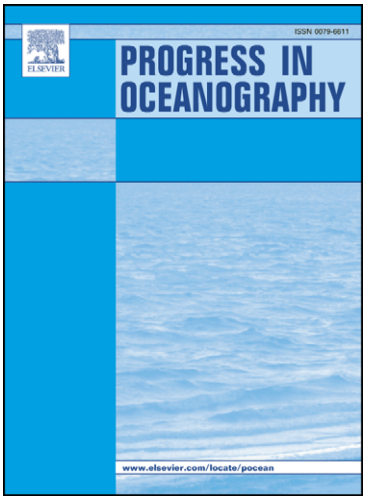

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Intercomparison of six Mediterranean zooplankton time series

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Abstract

We analyzed and compared Mediterranean mesozooplankton time series spanning 1957-2006 from six coastal stations in the Balearic, Ligurian, Tyrrhenian, North and Middle Adriatic and Aegean Sea. Our analysis focused on fluctuations of major zooplankton taxonomic groups and their relation with environmental and climatic variability. Average seasonal cycles and interannual trends were derived. Stations spanned a large range of trophic status from oligotrophic to moderately eutrophic. Intra-station analyses showed 1) coherent multi-taxa trends off Villefranche sur mer that diverge from the previous results found at species level, 2) in Baleares, covariation of zooplankton and water masses as a consequence of the boundary hydrographic regime in the middle Western Mediterranean 3) decrease in trophic status and abundance of some taxonomic groups off Naples, and 4) off Athens, an increase of zooplankton abundance and decrease in chlorophyll possibly caused by reduction of anthropogenic nutrient input, increase of microbial components, and more efficient grazing control on phytoplankton. 5) At basin scale, the analysis of temperature revealed significant positive correlations between Villefranche, Trieste and Naples for annual and/or winter average, and synchronous abrupt cooling and warming events centered in 1987 at the same three sites. After correction for multiple

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comparisons, we found no significant correlations between climate indices and local temperature or zooplankton abundance, nor between stations for zooplankton abundance, therefore we suggest that for these coastal stations local drivers (climatic, anthropogenic) are dominant and that the link between local and larger scale of climate should be investigated further if we are to understand zooplankton fluctuations.

Keywords
Zooplankton time series, taxonomic groups, climate indices, correlations, Mediterranean Sea, Balearic Sea, Ligurian Sea, Tyrrhenian Sea, Adriatic Sea, Aegean Sea

1. Introduction

The response of marine ecosystems to climate variability is a topic of high interest, from both observational and modeling points of view (e.g. Hänninen et al 2000, Beaugrand and Reid 2003, Sarmiento et al 2004, Frederiksen et al 2006, Richardson 2008). Zooplankton, because of its short life history, its sensitivity to temperature, and the fact that it is not harvested as fish, has been pointed out in several studies as an interesting candidate for studying the response of ecosystems to change in the climate system (Beaugrand 2005, Hays et al 2005, Richardson 2008). Zooplankters are affected by the primary producers' fluctuations, and propagate them to the higher trophic level of the pelagic ecosystem (squids, fishes and mammals). In particular, zooplankton fluctuations can reflect regional to basin scale climate fluctuations. Indeed, significant correlations between zooplankton communities and the main modes of climatic variability such as the North Atlantic Oscillation (NAO), El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) have been reported in many works and for various oceanic regions (e.g. Fromentin and Planque 1996, Mantua et al., 1997, Beaugrand et al 2000, McGowan et al., 2003, Greene et al 2003, Drinkwater et al 2003, Molinero et al 2008) and supported by direct (e.g. temperature, transport) or indirect (e.g. trophic interactions) causal links. Ecosystem change can also take the form of "regime shifts", which are "persistent radical shift in typical levels of abundance or productivity of multiple important components of marine biological community structure, occurring at multiple trophic levels and on a geographical scale that is at least regional in extent" (Bakun 2004, see also Reid et al 2001, deYoung et al 2004). Such transitions are generally forced by changes in the physical climate system or by anthropogenic factors (deYoung et al 2004).

In the Mediterranean Sea, broad scale studies of climate impact on zooplankton variability are not as common as in the Pacific and Atlantic oceans. However, in the past three decades, local changes in hydrography and biota have been reported. In the Western Mediterranean, changes were reported in the distribution of fish and benthic species following the gradual warming of surface, intermediate and deep waters (Astraldi et al. 1995, Bianchi and Morri 2000, Bianchi 2007, Bethoux et al 1990, Sparnocchia et al 1994, Sabatés et al 2006). Changes in the community structure of copepods in the Gulf of Lion were attributed to increased temperature and subsurface salinities (Kouwenberg 1998). An increase of gelatinous zooplankton relative abundance with respect to copepod at the end of the 1980s was reported in the Ligurian Sea (Molinero et al 2005a). In 1999, in the Ligurian Sea, a large mass-mortality event of benthic organisms was observed (Cerrano et al. 2000; Pérez et al. 2000), when a positive thermal anomaly during summer combined with an increase in the warm mixed layer down to a depth of 40 m. In the Adriatic, a warming trend was reported over 1970-2000 (Dulčić and Grbec 2002), a strong increase of primary production occurred during the 80s (Marasović et al., 1995, 2005) and large fluctuations of fish catch were recorded (Guidetti et al. 2002, Grbec et al. 2002, Santojanni et al. 2003). Changes at the end of the 80s in the abundance and phenology of several copepod taxa, and in total copepod abundance in the Gulf of Trieste were reported by Conversi et al. (2009), who hypothesized that these were due to the changes in the Eastern Basin circulation and to the area warming. In the Eastern Mediterranean Sea, a shift of the source of deep waters from its usual southern Adriatic source to a new Aegean source caused major changes in deep water masses and circulation at the end of the 1980s, a phenomenon called the Eastern Mediterranean Transient (EMT, Lascaratos et al. 1999). The EMT influenced zooplankton in the Ionian sea (Mazzocchi et al., 2003) and possibly in the North Adriatic (Kamburska and Fonda Umani 2006, Conversi et al., 2009). Anthropogenic changes such as eutrophication have also been identified in the NW Mediterranean, Adriatic and Ligurian Sea for instance, as reviewed in Duarte et al. (1999).

Previous studies reporting changes in mesozooplankton in the Mediterranean Sea have examined either several taxa at a single station (e.g. Molinero et al., 2005a, 2008, Fernández de Puelles et al., 2007) or a single species at several locations (Mazzocchi et al., 2007). Despite the need for a consistent picture of the climate-plankton variability over the entire basin and the existence of interesting time series data sets at several locations across the Mediterranean Sea, there is a lack of intercomparison of local data sets and common analysis with regards to climate variability at larger-than-local scale. This is due partly to restricted access to the data, to the heterogeneity of sampling efforts and to the absence of international collaborations. These limits are alleviated within the EU integrated project SESAME (Southern European Seas: Assessing and Modelling Ecosystem changes), aiming at the detection of climate change impact on Mediterranean plankton and thus encouraging the collection and comparative analysis of the existing long term data sets. The objective of the present work, conducted in the framework of the above project, was to gather zooplankton time series data sets spanning the last 50 years (1959-2006) collected at six coastal areas across the Mediterranean Sea, to conduct a joint analysis and comparison. Doing so, this work follows the lines of the SCOR 125 effort for a global comparison of zooplankton time series (Perry et al 2004). The analysis focuses on taxonomic group fluctuations in relation with environment and climate variability.

Section 2 provides a description of the areas under study, and the data and numerical methods applied. Sections 3, 4 and 5 contain results. Discussion and conclusions are given in sections 6 and 7.

2. The time series

2.1. Environmental setting of zooplankton time series

The location of sampling stations and main geographical names are presented in figure 1. For each time series from the Western to the Eastern basin, the abiotic setting is summarized.

Baleares station (BAL) is located 4.6 km from Mallorca Island, at 77 m bottom depth on a shelf strongly influenced by open ocean circulation, composed by a mixture of waters from the Northern Mediterranean current to the north and from Atlantic waters from the Alboran basin to the south (Fernández de Puelles et al., 2003a and b). Surface water temperature peaks in August (26.6°C) and is minimal in February (14.4°C). Salinity variations are very irregular, with no clear seasonal cycle, in relation to mesoscale processes in neighboring areas and the large variability of water masses advected to the station (Fernández de Puelles et al., 2007). Low values of chlorophyll are always recorded (annual mean 0.28 mg/m^3), as expected in this oligotrophic area. Large scale climate variability in the North Atlantic (e.g. NAO) explains a large part of the hydrographic changes and also the changes in abundance of main zooplankton groups (copepods, appendicularians, cladocerans, siphonophores, doliolids, and ostracods, Fernández de Puelles and Molinero, 2007, 2008).

Point B station of Villefranche (VLF) is located 400 m offshore at the mouth of Villefranche Bay, at 80m on a narrow continental shelf. Because water depth drops to 2000m at a few kilometers offshore, the site has a marked open ocean character. Water circulation is dominated by the Northern Mediterranean current, and the local hydroclimate is closely correlated with the NAO (Molinero et al., 2005a,b). Surface water temperature peaks in August (24°C) and is minimal in February (13.2°C), while chlorophyll concentration ranges from 0.3 to 0.5 mg/m^3. Chl-a shows a clear seasonal cycle, with a marked spring bloom.

MareChiara station (NPL) is located 3.7 km off Naples, a very densely populated area, close to the 80 m isobath, in the boundary region between the coastal and the offshore systems (Mazzocchi and Ribera d'Alcalà 1995, Ribera d'Alcalà et al 2004). Surface temperature peaks in August (25.7°C) and has its minimum in March (14°C), Chl-a ranges from 0.3 to 0.85 mg/m3, while surface salinity also follows a clear seasonal cycle from 36.5 to 38 pss. Nutrients are rarely depleted (only in late spring, summer), and anthropogenic nutrient inputs are potentially important. A very regular annual cycle of the environmental parameters and zooplankton species was observed by Ribera d'Alcalà et al. (2004).

Station C1 (TRI) in the Gulf of Trieste is located 200 m from the shore, over 18 m depth, in a shallow, semi-enclosed bay. The local hydrography and planktonic community show a marked seasonality, superimposed with a large interannual variability (Cataletto et al 1995), related to the Isonzo river run-off, anthropogenic nutrient discharge, and to the advection of middle Adriatic water masses

(Cataletto et al 1995, Kamburska and Fonda Umani 2006). Surface temperature peaks in August (24.5°C) and has its minimum in February (8.2°C). Run-off maxima cause low salinity events (below 36 pss), and highly variable Chl-a blooms. The large seasonal range of water temperature (8- 24°C) is due to strong NNE Bora wind, which cools and mixes the shallow water column in winter.

Stončica sampling station (SPL) (Baranović et al 1993, Šolić et al 1997) is located 3.7 km offshore of Vis Island, off Split in the middle Adriatic, at 100 m depth. Surface temperature peaks in August (23.8°C) and has its minimum in March (13.4°C), while depth averaged chlorophyll varies from around 0.1 mg/m^3 in August to 0.22 mg/m^3 in February. This station is typical of the open middle Adriatic, strongly influenced by incoming Mediterranean water masses (Zore-Armanda, 1963), known as Levantine Intermediate Water (LIW) (Artegiani et al 1993). Even though it is not affected by land-derived materials, increased primary production was observed in the 1980s (Pucher-Petković and Marasović 1988).

Station S11 (ATH) in the Saronikos Gulf (Siokou-Frangou, 1996, Siokou-Frangou et al., 1998) is situated in the eastern inner area of the Gulf, at 7 km from the Athens domestic sewage outfalls and at 78 m depth. Before 1994, waste waters were untreated and disposed in the sea surface, whereas afterwards they received primary treatment and were released at 60m depth, below the seasonal thermocline. Surface temperature peaks in August (26.5°C) and is minimum in February (14.2°C). Salinity ranges between 38 and 39 pss depending on the variability of the inflow of Aegean water (Kontoyiannis et al., 2005). In 2002, the area was classified as mesotrophic and having good water quality (Simboura et al 2005).

2.2. Abundance and environmental data

[insert tables 1 and 2]

Stations geographical coordinates and corresponding time series are described in table 1. Hereinafter, the station codes given in table 1 are used to refer to the time series or the site. Sampling and counting methodologies are given in the references listed in table 2. The entire dataset extends from 1959 to 2006. Overlapping periods between stations are from 5 to 18 years long. SPL and BAL zooplankton time series do not overlap in time. Large gaps were present in NPL from August 1991 through February 1995 and in TRI from January 1981 to December 1985. Since species level data were only available for Naples and Trieste, analysis was restricted to broader taxonomic groups (noted TG hereinafter) for all time series. Species data were analyzed elsewhere (Mazzocchi et al, this issue, Mackas et al, this issue, Conversi et al, 2009, Fernandez de Puelles et al., 2009, Kamburska and Fonda-Umani, 2006). The TG presented in this work are:

copepods, cladocerans, chaetognaths, available in all time series, and

appendicularians, ostracods, pteropods, medusae, siphonophores, salps and doliolids, available in at least three time series. Note that the availability of a TG only means that counts were available, not that this TG was present or absent at a station.

Except for salps and siphonophores, Villefranche abundance data originate from the Zooscan imaging system (Gorsky et al 2010), and not from manual counting as the other time series. The automatic recognition results were checked, and compared to manual counting to ensure a good accuracy (Garcia-Comas et al submitted).

To characterize the zooplankton environment, temperature, salinity and Chl-a data from the sampling site were collected for periods including the zooplankton time series. At SPL and VLF, T and S were available for a longer period than zooplankton data. In TRI, only surface temperature data was available for the whole period. To complement in time the in situ temperature data, sea surface temperature data were obtained from the ICOADS gridded database available at www.cdc.noaa.gov/data/gridded/data.coads.1deg.html, based on in-situ data (Worley et al 2005). Surface temperature for the grid point corresponding to the stations locations was extracted for the period 1960 to 2006. In addition, time series of several climate indices were downloaded from the web: the North Atlantic Oscillation (NAO) index from www.cgd.ucar.edu/cas/jhurrell/indices.html and all other indices (Eastern Atlantic (EA), Eastern Atlantic/Western Russian (EA/WR), Arctic Oscillation (AO), Northern Hemisphere temperature (NHT) and Scandinavian pattern (SCA)) from ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/tele_index.nh.

2.3. Data processing

Abundance and environmental (temperature, salinity, Chl-a) time series with weekly or fortnightly sampling (VLF, NPL) were averaged to a monthly frequency. Then abundances in ind/m^3 were multiplied by 1000 and added to 1 so that all values are greater than 1, then were log transformed to stabilize the variance and obtain close to normal data distributions. To compare long term average abundance to total food availability, water column integrals were used (Chl /m^2 and ind/m^2).

For between site comparison of the average seasonal cycles, surface temperature data were used. For the other analysis, depth integrated (surface to bottom) temperature and Chl-a were used.

The average seasonal cycle (12 months) was computed from the transformed monthly abundances. As in Mackas et al. (2001), monthly anomalies were computed by removing the average seasonal cycle from the monthly time series. Seasonal (JFM/AMJ/JAS/OND) and annual anomalies were derived as the seasonal and annual average of the monthly anomalies, thereby excluding any missing months (Mackas et al. 2001). Annual average was built from the annual anomaly plus the average of the mean annual cycle. Anomalies computed from the log transformed time series have the advantage of canceling out any systematic multiplicative bias (e.g. due to sampling) present in the abundances (see O'Brien et al 2008), thus allowing the comparison of samples from different mesh size. For the Athens seasonally sampled time series, only years with more than two months of sampling were kept to improve the robustness of the analysis.

TG average seasonal cycles. For between sites comparison of TG seasonal cycles, each cycle was linearly scaled between 0 and 1. The timing of the seasonal peak was determined as the day of the year corresponding to the 15th of the month of maximum abundance. The same baseline period (1994-2003) was used to compute the average cycle and peak timing at each station, in order to avoid possible effects of the period of averaging (e.g. warm/cool). For SPL, as the time series stopped in 1991, the 1976-1985 period was used.

Cumulative sums. To highlight the changes in the local average, anomalies were standardized (zero mean and unit variance) and cumulatively pooled to get cumulative sums. The cumulative sum is a simple way to detect local changes and homogeneous periods in a time series (Ibanez et al., 1993). The interpretation of the cumulative sum curve is based on its slope: a constant deviation from the mean of the time series shows a constant non-zero slope. Persistent changes from the mean of the time series cause a persistent change of the slope.

Correlation analysis. For environmental variables, climatic indices and TG abundance, correlations were calculated only between time series of more than 9 pairs (ie 9 shared years) to get sufficient confidence in the correlation and to reduce the number of possible comparison. Correlations of TG with climate indices were considered with 0, 1 and 2-year lags. No detrending was applied prior to correlation to keep a potential common climatic trend. Pearson correlation coefficient was computed taking into account the reduction of degree of freedom due to autocorrelation (Pyper and Peterman 1998). Annual and seasonal anomalies were used. To ensure the robustness of correlation to outliers, a bootstrap resampling technique (10000 x) was used to get a 95% confidence interval for the correlation coefficient. Only correlations with confidence bounds of same sign were retained. As multiple comparisons are computed, the significance level of individual correlations should be corrected. The Benjamini and Hochberg (1995) correction was used to get the corrected significance levels.

Principal component analysis (PCA) was performed on standardized anomalies (zero mean and unit variance) of winter temperatures, so that each time series has the same weight. For comparison of TG abundance between sites, correlation analysis was preferred over PCA because all sampling periods do not overlap in time, preventing a global comparison. For salinity and Chl-a, correlation analysis was also preferred over PCA as overlapping periods were short and no additional data were available to complement the analysis.

3. Long term average and seasonal time scale

3.1. Temperature and Chl-a

[insert Figure 2]

The mean seasonal cycle of surface temperature and depth integrated chlorophyll concentration (Fig. 2) illustrates the contrast between the sites in the trophic status and hydroclimate. We define here the average Chl-a concentration as a proxy for nutrient availability, which we call trophic status. Largest temperature fluctuations were observed in the Gulf of Trieste, where the sampling site is very shallow and where strong Bora wind cools the water column in winter. In contrast, SPL had the smallest temperature range, while ATH was the warmest. From the Chl-a mean value and range, two groups of stations can be defined: oligotrophic, open sea stations (SPL, VLF, BAL) with low average and small ranges and mesotrophic-coastal stations (NPL, ATH, TRI) with large ranges and higher average. TRI low average Chl-a is due to its low depth compared to the other stations. SPL had the smallest Chl-a range while ATH had the largest. Chl-a peaks in winter for all series (February to March), while TRI and ATH have an additional autumn Chl-a peak (respectively in October and December).

3.2. Taxonomic groups (TG) long term average

[insert Figure 3]

As the average Chl-a partly differentiated the stations, TG abundances were plotted against Chl-a (Fig. 3). As TRI is very shallow (18m) compared to the other stations with depth ranging from 75 to 100m, depth integrated zooplankton and Chl-a is limited by the depth of the water column and not by productivity, therefore TRI is not included in the following comparison. Comparison is limited to the groups of stations with comparable mesh size (200-250 µm, BAL, NPL, ATH, TRI and 330µm, SPL, VLF). For copepods, cladocerans, and to a lesser degree appendicularians, the average abundances over the entire time series increased approximately steadily with average Chl-a. The two groups of stations could still be identified from these abundances, open-ocean with lower abundance and coastal with higher abundance. BAL stood apart with more abundant appendicularians compared to VLF, for a comparable Chl-a concentration. This may be due to a different community composition, or to the relatively short duration of the time series (10 years)

For other TGs, abundance was not increasing with Chl-a for several possible reasons:

Trophic behaviour: some TG do not feed directly, or exclusively on phytoplankton (carnivorous, as chaetognaths, medusae, siphonophores). Although many copepods are omnivorous, their total appears to depend on phytoplankton.

Community structure: the community structure can differ among stations of similar Chl-a concentration. Therefore difference in taxa dominance (mainly at species level) among stations can lead to differences in TG abundance, independently of Chl-a.

Sampling bias: certain TG, abundant or well sampled in some stations, are quasi-absent or poorly sampled in others (e.g. medusae, doliolids, siphonophores, appendicularians). Undersampling of small organisms (e.g. ostracods, pteropods, appendicularians) is expected at stations sampled with mesh size 330 µm (SPL, VLF). A bias is also expected for large organisms (e.g. medusae, siphonophores, salps), function of the volume sampled by the net with respect to the field density of the organisms and their swimming behavior. For these TG, abundances are not quantitative, and thus not easily comparable between stations.

Interestingly, for ostracods, pteropods and siphonophores, the abundance decreases with increasing chlorophyll concentration from BAL to ATH to NPL. The relative contribution of the first four TG was stable among stations (not shown): copepods (>50% of total abundance), then cladocerans, appendicularians and chaetognaths, except for BAL where appendicularians ranked second. The abundance of cladocerans (mainly *Penilia avirostris*) in neritic environment such as TRI, NPL and ATH decreases the copepod fraction (Ribera d'Alcalà et al. 2004, Siokou-Frangou 1996). Chaetognaths relative abundance was largest in SPL. Copepod dominance was often maintained throughout the year, although cladocerans could equal copepods abundance in late spring and summer.

3.3. TG average seasonal cycles

[insert Figure 4]

Average seasonal cycles are scaled to a unit range to compare only the pattern, and not the amplitude of abundances (Fig. 4). The shapes of the seasonal peaks are very similar for copepods, cladocerans, chaetognaths, and to a lesser degree ostracods and doliolids. On the contrary, there is no dominant pattern for appendicularians, siphonophores and medusae.

Five classes of pattern can be defined according to the season of the annual maxima:

late-winter-early spring TG - copepod
summer TG - cladocerans
fall-winter TG - ostracods
late-summer - fall TG: chaetognaths, pteropods (except for ATH), and doliolids (except for BAL)
Irregular TG - siphonophores, medusae, appendicularians

For copepods, several stations showed a large peak in March-April followed by a second peak in August-September. NPL cycle was peculiar as the peak intensified from April through summer. TRI had a second peak in November, nearly as high as the spring peak. This is consistent with the second peak observed in Chl-a (Fig. 2). Cladocerans showed a strong regularity in the peak, always in July-August, mainly due to *Penilia avirostris* outbursts. Although slightly shifted in time, VLF and NPL have similar seasonal cycles for most TG.

ATH abundances have a significant increasing trend for siphonophores and chaetognaths (see section 4, interannual variations), therefore their mean seasonal cycle is biased toward the recent years (2002-2004) with higher abundance. ATH pattern for ostracods and chaetognaths is different from the other stations, probably because of the short sampling period and large interannual variability at this station.

3.4. Between site comparison of TG peak timing

[insert Figure 5]

The median date and range of the seasonal peak of abundance is summarized in fig. 5 for copepods, cladocerans, chaetognaths, and Chl-a. Abundances peak successively at BAL, VLF and NPL for copepods and chaetognaths, and at BAL to VLF for cladocerans. The spring Chl-a peak (Fig. 5, stars) consistently precedes the copepod peak. For ATH and TRI, the respective timing differ between TGs. Apart from differences linked to the species composition of TG, this can be due to the larger interannual variability of the seasonal cycle in these stations, and to fewer data points (5 and 6 years respectively).

4. Interannual time scale

For each time series, interannual variations are analyzed based on annual averages and cumulative sums of annual anomalies.

4.1. Baleares

[insert Figure 6]

In BAL (Fig. 6), high copepod abundance was observed in 1996, 2000, 2001, 2002, and low abundance in 1994, 1995, 1997, 1998 and 1999. Appendicularians, cladocerans and siphonophores followed a similar pattern, while chaetognaths and doliolids showed a decreasing trend over the period. Environmental variables (T,S,Chl-a) were strongly covarying: higher temperature was associated with lower salinity and Chla as a result of water mass alternation. 1994-1996 and 2001, 2002, 2003 years were cold, saline and Chl-rich with a high influence of northern Mediterranean waters, while 1997, 1998 were warm and Chl-poor. Variations in hydrography were coherent with variations in zooplankton, with years 1997-1998 (warm and Chl-poor) standing out from the other years. No long term trend was detected.

4.2. Villefranche

[insert Figure 7]

In VLF (Fig. 7, middle panel), four transition periods of zooplankton abundance are identified on the cumulative sum chart (ca. 1979, 1982, 1990 and 1999), with an alternation between low and high abundance (a ca two fold change) coherent for copepods, cladocerans and chaetognaths. Medusae are less abundant before 1980. Doliolids and medusae are more abundant than average from ca. 1984 to 1990. After 2000, medusae and doliolids have opposite trends. Environment variables also show four distinct periods: a cool period from 1974 to 1985 (1987 for winter), then a warm period from 1985 to 1990, then cool until 1993, then warm again since 1993. Salinity cumulative sum approximately follows the zooplankton cumulative sum, with above average values from 1980 to 1990. From 1990 to ca. 2000, cooler and fresher waters coincided with lower zooplankton abundance.

4.3. Naples

[insert Figure 8]

In NPL (Fig. 8), mean abundances of copepods and cladocerans were 10 to 20% higher in the first (1984-1990) than in the second (1995-2006) part of the time series, although the slope of the trend reversed in 2002. Conversely, lower (resp. four and ten fold) abundances before than after the gap were observed for chaetognaths and pteropods. Abundances remained low and steady for appendicularians, medusae and doliolids, while siphonophores abundances were below average until 2001. Chl-a was 80% higher in the first period than in the second, paralleling copepods and cladocerans abundances. Salinity and temperature had a common pattern of variation except for recent years 2004-2006, with higher temperature after 1999.

4.4. Trieste

[insert Figure 9]

In TRI (Fig. 9), only copepods were analyzed (other groups were only available for 7 years). During 1970-1980, copepod abundance was below average. After the 1981-1985 gap, abundance was low in 1986, followed by a five fold increase in 1987. After 1987, the abundance stayed ca two fold higher than before the gap. Temperature, especially the winter average was cool from 1980-87, followed by a large warm anomaly that began in 1988 and lasted through 1994 for the annual average temperature, while winter temperature was more variable. Assuming that the copepod abundance stayed low during the gap, then the 1987-1988 changes in temperature (cool to warm) and copepod abundance (low to high) were synchronous. However, after 1994 low annual temperatures came back while copepod abundance stayed high.

4.5. Split

[insert Figure 10]

In SPL (Fig. 10), year 1971 was peculiar with lower than average abundances for all taxa. Several changes occurred after 1980, with a halving of chaetognaths, medusae and appendicularians abundance, while cladocerans abundance increased five-fold since approximately 1974. Chaetognaths, appendicularians and medusae displayed higher variability after 1980. At a lesser degree, copepod abundance started to decrease by 20% after 1983. Annual temperature was above average from 1960 to 1971, then slightly below average until 1985, then temperature dropped after 1986, while winter temperature was more variable. Winter 1971 was particularly warm, while winter 1981 and 1983 were particularly cold. Salinity fluctuations showed a general decreasing trend before 1977 and an increase afterwards.

4.6. Athens

[insert Figure 11]

In ATH (Fig. 11), copepods, appendicularians and chaetognaths abundances show a two to fourfold increase over the period, while doliolids and siphonophores do not show a particular trend. Conversely, medusae declined 50% over the period. Cladocerans showed a seven fold increase from 1987 to 94, then decreased until 2000. Over the whole period, temperature was lower before 1996 than after, and Chl-a concentration was higher before 1998 than after. Salinity was higher in 1990-1995 than in 1997-2001.

5. Between sites comparisons and correlation with climate indices

Station pairs are compared based on their overlapping periods. First, comparisons of local hydrography (T,S,Chl-a) are presented, then comparisons of TG.

5.1. Environmental parameters

[insert Figure 12]

A principal component analysis of winter water temperatures (Fig. 12, left panels) reveals a high correlation between temperature at VLF, TRI and NPL and the first axis, while BAL temperature is mainly correlated to the second axis. This is true both for in situ and ICOADS temperature. For in situ temperature, exceptionally warm winters occurred in 1988, 1990, 1998 and 2001. The first principal components time series of in situ and ICOADS surface temperature (Fig. 12, right panels) show an abrupt change ca. 1987, from a below average to an above average winter temperature. Note that this pattern is robust if the PCA is performed without the time series from TRI that is surface temperature. Between sites correlations of winter temperature are positive: VLF vs NPL ($r=0.8$, $p<0.001$, $n=17$), TRI vs NPL ($r=0.72$, $p<0.001$, $n=19$), and TRI vs VLF ($r=0.53$, $p<0.01$, $n=30$). VLF and NPL are also correlated for annual temperature ($r=0.73$, $p<0.01$, $n=17$). For salinity and Chl-a, no significant between sites correlations were found for annual and seasonal averages, except a negative correlation of Chl-a between TRI and SPL ($r=-0.7$, $p<0.01$, $n=14$).

5.2. Taxonomic groups

To quantify relationships between stations for TG annual average time series, correlation analysis was used. After correction for multiple comparisons, no correlations were significant.

5.3. Correlation with climate indices

Correlations between the winter (JFM) average water temperature and winter NAO index (Hurrell et al 1995) and other indices (EA, EA/WR, AO, NHT, SCA) that are linked to the Mediterranean climate were computed, ie a total of 36 pairwise comparisons. After correction for multiple comparisons, the smallest p-value was 0.26, not significant.

To analyze direct and indirect climate-plankton relationships, correlations between climate indices and TG were computed with zero, one and two-year lags, ie a total of 683 pairwise comparisons. No significant correlations were found, as the smallest p-value was 0.43.

For both comparisons, individually significant correlations (ie before correction) found are listed in tables 3 and 4 for further reference.

[insert tables 3 and 4]

6. Discussion

According to the average Chl-a (Fig. 2), stations scaled from an open-ocean type to a coastal type (respectively SPL, VLF, BAL, ATH, and NPL), TRI being coastal but peculiar due to its shallowness. The coastal group is potentially influenced by anthropogenic nutrient inputs from large cities (Athens, Naples and Trieste). This gradient coast/open ocean dominates over the well known large scale East-West gradient in the productivity shown on a map of average Chl-a (e.g. Bosc et al 2004 Fig. 13).

The average abundance of copepods and cladocerans follows basically the same pattern as the average Chl-a, except for TRI. This relationship suggests a bottom-up effect, plausible for the long term averages considered, which filter out the effect of other environmental factors and natural variability (Richardson and Schoeman 2004). However, this relationship does not ensure a direct trophic relationship between phytoplankton (Chl-a) and these zooplankton groups, taking into account the great role of the microbial food web (based on picoautotrophs and bacteria) in the Mediterranean (Thingstad and Rassoulzadegan 1999, Turley and Stutt, 2000). Indeed, within sites this bottom-up effect is not always observed for copepods or cladocerans (e.g. in VLF). Additional data on zooplankton species or functional groups, as well as on chlorophyll size fractions, bacteria and protists would be needed to better decipher these trophic relationships. The decreasing abundance of pteropods, ostracods and siphonophores with increasing Chl-a might be attributed to increasing competition in richer environment. Further dedicated investigation, including species information, is required.

6.1. Seasonal scale

We noted a successive peaking of Chl-a, copepods, cladocerans and chaetognaths abundance at BAL, VLF and NPL, in this order (Fig. 5). Mazzocchi et al. (2007), analyzing *Centropages typicus* abundance in five Mediterranean time series, noticed that the main peak occurred in May in BAL and VLF, and a month later in NPL. As TGs, and not species, are considered here, the peak is the result of the integrated community structure. The peak shift can be therefore a shift in the species composition, or a shift in the timing within species (Mazzocchi et al. 2007). The BAL-VLF time lag in Chl-a is also consistent with shift in surface Chl-a cycles from satellite (Bosc et al., 2004) over Ligurian and Balearic regions (Fernández de Puelles et al., 2007). On the contrary, the NPL mean cycle is different from the cycle over the full Tyrrhenian Sea region (Bosc et al., 2004), which suggests that NPL Chl-a cycle is driven by local processes such as anthropogenic factors or circulation features. For NPL, ATH and TRI, the Chl-a peak timing does not match the mean seasonal cycle classification obtained from satellite surface Chl-a data by D'Ortenzio and Ribera d'Alcalà (2009), but matches within one month the classification for BAL, VLF and SPL. This may indicate a significant contrast between surface (satellite) and depth integrated Chl-a peaking, dominant local processes not seen by satellite in coastal stations, or a strong interannual variability. Therefore, the timing of the peak in the coastal stations seems to result from a combination of factors mostly acting at local scale.

6.2. Interannual scale

Nutrient input, temperature and water masses are the drivers most commonly invoked to explain local zooplankton changes. However, each local scenario of change is unique.

Baleares

At BAL, zooplankton variability is dominated by water masses alternation, as the station is located in a boundary area between northern and southern western Mediterranean waters (Fernández de Puelles et al. 2003b, 2004, 2007, Fernández de Puelles and Molinero, 2007, 2008). Two water masses compete in the region: Atlantic (fresh, nutrient poor coming from the south), and Northern Mediterranean water (saline, cool and nutrient rich coming from the north). Zooplankton variability was related to the hydrographic regime, with higher abundance of copepods and appendicularians when northern Mediterranean waters prevailed in the area (Fernández de Puelles et al. 2007, 2009). The warmer years were those with lowest zooplankton biomass, associated with the inflow of less saline and nutrient depleted Atlantic waters. But the water mass and associated zooplankton variability are also related to large scale climate patterns, suggesting that the latter are the ultimate drivers of the variability (Fernández de Puelles and Molinero, 2007). Climate patterns act through regulation of the winter atmospheric conditions, nutrients, and subsequent primary production, as well as through the spread of the Northern Mediterranean water (Fernández de Puelles and Molinero, 2007). Therefore the main changes observed in the Balearic region seem to be tightly modulated by large scale forcing in the North Atlantic. These findings were confirmed by the results presented here.

Villefranche

Previous studies in VLF emphasized the role of increasing temperature and the response of gelatinous taxa. From the 1970s to the 1980s, following a warming of the water column and calmer weather, modifications of abundance were reported for several taxa: siphonophores and medusae (Buecher et al 1997, 1999, Goy et al 1989), salps and doliolids (Braconnot et al. 1990, Ménard et al 1994, 1997, Licandro et al 2006), whole zooplankton community (Licandro and Ibanez 2000). Ménard et al (1994, 1997) reported a steady increase in salps and doliolids from 1967 to the early 1980s, followed by a stable level until 1990. Molinero et al. (2005a, 2008) observed an abrupt drop ca. 1987 of summer-autumn copepod and chaetognaths species synchronous to an increase in gelatinous predators (medusae, siphonophores, ctenophores), and put forward a top down hypothesis.

The subsequent years (1974-2003) included in our analysis, but not in Molinero et al (2005a, 2008) do not depict this opposite behavior of copepods and chaetognaths vs gelatinous species, but instead show an alternation of high and low abundance periods synchronous and in phase across several TGs (copepods, cladocerans, chaetognaths, medusae). The main change ca 1990 was from high to low abundance, coinciding with a shift toward cooler and fresher waters. A warmer and drier climate in the 1980s (especially 1985-1990) than in the 1970s was linked to the increase in gelatinous zooplankters such as salps, medusae and doliolids by many authors (Goy et al. 1989, Ménard et al 1997, Buecher 1999, CIESM 2001, Molinero et al 2005a). However, this hypothesis (warmer and drier) cannot explain the higher abundance in copepods, cladocerans and chaetognaths observed here from ca 1983 to the early 1990s. Although several processes may be at work, we hypothesize that synchronous changes across TG arise from variations in phytoplankton and microbial biomass propagating through the food web and benefiting several TG. This bottom-up hypothesis was suggested by Garcia Comas et al. (submitted), who reported coherent fluctuations between comprehensive local environmental data and TG. Higher abundance could also arise from change in water mass composition.

Although our results do not show the large drop ca. 1987 reported for some copepod species (Molinero et al 2005a, 2008), it is probable that this signal is lost in the summation of all copepod species. Therefore TG and species level analysis are not comparable, but complementary.

Naples

The main variability at NPL is a decrease in chlorophyll a concentration, copepod and cladoceran abundance from the first to the second part of the time series and an increase of pteropods and chaetognaths population. Decreasing Chl-a, copepods and cladocerans abundances can be interpreted as a bottom up control, with the copepod decrease essentially driven by less abundant juveniles (not shown). Alternatively, chaetognaths could also exert a top-down control on copepods and cladocerans. Whether the decrease in Chl-a is linked with the warming since 1997 is not clear. As NPL station is subject to varying anthropogenic nutrient input (Mazzocchi and Ribera d'Alcalà, 1995), fluctuations in autotrophic abundance can be partly independent of the 'natural' nutrient input fluctuations through winter mixing. Ribera d'Alcalà et al., (2004) reported a decreasing trend of autotrophic biomass over the period 1984-2000, as well as a reduction of the average phytoplankton cell size likely related to changes in the contribution of different phytoplankton groups. Although it is plausible that zooplankton (copepod) species composition were affected by phytoplankton changes, our analysis was not conclusive. Increase in temperature, variability in water exchanges between coastal and offshore areas and in anthropogenic influence likely represent the factors interplaying in affecting plankton variability in the inner Gulf of Naples.

Trieste

TRI showed the most abrupt change in copepod abundance. Over the period, warming, circulation and nutrient input changes also occurred. After 1986, copepod abundance doubled: average abundance over 1987-2005 is approximately twice its value over 1970-1980. Meanwhile, after a period of cold winters (1981-1987), the 1987 annual temperature was high, and 1988 winter was very warm. Mozetic et al. (2002) noted large changes before vs after the 1981-1985 sampling gap for both temperature (warmer) and copepods (more abundant). Analyzing species composition, Kamburska and Fonda-Umani (2006) and Conversi et al (2009) reported changes ca. 1987 (resp. in 1986 and 1988). Distinct species assemblages were observed with more abundant small-size copepods, new copepod species (*Diaixis pygmoea)* and declining species (*Pseudocalanus elongatus)*. As causes, Kamburska and Fonda-Umani (2006) suggested a decrease in nutrient input, a reduction of the average phytoplankton size, and more frequent injections of modified Levantine Intermediate waters in the area. Conversi et al. (2009) invoked a warming trend, a change in precipitation and wind regime as noted Demirov and Pinardi (2002) and a change in the surface circulation of the Adriatic, consequence of the Eastern Mediterranean Transient (Roether et al. 1996). To summarize, changes in the copepod community result not only from the short, abrupt circulation and possibly climatic event of ca. 1987 but also from a more gradual warming and trophic changes. Abruptness of change is possibly amplified by the very shallow sampling site, the highly variable freshwater flux, and the northern location of the Gulf of Trieste, all of which makes it a very sensitive ecosystem compared with other sites. From our data, only autumn temperature showed a significant positive trend over 1970-2005. A positive correlation of copepod abundance with temperature is probably linked with new "warm water" copepod species as suggested by Kamburska and Fonda Umani (2006). Although atmospheric forcing may contribute to changes, we found no correlation with climate indices. Specifically, the correlation between NAO and copepod abundance found by Piontovsky et al. (2006) between 1970-1999 is not significant over the longer 1970-2005 period.

Split

In SPL, changes of primary production, phytoplankton community and zooplankton were linked to water masses changes. The increase of cladocerans and decrease of chaetognath, medusa and appendicularian reported here was previously detected over the period 1960-1982, along with an increasing trend of primary production (Vučetić 1980, Marasović et al 1995, 2005), phytoplankton and bacteria, and oscillations with periodicities of 8 and 10 years of salinity and temperature (Vučetić 1980, Baranović et al 1992, 1993, Šolić et al 1997). Several hypotheses can be proposed to explain these fluctuations. Increased primary production over 1960-1991, first attributed to eutrophication spreading from the coast (Baranović et al 1993, Šolić et al. 1997), was recently related to enhanced input of Mediterranean water into the area (Marasović et al. 1995, 2005). The Mediterranean influx is seen here in the increasing salinity trend. This change of water masses may also have altered the zooplankton community composition. An increased proportion of smaller phytoplankton (coccolithophorids) at Stončica after 1974 (from 50% to 80%, Šolić et al. 1997) could favor cladocerans, and disfavor appendicularians through increased competition with cladocerans (Sommer and Sommer, 2006). Decrease in chaetognaths could be attributed to cooling (Baranović et al 1992) and to higher predation by small pelagic fish (Batistić et al 1997). Seasonal temperature extrema also seem to play a role: particularly cold winter of 1981 and 1983 had very low chaetognaths and medusae abundances. Conversely, the warm winter of 1971 had very low abundance for all TG. Therefore SPL zooplankton seems both affected by long term increase in productivity and short term events.

Athens

In ATH, large zooplankton changes appear linked to changes in anthropogenic nutrient inputs but also to climatic effects. Over the period 1987-2004, copepods, appendicularians and chaetognaths increased by two to four fold, in parallel to the total mesozooplankton abundance and biomass in the area (Siokou-Frangou et al., 2007), while medusae decreased by 50%. Chl-a decreased after 1998, while temperature increased after 1995. One factor to explain these changes is the anthropogenic nutrient input. Within the study period nutrients inputs have increased due to the increase of sewage outflow volume (Siokou-Frangou et al., 2007), but the depth of discharge was moved to 60m after 1994 (Siokou-Frangou et al., 2007, Makra et al 2001, Simboura et al 2005). After 1994 nutrients were therefore less available for phytoplankton growth in the surface layer (Pagou, pers. comm.). In addition, at depth, high availability of dissolved organic carbon and nutrients close to the sewage outfalls favors bacterial production and ciliates rather than primary production (Saridou et al., 2009; Zeri et al, 2009). Thus copepods and appendicularians could graze on the increased abundance of the microbial components at depth after 1994. Apart from the surface nutrient reduction after 1994, the decrease of chlorophyll could also result from an intensified grazing control by mesozooplankton on lower quantity of

phytoplankton, or from changes in phytoplankton groups and/or size composition as observed in NPL (Ribera d'Alcala et al., 2004).
As the timing of nutrient input changes and ecosystem response do not correspond perfectly, other factor such as climate variability could play a role. Therefore, ATH zooplankton variability seems to be driven by several processes and the determination of the ultimate driver of the change awaits additional data. Because ATH sampling is sparse in time (only 3 samples for some years), increased uncertainty in the values of the anomalies limits the confidence in our interpretation.

6.3. Intercomparison of fluctuations at the different sites, and links with main modes of atmospheric variability

For the physical variables, winter temperature at VLF, TRI and NPL showed coherent abrupt drops in 1985-1987 followed by abrupt increases during 1988-1990 (Fig. 12). Annual average temperature at VLF and NPL, at NPL and TRI stations, and winter temperature at TRI and VLF are also correlated. Positive correlation between NPL and VLF can be expected given their geographical proximity, the cyclonic surface water circulation pattern (Millot, 1987) and the absence of high altitude orography. Correlation between VLF and TRI may be linked to their geographic proximity and similar latitude, although they are in different sub-basins.

Water temperature was not significantly correlated to any atmospheric teleconnection pattern after correction for multiple comparisons. In particular, we found no significant correlation of NAO with water temperature. However, correlations between NAO and air temperature were reported over several of the regions (Ligurian Sea, Northern Adriatic and Aegean Sea, Xoplaki 2002, Fig. 6.3, p165). Rixen et al. (2005) showed covariation between the surface heat flux in the Western Mediterranean, Western Mediterranean deep water temperature and the NAO. This non-significance of correlations can be due to the weak influence of teleconnection patterns locally, local processes (e.g. advection, run-off) driving the water temperature, to the relatively short periods considered (≤ 30 years), or to the depth averaged temperature used here that can mask existing signals. Finally, the strength of the correlation between NAO and temperature at VLF may vary with time, as correlation (not corrected for multiple comparison) was just significant over the period 1966-1993 (r=0.39, p=0.04, consistent with Molinero et al. 2005a, 2008), but was not significant over 1974-2003, nor over 1957-2007 (not shown).

For TGs as for temperature, no significant correlations with climate indices were found. This is coherent with the high sensitivity of zooplankton to temperature. Although temperature was correlated at VLF, TRI and NPL, zooplankton was not correlated between these sites. This may be due to a compensation effect within taxonomic groups that contain species that do not respond equally to changes.

7. Conclusions

Average seasonal cycles and long term trends of zooplankton groups in six sampling sites located in Balearic, Ligurian, Tyrrhenian, Adriatic and Aegean Sea were analyzed and compared. These data will be useful to modelers for validation of their simulations of zooplankton groups at regional scale.

This study dealt with broad taxonomic groups. By essence, their response to change in their environment is more integrated (*sensu* Ottersen et al 2001) and less direct than response of individual species. As a consequence, TG sensitivity to changes in the environment may be lower, but TG level response may be more significant in term of, for instance, average secondary production available for higher trophic levels, or other biogeochemical fluxes in the ecosystem. Therefore taxonomic groups and species level approaches are complementary. An important practical advantage of TG is that their identification requires less taxonomic knowledge; thus sample analysis is easier and faster. In several sites (NPL, SPL, TRI, ATH), information on phytoplankton species or size composition helped the interpretation of zooplankton changes. Therefore phytoplankton data should be collected together with zooplankton when possible.

For the Mediterranean as a whole, a general west to east gradient in productivity and zooplankton abundance exists, but it was largely dominated at our sites by the coastal-open ocean gradient. Anthropogenic influence was also potentially non negligible at three stations (NPL, ATH, TRI). In every station, local zooplankton variations could not be explained by one or two simple factors. After correction for multiple comparisons, neither temperature nor zooplankton time series had significant correlations with climate indices. No correlations were found between temperature and NAO neither at VLF nor at ATH, although previous studies suggest a link (Xoplaki 2002, Molinero et al 2005a). Between several northwestern stations (VLF, NPL, TRI), temperature was positively correlated. Extreme events such as the cold winter of 1987, warm winters of 1988, 1990, 1998, 2001 were observed in three to four stations (VLF, TRI, SPL, NPL), revealing a basin scale coherence for at least some climatic events.

Except for the temperature correlations noted in the previous paragraph, no coherent hydroclimatic or zooplankton behavior emerged at the scale of the Mediterranean, and no ‘regime shift’ could be detected. This can be attributed to noise from the heterogeneous sampling methodology, the relatively short overlapping periods, or to the anthropogenic influence masking the climate signal. However, as no correlation between temperature and climate indices were found, it may also be a result of the highly spatially differentiated climate typical of the Mediterranean (e.g. wind regime with Mistral, Bora, Tramontane, Xoplaki 2002). In such a heterogeneous area, to understand the coupled climate-hydroclimate-plankton system, it will be critical to develop downscaling studies, i.e. to make explicit the links from the larger scales of atmosphere down to the local hydroclimate that directly impacts the zooplankton. Statistical, dynamical approaches as well as local expertise should combine towards this aim.

Although some correlations found here were individually significant (tables 3 and 4), they were not significant after the Benjamini and Hochberg (1995) correction. Indeed, when computing a large number of pairwise comparisons, it is important to consider the number of significant correlations found with respect to the total number computed. Otherwise, showing only the few significant correlations out of a much larger set of correlations actually computed but not shown means misrepresenting (overestimating) the real significance of the relationships. However, the Benjamini and Hochberg (1995) correction limits the likelihood of Type I error (rejecting H0 while it is true) but increase the risk of a Type II error (accepting H0 while it is false) to a level of about 50%.

Finally, for a thorough understanding of zooplankton fluctuations, long term (>10 years) zooplankton time series are strongly needed, but with adequate frequency (at least monthly), and additional environmental data (physical, biogeochemical) collected together with zooplankton. New technologies (eg automated buoys with multi sensors) are now available to set up the future in situ observatories.

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Figure captions

Figure 1. Location of sampling stations (black crosses), stations codes, and main geographical names used in the text. The long term averages of depth integrated Chl-a concentration are represented as grey circles, sized proportional to the.value. *Tyrr.* : Tyrrhenian, *Lig.* : Ligurian.

Figure 2. Mean seasonal cycle of depth integrated (surface to bottom) Chl-a versus surface temperature for each station. Naples Chl-a is from Ribera d'Alcalà (2004). January (J) and February (F) months are indicated.

Figure 3. Log10 of average abundance versus depth-integrated Chl-a at each station for different TG. The open sea stations are marked with crosses, the coastal stations as stars. Comparison is limited to the two groups of stations with comparable mesh size (200 µm, BAL, NPL, ATH, TRI) and 330µm (SPL, VLF). Note the changes in y axis limits.

Figure 4. Scaled mean seasonal cycle for each TG. Average computed over 1994-2003, except for SPL (1976-1985). All cycles have a unit range and the y-intersect of the curves is incremented for clarity. Each line corresponds to a station, from bottom to top, BAL (black diamonds), VLF (black stars), NPL (black circles), TRI (grey triangles), SPL (solid grey) and ATH (grey squares).

Figure 5. Median of the day of the year (symbols) and 0.25 and 0.75 quantiles (horizontal lines) of the annual peak for Chl-a, copepods (cop), cladocerans (cla), and chaetognaths (cha) at each site. Day of the year computed over 1994-2003, except for SPL (1976-1985).

Figure 6. BAL time series of annual average abundance for available groups (top panel), cumulative sum of the annual abundance anomalies (middle), cumulative sum of anomalies of temperature, winter temperature (JFM), Chl-a and salinity (bottom). Cumulative sum of some TG are shifted on the y-axis for clarity. TG abbreviations are cop, copepods, cla, cladocerans, app, appendicularians, cha, chaetognaths, ost, ostracods, pte, pteropods, sip, siphonophores, dol, doliolids, med, medusae, sal, salps,

Figure 7. VLF time series of annual average abundance for available groups (top panel), cumulative sum of the annual abundance anomalies (middle), cumulative sum of anomalies of temperature, winter temperature (JFM) and salinity (bottom). Cumulative sum of some TG are shifted on the y-axis for clarity. TG abbreviations as figure 6

Figure 8. NPL time series of annual average abundance for available groups (top panel), cumulative sum of the annual abundance anomalies (middle), cumulative sum of anomalies of temperature, winter temperature (JFM), Chl-a and salinity (bottom). Cumulative sum of some TG are shifted on the y-axis for clarity. TG abbreviations as figure 6

Figure 9. TRI time series of annual average abundance for available groups (top panel), cumulative sum of the annual abundance anomalies (middle), cumulative sum of anomalies of temperature, winter temperature (JFM) and salinity. The temperature anomalies are computed taking into account the 1981-1984 gap to compare with abundance. TG abbreviations as figure 6

Figure 10. SPL time series of annual average abundance for available groups (top panel), cumulative sum of the annual abundance anomalies (middle), cumulative sum of anomalies of temperature, winter temperature (JFM) and salinity (bottom). For some TG, the y-axis intersect of the cumulative sum is shifted for clarity. TG abbreviations as figure 6

Figure 11. ATH time series of annual average abundance for available groups (top panel), cumulative sum of the annual abundance anomalies (middle), cumulative sum of anomalies of temperature, winter temperature (JFM), sea surface temperature from ICOADS,), Chl-a and salinity (bottom). Cumulative sum of some TG are shifted on the y-axis for clarity. TG abbreviations as figure 6

Figure 12. Principal component analysis results for winter in situ temperature (top), and for ICOADS winter SST (bottom) over 1960-2005. Correlation biplot of site temperature (left panels), and corresponding first two principal components time series (right panels) in thin line. The cumulated sums of the principal components are in thick line. The proportion of explained variance (%) is indicated on each axis.

name	**code**	**Position**	**Bottom depth (m)**	**Period**	**Mesh size (µm)**	**Haul, net**	**Sampling frequency**	**Taxonomic resolution**
Baleares	**BAL**	39º28'59 N 2º25'63E	77	1994-2003	250	Oblique hauls 75-0m, Bongo -20 net	10 days	TG
Point B	**VLF**	43°41'10 N, 7°19'00 E	80	1966-2003	330	Vertical, 75-0m Juday Bogorov	Weekly	TG
Marechiara	**NPL**	40°48.5' N, 14°15' E	80	1984-2006	200	two vertical hauls 50-0m, Nansen net	Weekly and fornightly	Species
Trieste	**TRI**	45°42.05'	18	1970-	200	Vertica	Monthly	Species

		N, 13°42.6' E		2005		l haul, 18-0m, WP-2		
Stončica	**SPL**	43°2.63' N 16°17.12' E	100	1959-1992	330	Vertical hauls, 100-0 m, Hensen net	Monthly	TG
HCMR station 11	**ATH**	37º52.37 N, 23º 38.27E	78	1987-2004	200	double oblique hauls, 78-0m, WP-2	Seasonally and monthly	TG

Table 1: Main characteristics of the zooplankton and environment (T, S) time series.

code	Reference zooplankton	Reference for T, S, Chl-a if different
BAL	Fernández de Puelles et al 2004, 2007	
VLF	Buecher et al 1997, Ménard et al 1997, Licandro et al 2006, Molinero et al 2005a, 2008, Garcia-Comas et al submitted	SOMLIT
NPL	Mazzocchi and Ribera d'Alcalà 1995, Ribera d'Alcalà et al 2004	MC permanent sampling
TRI	Fonda-Umani et al 2004, Kamburska and Fonda-Umani, 2006	
SPL	Šolić et al 1997	
ATH	Siokou-Frangou 1996	Harilaos Kontoyiannis, Kalliopi Pagou, Georgia Assimakopoulou, Soultana Zervoudaki (unpub. data)

Table 2: References for time series

index	site	r	N
NAO	SPL	-0.34	33
EA	VLF	0.36	30
EA/WR	ATH	-0.51	14
NHT	SPL	-0.38	33
SCA	SPL	0.45	33

Table 3: Pearson correlation between winter (JFM) average temperature and climate indices. These correlations are not significant after Bonferroni correction, but are individually significant at $p<0.05$.

index	Lag (year)	TG, site	r	N
NAO	2	dol, VLF	-0.45	38
EA	1	app, SPL	-0.44	33
	2	sal, VLF	0.49	30
EA/WR	1	cla, SPL	0.50	33
		cop, ATH	0.63	16
AO	2	cla, SPL	0.48	33
	1	app, SPL	-0.51	33
NHT	0	cop, BAL	0.76	10
SCA	1	cha, SPL	0.52	33

Table 4: Pearson correlation for annual average TG and climate indices. These correlations are not significant after Bonferroni correction, but are individually significant at $p<0.01$. Cop, copepod, cla, cladocerans, app, appendicularians, sal, salps, dol, doliolids, cha, chaetognaths.

Figure 1

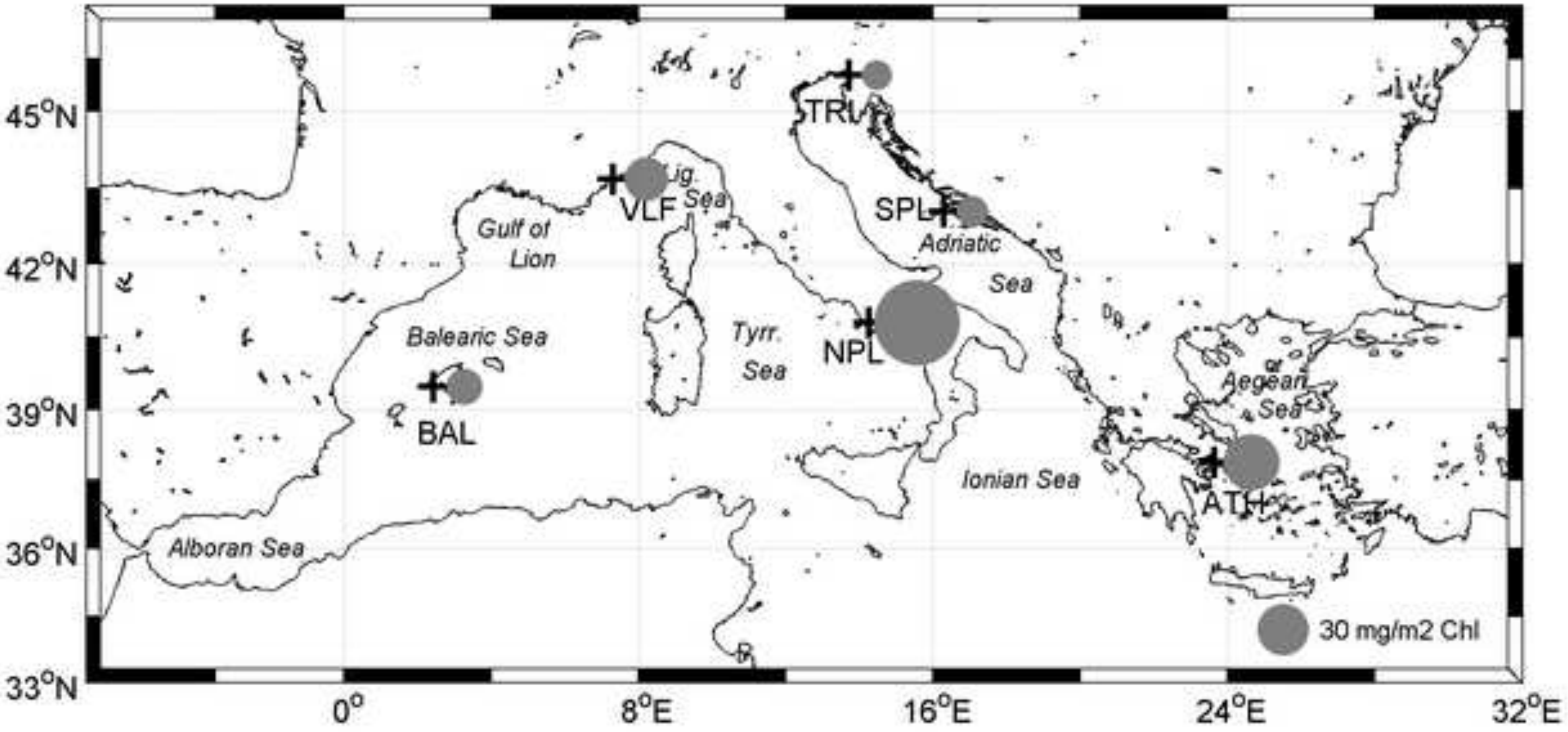
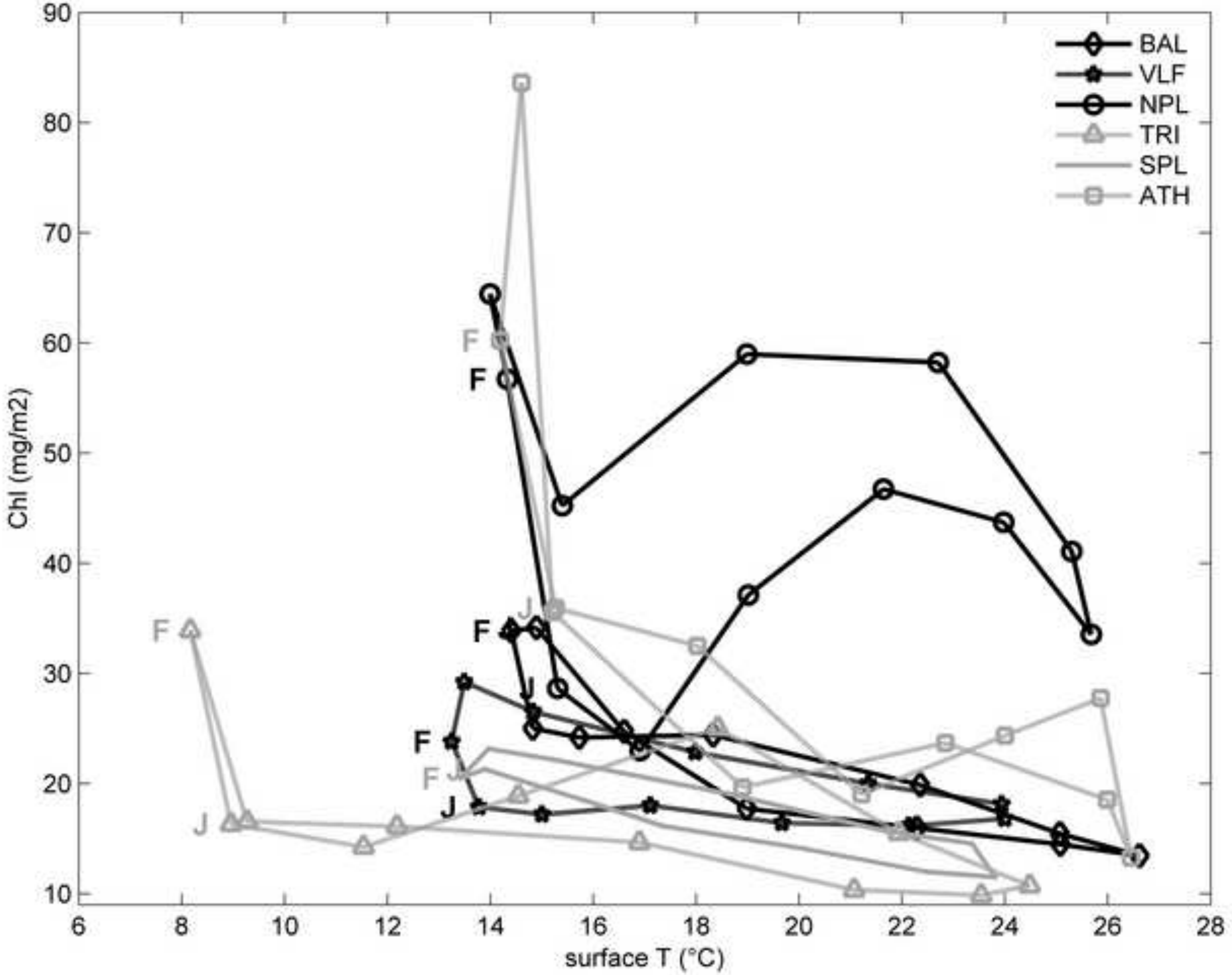

45°N
42°N
39°N
36°N
33°N
0°
8°E
16°E
24°E
32°E
TRI
VLF
Lig. Sea
SPL
Gulf of Lion
Adriatic Sea
Balearic Sea
Tyrr. Sea
NPL
BAL
Aegean Sea
Ionian Sea
ATH
Alboran Sea
30 mg/m2 Chl

Figure 2


Chl (mg/m2)
surface T (°C)
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20
30
40
50
60
70
80
90
6
8
10
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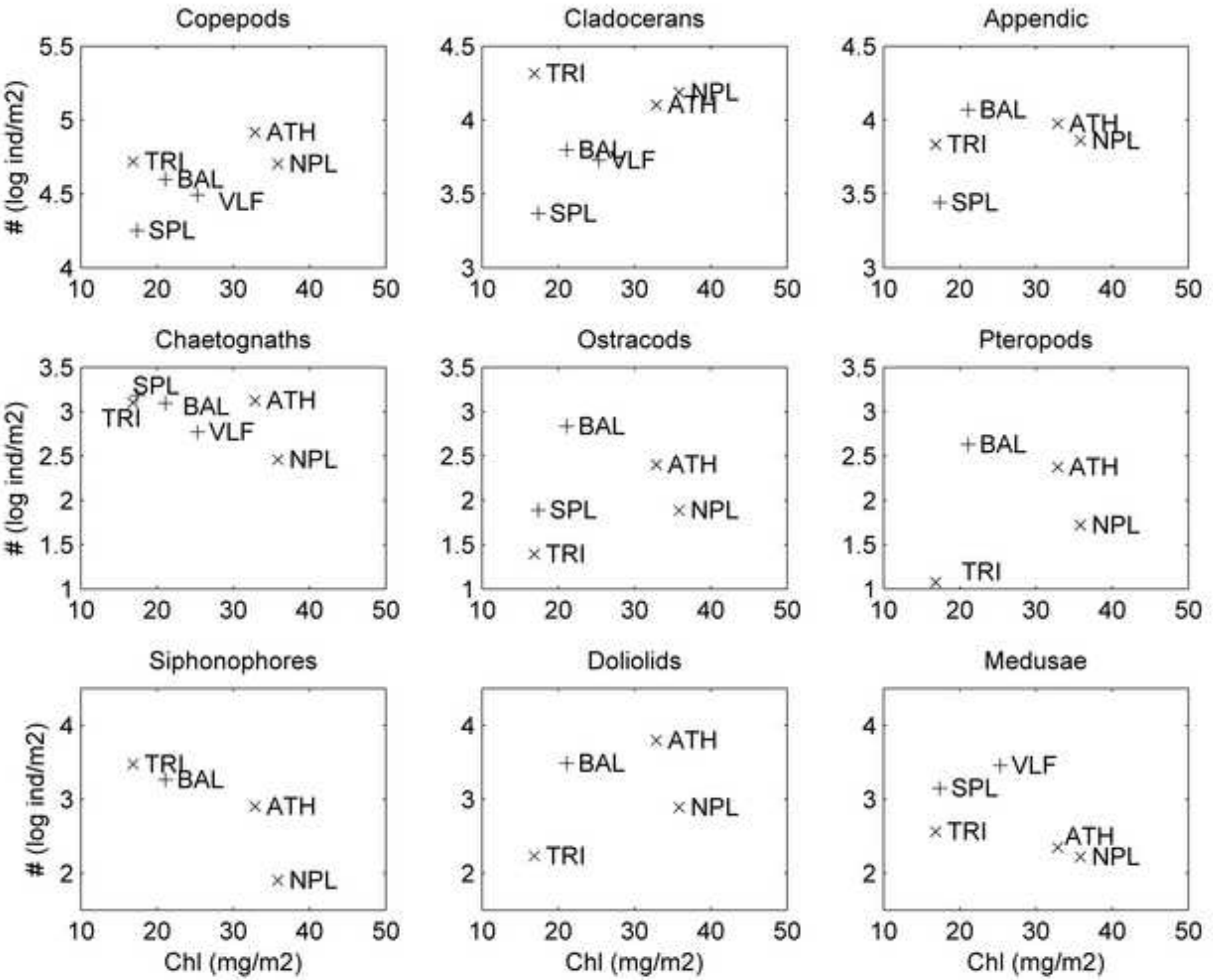
22
24
26
28
BAL
VLF
NPL
TRI
SPL
ATH
F
J

Figure 3


Copepods
5.5
5
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20
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40
50
(log ind/m2)
ATH
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NPL
VLF
SPL
Cladocerans
4.5
4
3.5
3
TRI
NPL
ATH
BAL
VLF
SPL
Appendic
BAL
ATH
TRI
NPL
SPL
Chaetognaths
3.5
3
2.5
2
1.5
1
SPL
TRI
BAL
ATH
VLF
NPL
Ostracods
BAL
ATH
SPL
NPL
TRI
Pteropods
BAL
ATH
NPL
TRI
Siphonophores
TRI
BAL
ATH
NPL
Doliolids
ATH
BAL
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TRI
Medusae
VLF
SPL
TRI
ATH
NPL
Chl (mg/m2)

Figure 4

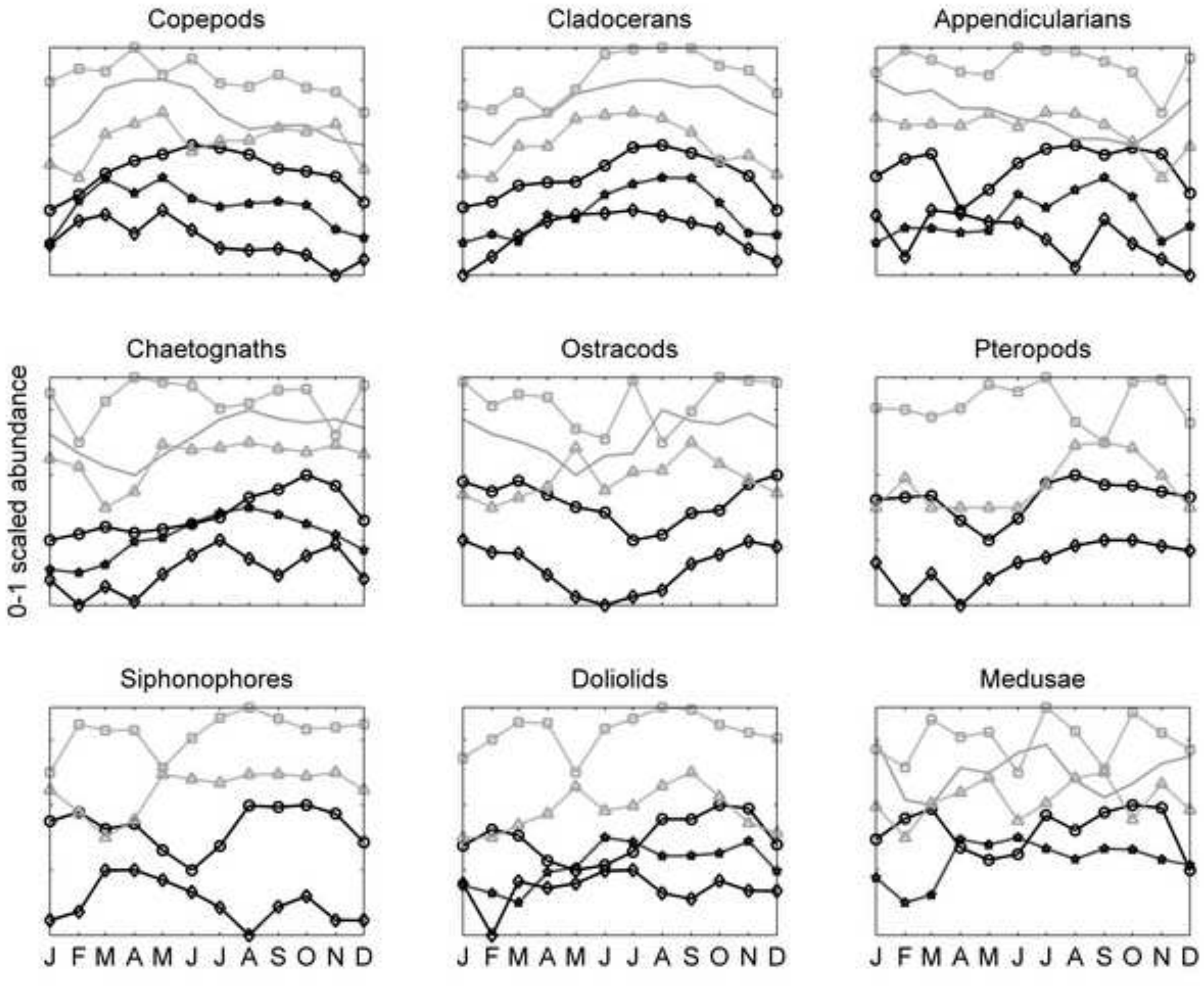

Copepods
Cladocerans
Appendicularians
Chaetognaths
Ostracods
Pteropods
Siphonophores
Doliolids
Medusae
0-1 scaled abundance
J F M A M J J A S O N D
J F M A M J J A S O N D
J F M A M J J A S O N D

Figure 5

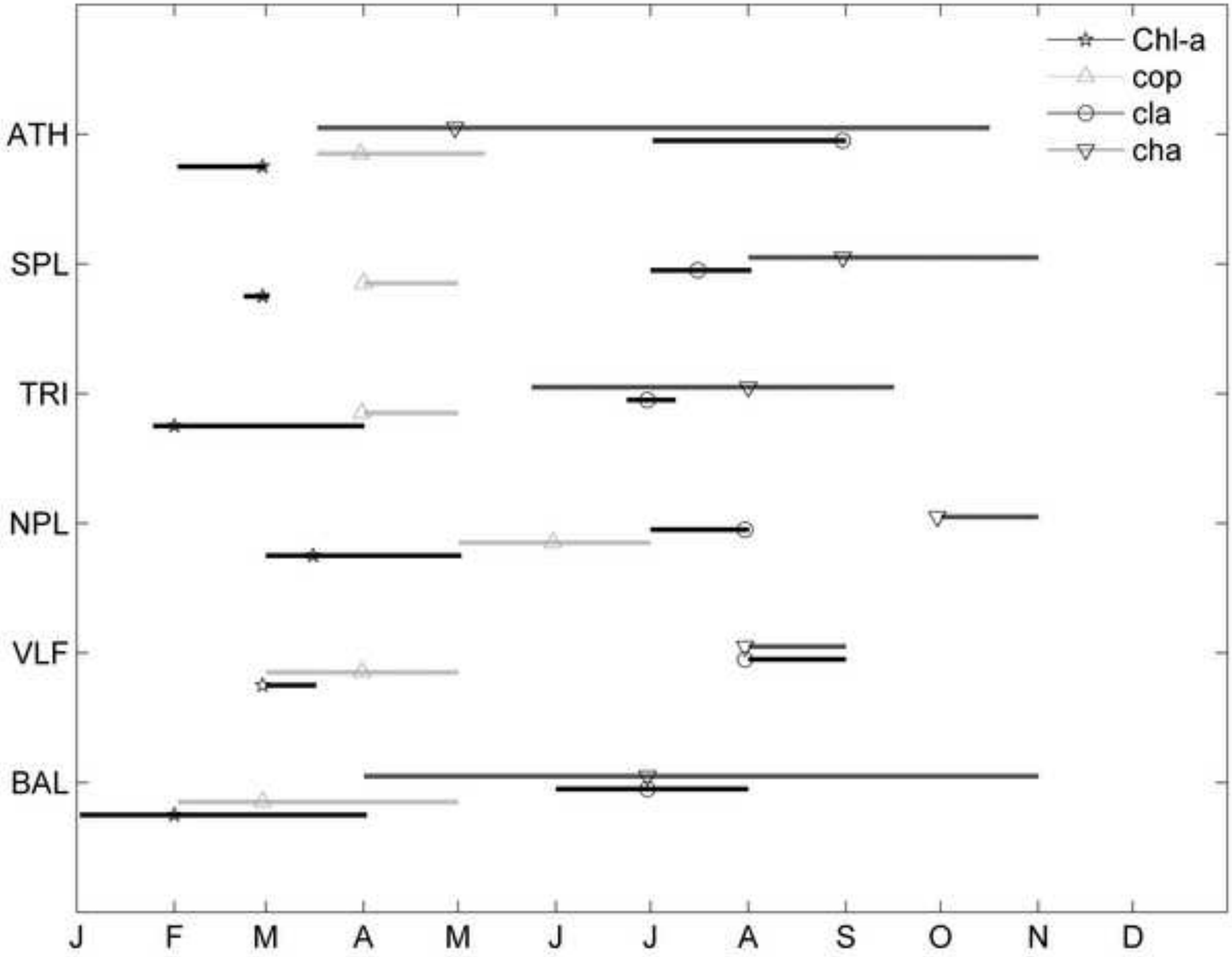
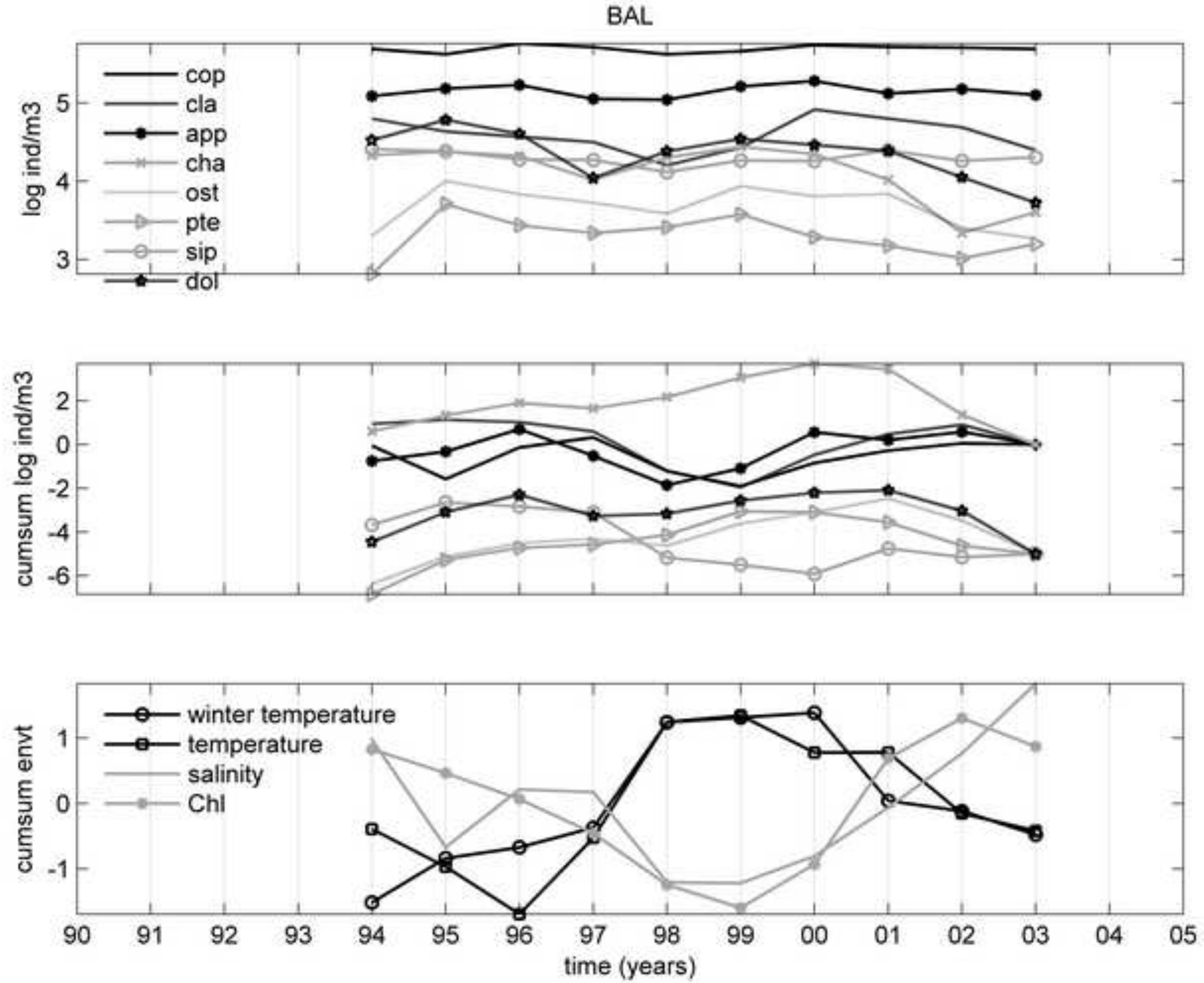


Figure 6


BAL
log ind/m3
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-4
-6
cumsum envt
1
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-1
winter temperature
temperature
salinity
Chl
90
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92
93
94
95
96
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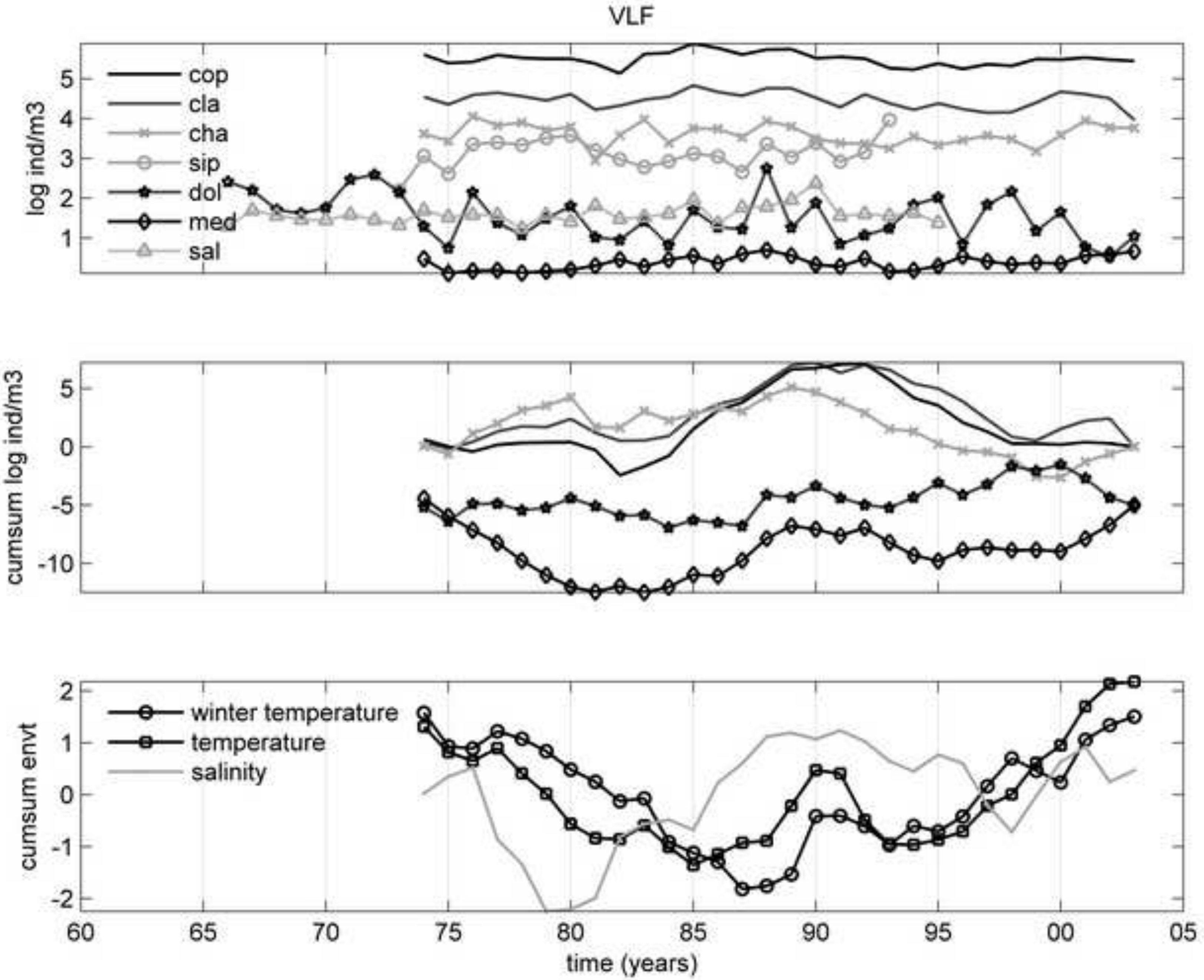
03
04
05
time (years)

Figure 7


VLF
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cumsum log ind/m3
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-5
-10
winter temperature
temperature
salinity
cumsum envt
2
1
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-1
-2
60
65
70
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95
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05
time (years)

Figure 8

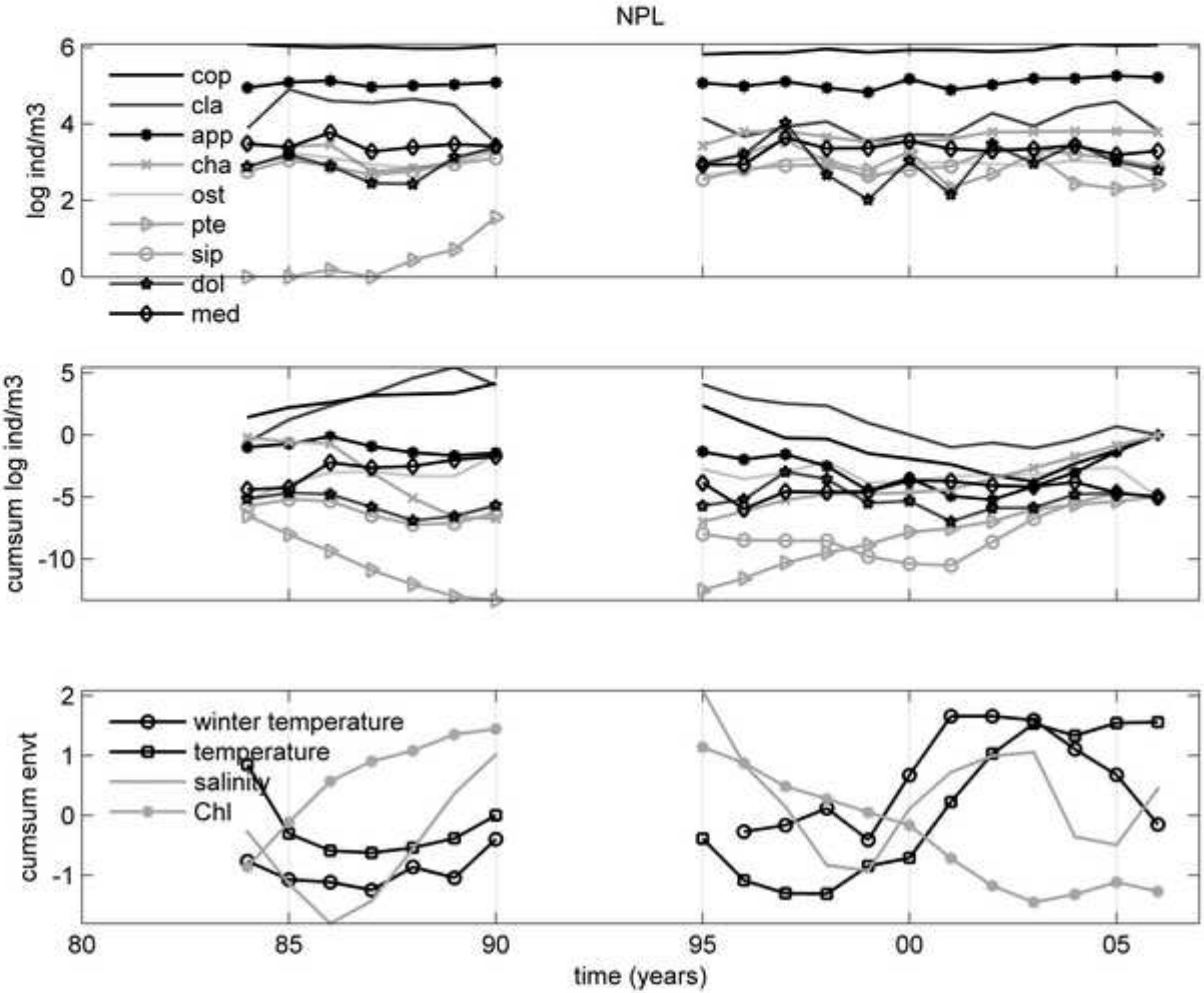

NPL
log ind/m3
6
4
2
0
cop
cla
app
cha
ost
pte
sip
dol
med
cumsum log ind/m3
5
0
-5
-10
cumsum envt
2
1
0
-1
winter temperature
temperature
salinity
Chl
80
85
90
95
00
05
time (years)

Figure 9

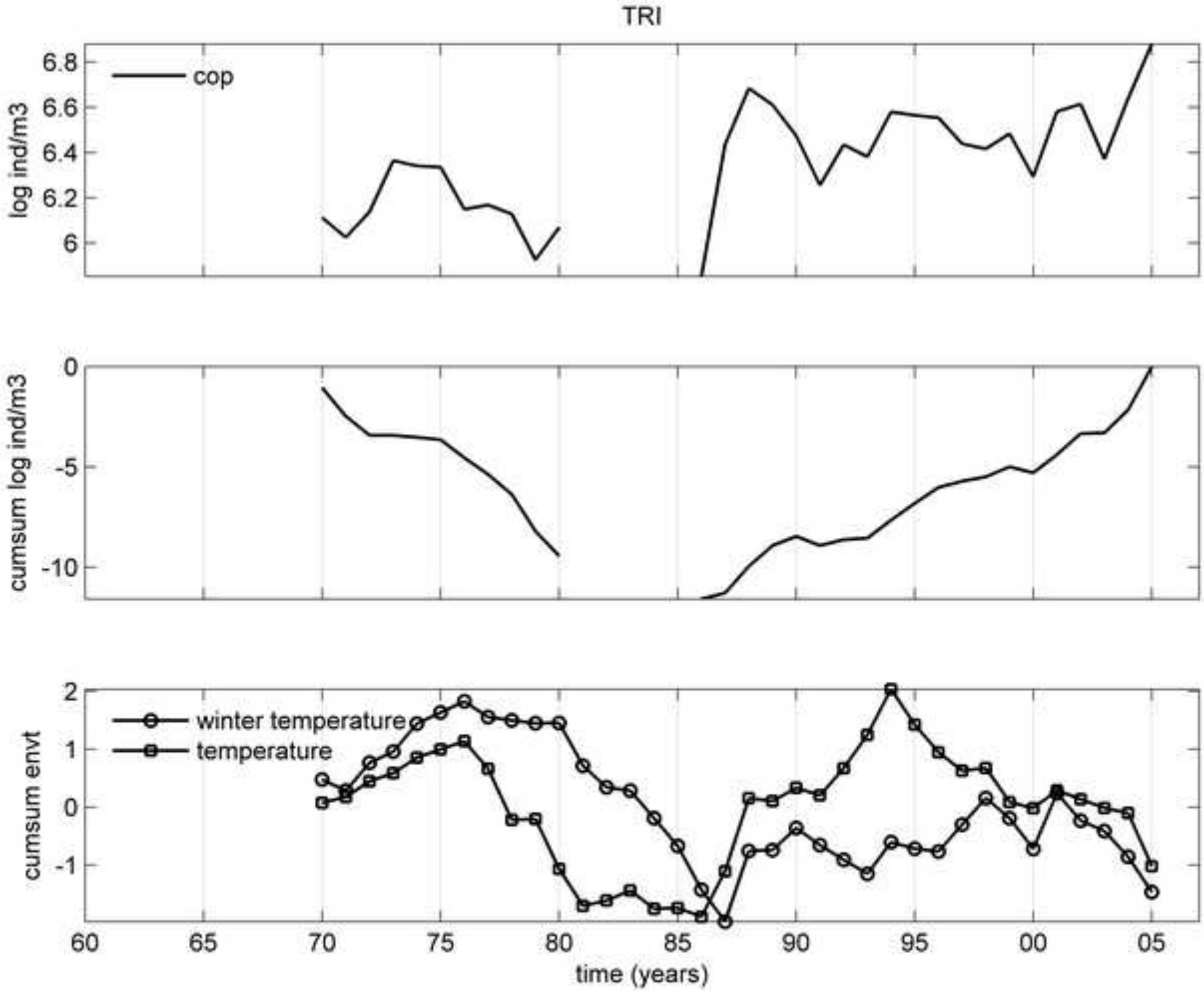

TRI
log ind/m3
6.8
6.6
6.4
6.2
6
cop
cumsum log ind/m3
0
-5
-10
cumsum envt
2
1
0
-1
winter temperature
temperature
60
65
70
75
80
85
90
95
00
05
time (years)

Figure 10

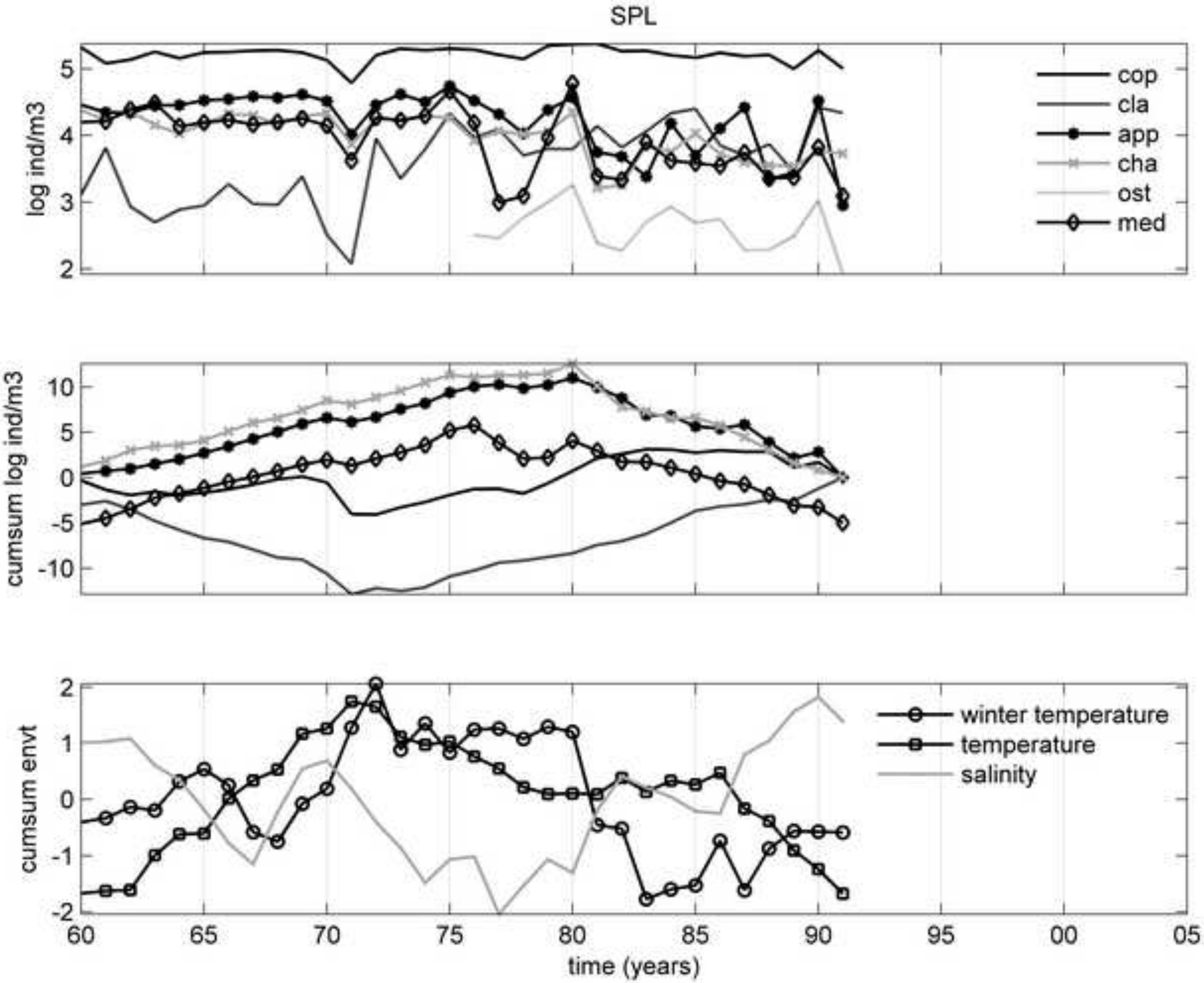

SPL
log ind/m3
5
4
3
2
cop
cla
app
cha
ost
med
cumsum log ind/m3
10
5
0
-5
-10
cumsum envt
2
1
0
-1
-2
winter temperature
temperature
salinity
60
65
70
75
80
85
90
95
00
05
time (years)

Figure 11

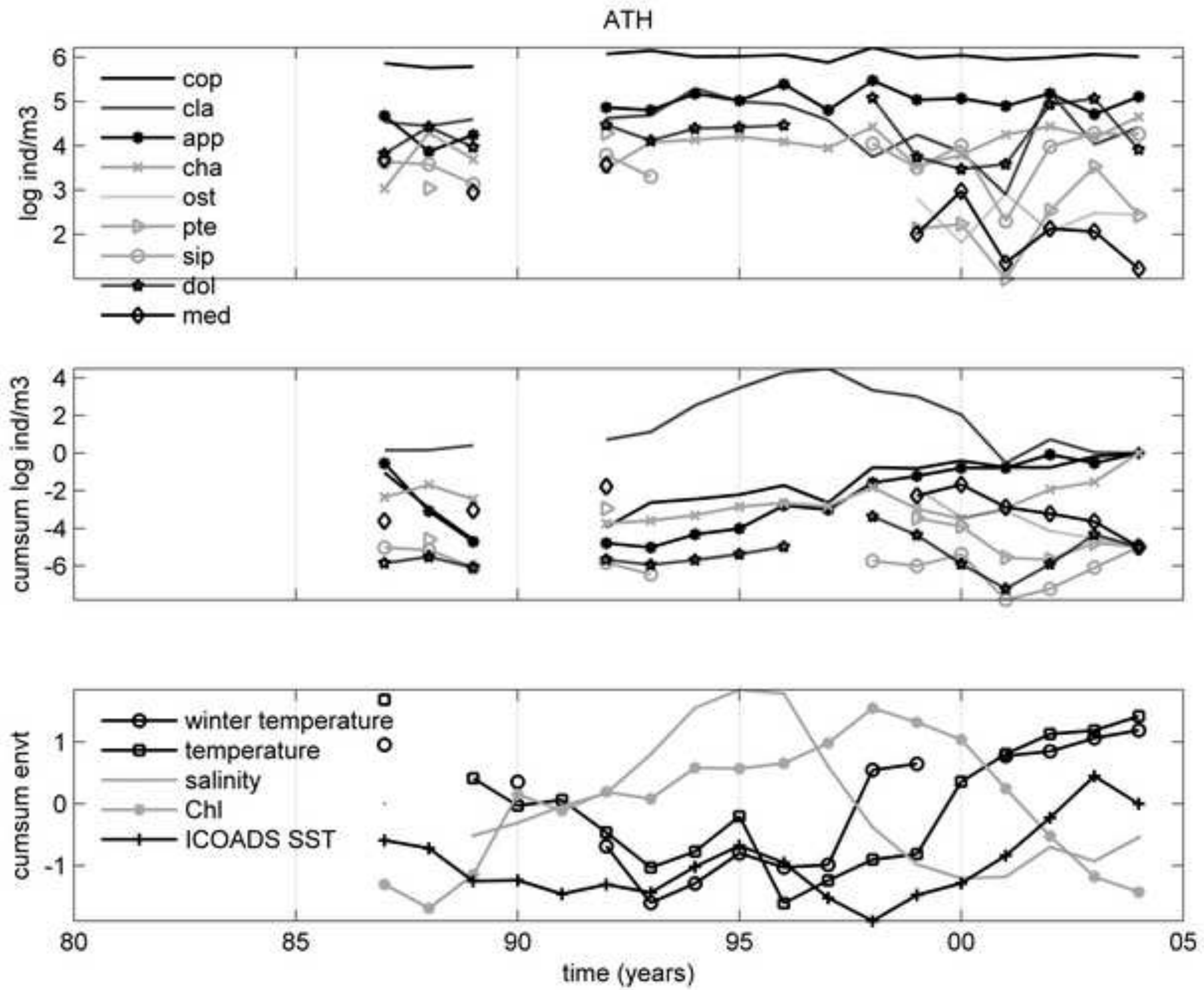
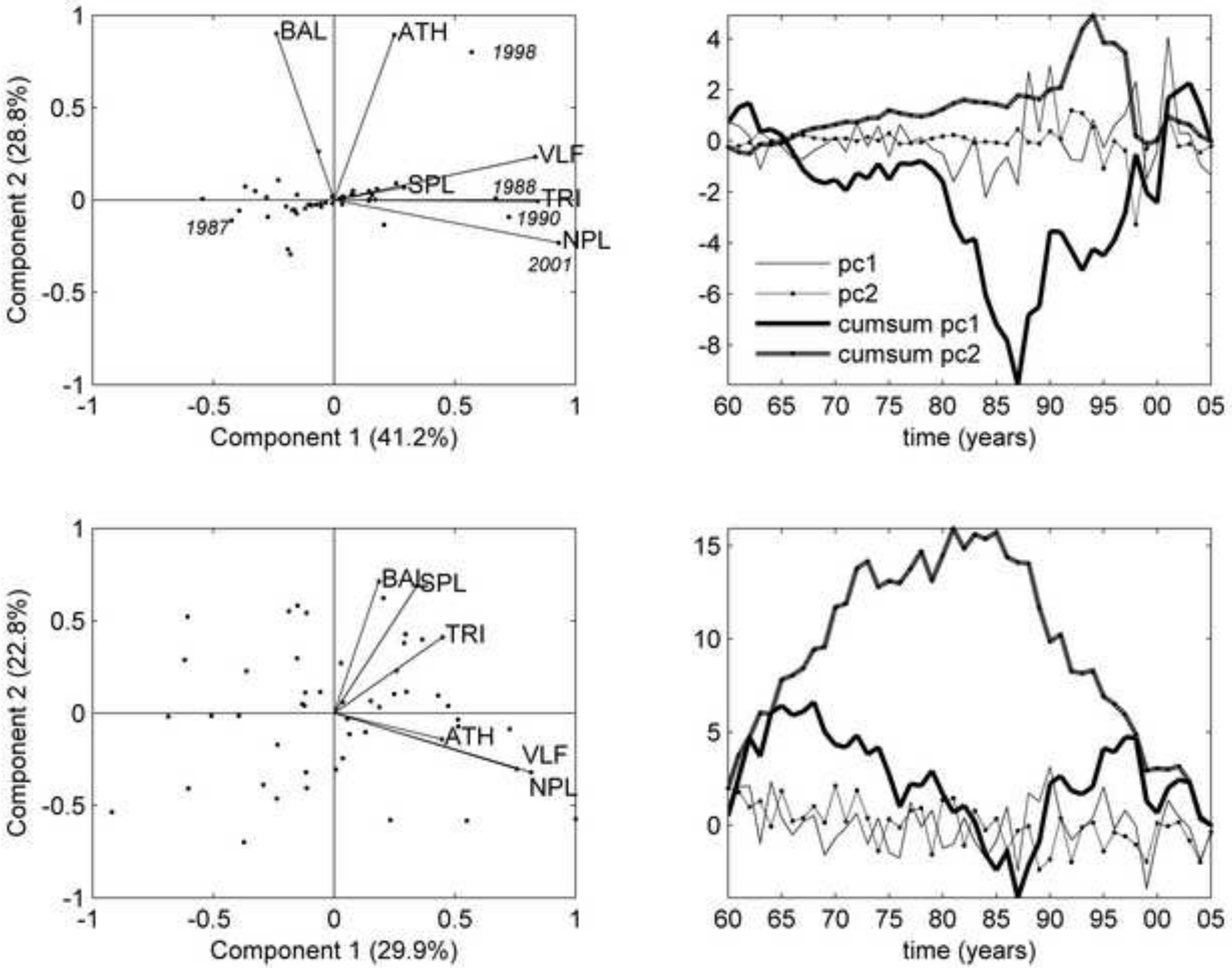

ATH
log ind/m3
6
5
4
3
2
cop
cla
app
cha
ost
pte
sip
dol
med
cumsum log ind/m3
4
2
0
-2
-4
-6
cumsum envt
1
0
-1
winter temperature
temperature
salinity
Chl
ICOADS SST
80
85
90
95
00
05
time (years)

Figure 12


BAL
ATH
1998
VLF
SPL
1988
TRI
1990
NPL
2001
1987
Component 1 (41.2%)
Component 2 (28.8%)
pc1
pc2
cumsum pc1
cumsum pc2
time (years)
60
65
70
75
80
85
90
95
00
05
BAL
SPL
TRI
ATH
VLF
NPL
Component 1 (29.9%)
Component 2 (22.8%)
time (years)