate with salinity below 50 m depth. Limacinidae do not show a close association with any of the environmental variables. Copepods also have no close correlation with any environmental variables; however, this may be due to the coarser taxonomic sorting of this group as the copepod group contains both herbivorous and carnivorous species. The cumulative sums of both PC1s for the environmental PCA and the biological PCA show an oscillating pattern of 4 periods, with turning points at 1981, 1989, and 1994 for biological variables, and 1979, 1991 and 1998 for environmental variables (Fig. 6B,C).

SSA performed on non-log-transformed abundances showed an increasing trend associated with the 1st eigenvalue for all pteropod species. The trend accounts for 10, 13 and 19% of the total variance in Cavoliniidae, Creseidae and Limacinidae, respectively. No significant trend was found for copepods. SSA analysis revealed a clear annual component in all zooplankton groups, which is expected in a temperate, seasonal environment. All pteropod groups

exhibited a quasi-decadal oscillation (Fig. 7A–C) above the noise level for all pteropod species groups, which explains 2, 4 and 5% of the variation in Creseidae, Cavoliniidae and Limacinidae, respectively. The oscillations occur every 11.2, 9.9 and 16.7 yr for Cavoliniidae, Creseidae and Limacinidae, respectively. Sea temperature (averaged over depths 0, 20, 30, 50 and 70 m) also displayed a quasi-decadal component of ~15.3 yr oscillations associated with the 1st and 2nd eigenvalues (Fig. 7D), which accounted for 10% of the total variance. Copepods did not show a significant decadal component; however, a 6.3 yr oscillation (Fig. 8A) associated with the 9th and 10th eigenvalues was identified. This component was barely above the noise level and explained only 0.2% of the variance, as the series is strongly dominated by the annual component. Density displayed a similar pattern, with a 6.9 yr oscillation (Fig. 8B) on the 1st and 2nd eigenvalues, accounting for 17% of the variance in the series.

DISCUSSION

The objective of this study was to investigate the inter-annual changes in pteropod populations, assessing their response to long-term climate (tempera-
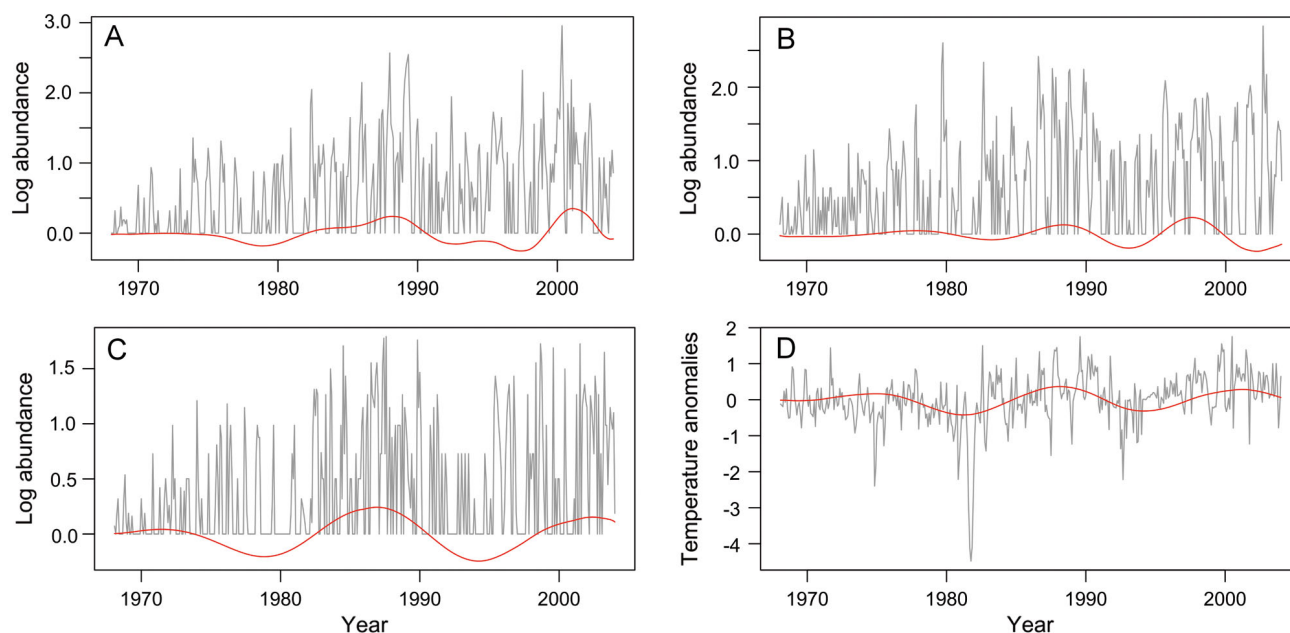
Fig. 7. Quasi-decadal periodic component (red line) extracted from the time series: (A) Cavoliniidae, (B) Creseidae, (C) Lima-cinidae and (D) normalised sea temperature for integrated 0–75 m depth
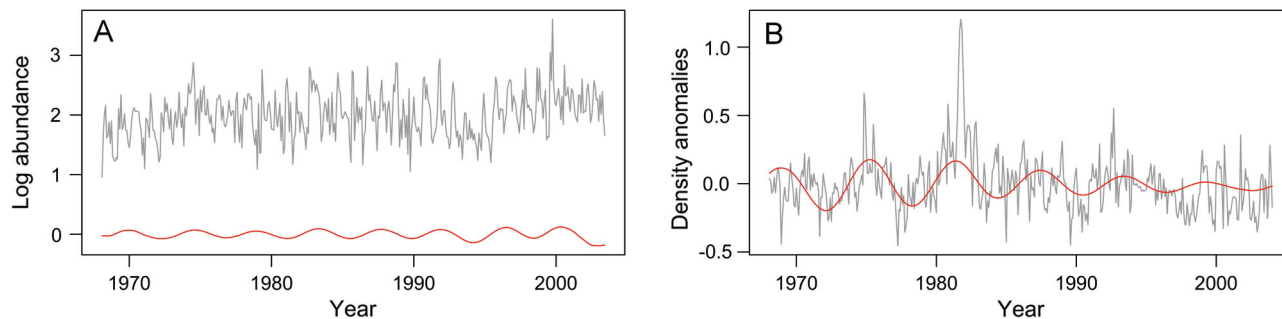

Fig. 8. Approximately 6.5–7 yr periodic component (red line) in (A) copepod abundance and (B) normalised seawater density for integrated 0–75 m depth

ture) and decreasing pH. Comparison with the bet-ter-studied copepod time series was used to highlight any differences in abundance which may have been directly caused by pH and saturation state.

Pteropods were present in lower numbers than copepods, with less consistent patterns of abun-dance. The vertical sampling depth of 0–70 m is not ideal for year round sampling of pteropods, as the depth ranges of the main species present at the site reach far deeper, down to 1000 m (Rampal 1975). The site depth of 200 m is also a relatively shallow envi-ronment for pteropods. Despite these factors, the average abundances of Cavoliniidae found in this study are comparable to those found across the wider Ligurian and Tyrrhenian Seas by Andersen et al. (1998). Limacinidae are particularly underrepre-

sented relative to the other 2 groups, likely due to sampling bias. The small body size of *Heliconoides inflatus* (the most abundant limacinid at the site, maximum shell diameter = 1200 µm) may have led to undersampling of the juvenile population by the 330 µm mesh net (Wells 1973). Despite these consid-erations, this time series was the longest running in the area that was taken with a mesh size appropriate for catching a wide range of both adults and juve-niles of the species present at Point B. The mesh size used also excluded veligers of all species groups. As veligers can constitute a significant portion of the population (Gannefors et al. 2005), it is likely that a significant proportion of the population was not col-lected. As the proportion of the sampled population was size dependent, it is possible that the observed

seasonal 'blooms' may be the result of size biased sampling rather than the presence or absence of the animals from the sampled water column (Wells 1973).

Fluctuations in global and local temperatures are well documented (Bethoux & Gentili 1996, Vargas-Yanez et al. 2008, Levitus et al. 2009), but there is paucity of long-term pH and seawater carbonate system measurements. Records of atmospheric CO_2 are better documented, although the only northern hemisphere time series that covers the entire study period was the series at Mauna Loa. The effects of biological activity are not considered in the pCO_{2sw} estimation of this study; however, the comparison of the model results with data calculated from 'real' values (calculated from measured A_T and C_T) was highly robust. Despite inaccuracies in predicting extreme low values, the pH hind-cast produced a decreasing trend that is towards the lower end of the range of −0.0014 and −0.0024 yr^{-1} reported in the 5th Assessment Report of the Intergovernmental Panel on Climate Change (Rhein et al. 2013). This rate is comparable to the one reported by Touratier & Goyet (2011) for the Western Mediterranean from 1870 to the present. Due to the short residence time of Mediterranean waters, it has been estimated that the entire water column has been contaminated with anthropogenic CO_2 (C_{ant}; Touratier & Goyet 2011). Touratier & Goyet (2011) also show that, in the area surrounding Point B, C_{ant} is homogeneously distributed over the first 500 m water depth, thus the calculation of surface water pH_T should be representative of the net sampling depth.

Despite a clear decreasing trend in estimated pH of 0.05 units as a result of anthropogenic CO_2, neither pteropod nor copepod abundances have been affected. It is important to note that seasonal pH fluctuations are high: ~0.1 units larger than the average decrease over the study period. The Mediterranean is an evaporation basin, resulting in high alkalinity, which maintains supersaturated conditions with respect to calcite and aragonite. At its highest during the study period (1967–2003), estimated Ω_{ar} was 4.3 (1968), with a minimum of 3.1 in 2003. Studies that have shown Mediterranean pteropods to be sensitive to changes in carbonate chemistry have focused on future conditions and exposed individuals to saturation states that are well below those experienced during our study period, starting with Ω_{ar} of 3.1 as a control treatment and decreasing to 0.3 (Comeau et al. 2010a, Comeau et al. 2012b). Comeau et al. (2012a) show evidence that during short-term incubations (8 d), Arctic pteropods are capable of extending their

shells in waters undersaturated with respect to aragonite, suggesting a degree of short-term adaptability to changes in Ω_{ar} that may also be present in Mediterranean species. The results of Comeau et al. (2012a) suggest that the change in supersaturation during the study period might not have significantly affected net calcification, as the conditions in the Mediterranean remain highly saturated with respect to aragonite. Despite the apparently favourable conditions, the long-term effects of a decrease in supersaturation state are unknown, and long-term laboratory studies are required to clarify this point.

The observed insensitivity of pteropod abundances to recent decreases in pH agrees with time series observations in other ocean basins. Mackas & Galbraith (2011) state that it is unlikely that pH was the main driver behind changes in pteropod abundances in the NE Pacific (pH trends not analysed), as they observed a weak to significant increasing trend in *Clio pyramidata* but a decrease in the subarctic species, *Limacina helicina*. The authors deem it unlikely that ocean acidification response would be positive in one species and negative in another. The abundance of *C. pyramidata* also increased over a 57 yr time series (1951–2008) in the Central California Current System, while *L. helicina* remained constant (pH trends not analysed; Ohman et al. 2009). The same study also looked at the Southern California Current System where neither species displayed any changes in abundances. The analysis of a short time series (1994–2009) off the Antarctic Peninsula did not show any decreasing trend in pteropod populations but, instead, significant increases in the abundance of *L. helicina* and *Spongiobranchaea australis* associated with a climate regime shift to cooler conditions (Loeb & Santora 2013). This is in contrast to recent work by Beare et al. (2013) who reported a decline in pteropods in the North Sea over the last 50 yr. Unfortunately, pH records for this period are sparse and it is unclear whether pH is the driving factor controlling pteropod abundances; the authors concluded that the decrease is caused by a combination of climatic, chemical and biological factors. Beaugrand et al. (2013) also observed a decline in *Limacina* spp. in the North Atlantic between 1960 and 2009; they concluded that temperature, rather than pH, was the major driver, but did not discount a secondary effect of pH.

The effect of temperature on pteropod abundances appears to be more critical than that of pH, which can be seen in the results of the PCA. A large portion of the variance (44 %) in the zooplankton time series is explained by the oscillating trend shown in PC1

(Fig. 6B). This trend is similar to that identified for other zooplankton groups at Point B (Garcia-Comas et al. 2011, Berline et al. 2012) and bears a close resemblance to PC1 of the environmental data (Fig. 6C). This alternating trend is linked to inter-annual alternations between dry and wet years (Buecher et al. 1997), which was suggested by Garcia-Comas et al. (2011) to drive a nutrient enrichment process, suggesting that food availability is the main driver of changes in zooplankton abundance.

Prior to 1990, winter temperatures and salinity interacted to produce deep convection, loading nutrients to the surface waters to provide favourable conditions the following spring. The 1968–1970 low pteropod and copepod abundance period corresponded to a cool period with low salinity. The 1980s experienced warmer than average years, due to warm summers but also very cold winters and high salinities, leading to better mixing and the build-up of zooplankton populations. From the 1990s onwards, pteropod abundances were decoupled from changes in salinity and co-varied closely with temperature, being higher during warmer periods. The period of low pteropod abundance at the start of the 1990s is correlated with a decrease in both winter and summer sea temperatures, and above average winter salinity. The subsequent recovery of pteropod abundance coincided with a shift back to warmer summer temperatures (Fig. 3) and lower rainfall at the end of the 90s (not shown).

It is well documented that zooplankton populations are highly sensitive to temperature, and often show complex and unpredictable responses (Richardson 2008). The most commonly occurring species of each of the pteropod family groups included in the analysis have tropical to sub-tropical distributions and are found in waters up to 28°C (van der Spoel 1967). Conditions at Point B do not currently reach the maximum temperature ranges of the dominant pteropod species; therefore, it is feasible that warmer periods are conducive to increased fitness and the observed higher abundances. It is possible that higher temperatures at Point B in the late 1990s allowed faster pteropod growth and development, leading to a larger breeding population. The sensitivity to temperature can also be observed in the extended bloom periods of Cavoliniidae and the earlier timing of Creseidae blooms throughout the year (Fig. 5A,B).

The singular spectrum analysis highlighted similar oscillating quasi-decadal periodicity between sea temperatures and all pteropod groups. The periodicity identified in this study for both temperature and the abundances of pteropod groups is in the same range as the quasi-decadal oscillations of the NAO (Deser & Blackmon 1993). This supports the findings of past work that have identified the NAO as a controlling factor of zooplankton abundances in the region (Molinero et al. 2005, 2008a,b, Garcia-Comas et al. 2011). The cyclical population fluctuations caused by the NAO have the potential to be further impacted by climate change stressors, which could push organisms already at the limits of their thermal tolerance (Beaugrand et al. 2008). A correlation with inter-annual temperature oscillations was not seen in the copepod time series, which showed a closer link to seawater density; both copepod and seawater density time series exhibited a ~6 yr cycle, supporting the strong link proposed by the 'bottom-up' hypothesis.

Explanations for the differences in pteropod and copepod abundances could be due to the differences in life history traits or trophic regimes. Copepod peaks of abundance at Point B are correlated with optimum feeding conditions during spring phytoplankton blooms. The annual blooms of pteropods at Point B begin later in the year than the copepod blooms, with most pteropods appearing in summer or autumn. Pteropod peaks in abundance are thought to be related to seasonal vertical migrations linked to reproduction more than to food availability (Rampal 1975). Pteropods are passive feeders, utilising large mucous webs to collect food particles (Lalli & Gilmer 1989), and thus have a more omnivorous diet than many copepod species. Inter-annual fluctuations of the pteropod time series co-vary more closely with those displayed by jellyfish at Point B (Garcia-Comas et al. 2011). Like pteropods, the gelatinous predators (chaetognaths and jellyfish) at Point B bloom later in the year compared to copepods, suggesting that differences in the copepod and pteropod abundances may be related to trophic regime. It should also be noted that the taxonomic resolution of the pteropod groups was higher than that of the copepods, which included both herbivorous and carnivorous species. It is possible that sorting to a higher taxonomic resolution may diminish or accentuate differences between pteropod and copepod abundances, depending on their trophic regime.

While high temperatures are currently favouring high abundances of pteropods at Point B, this sensitivity may make them vulnerable to the effects of climate change. The highest SST observed in the time series was 27°C; an increase of 2–2.5°C (predicted for the end of the century; Lazzari et al. 2013) produces maxima in SSTs that could exceed the upper tolerance limit of these species (van der Spoel 1967). As

these values represent surface maxima, the entire water column will be within the optimum temperature window for these species for most of the year. However, the highest temperatures will occur during late summer and early autumn, coinciding with the breeding seasons of *Creseis clava* and *H. inflatus*, and the presence of juveniles in surface waters (Rampal 1975). As juvenile stages are often more sensitive than adult stages (Pineda et al. 2012), thermal stress may have a disproportionately severe impact on population fitness. Despite these projections, the results of this work suggest that the Mediterranean is, and will probably continue to be, one of the more favourable habitats for pteropods under changing climate. A decline in pH has, so far, had no deleterious effect on abundances and high temperatures correlate with increased numbers. Although this does not guarantee that saturation state or thermal limits will not be reached in the near future, the Mediterranean is likely to be one of the more suitable habitats for pteropods by 2100.

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