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Zooplankton dynamics in a changing environment: A 13-year survey in the northwestern Mediterranean Sea

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ARTICLE INFO

ABSTRACT

Dynamics of the subsurface (2–3 m) mesozooplankton (i.e., > 200 μm) in the Bay of Calvi (Corsica, France) were explored, combining time series (2004–2016) of 14 zooplankton groups, wind gusts, water temperature, nitrate and chlorophyll-*a*. Zooplankton data was obtained through image analysis. While contrasted group-specific seasonal patterns were observed, the most productive zooplankton annual event occurred in April (spring peak), concentrating on average 25% of the total annual abundance. A "typical" year was defined based on the annual succession of different community states, highlighting particular years (2007, 2015 and 2012), mainly characterized by weak spring peak. Environmental influences on the interannual variability of zooplankton were explored and while relationship between chlorophyll-*a* and zooplankton abundance was unclear, the availability of nutrients (December–March), potentially mediated via the wind regime (October–January) seemed to be essential to the occurrence of the spring peak. Additionally, we observed an influence of temperature, with winter thermal thresholds (between 12.1 °C and 13.4 °C) conditioning the spring peak. Also, the occurrence of lower annual abundances after 2010 was synchronous with the sharp increase of seawater warming trend, especially regarding winter temperature (0.30 °C.year^{-1}). Finally, winter North Atlantic Oscillation (NAO) was found to be correlated to both winter water temperature and spring peak abundance, which suggests large-scale processes to impact regional zooplankton community.

1. Introduction

On top of their central role in marine trophic food webs (Melle et al., 2004; Pinnegar and Polunin, 2000; Zöllner et al., 2009) and in biochemical processes (Banse, 1996; Cavan et al., 2017; Steinberg and Landry, 2017; Turner, 2015), zooplankton have also been pointed out as bio-indicators of environmental changes (Fernandez de Puelles et al., 2009; Perry et al., 2004) also referred as "beacons of climate change" (Richardson, 2008). A large number of studies have reported covariations between climate change and alterations of zooplankton spatial distribution, phenology, assemblages and abundance (Edwards and Richardson, 2004; Kamburska and Fonda-Umani, 2006; Mackas et al., 2012; Melle et al., 2014; Villarino et al., 2020, 2015) that may result in cascading impacts on a large variety of aspects including the biological pump, fisheries or even coastal habitats (Beaugrand et al., 2010; Dam and Baumann, 2017; Hays et al., 2005; Möllmann et al., 2008; Steinberg and Landry, 2017; Stempniewicz et al., 2007; Turner, 2015). Given the complexity of these cascading processes, the necessity of understanding the factors driving zooplankton dynamics in a first place seems self-evident. The best if not only way to gather such information requires continuous monitoring leading to the generation of time series (Southward, 1995) which, in turn, enables to detect recurrent patterns, changes, trends and to predict the likely amplitude and steepness of future changes (Mackas and Beaugrand, 2010). Image analysis based on a machine learning approach seems like an appropriate, rapid and non-destructive tool to process such long-term plankton data (Benfield et

al., 2007; Faillettaz et al., 2016; García-Comas et al., 2011; Ouba et al., 2016; Zarauz et al., 2008).

In the Mediterranean, previous studies of zooplankton time series provided evidence for tightly coupled hydroclimate-zooplankton systems, differing amongst studied areas (Berline et al., 2012; Mazzocchi et al., 2007), yet likely to undergo synchronous changes at basin-scale (Conversi et al., 2010). In the past four decades, local changes in hydrography, climate and zooplankton have been reported, along with overall warming waters (Adloff et al., 2015; Berline et al., 2012; Vargas-Yáñez et al., 2017). Drastic changes in the Eastern Basin circulation of deep water masses in the 1980s (named EMT, Eastern Mediterranean Transient) were linked, for example, to changes in the epipelagic zooplankton distribution and composition in the Ionan Sea (Mazzocchi et al., 2003) and to the increase of copepod abundance in the eastern Saronikos (Christou, 1998). Rising temperatures associated to the EMT event was found to affect the phenology, community composition and abundance of copepods in the northern Adriatic Sea (Conversi et al., 2009; Kamburska and Fonda-Umani, 2006). More recently, while in the Lebanese Sea, interannual zooplankton changes in phenology and total abundance appeared to be more related to hydrological dynamics than to sea surface warming (Ouba et al., 2016), in the Saronikos Gulf, the strong local water warming was found to drive important community rearrangements whereby warm-adapted species would replace shrinking populations of cold-adapted ones (Villarino et al., 2020). Overall, resilience capacity to buffer community structure changes due to environmental changes (Bernhardt and Leslie, 2013) might vary depending on the site-specific environmental properties such as circulation patterns (Batistić et al., 2014) and the internal community dynamics (Mazzocchi and Ribera d'Alcalà, 1995; Mazzocchi et al., 2012; Villarino et al., 2020). In the Ligurian Sea, warmer conditions have been linked, amongst others, to changes in the phenology of copepods (Molinero et al., 2005) and to the increase of jellyfish outbreaks, suggested to negatively impact on copepod abundances through increased predation pressure (Molinero et al., 2008). In the Balearic Sea, remarkable interannual changes were observed whereby years with lowest zooplankton abundances corresponded to warmest years including less saline and nutrient-depleted water conditions (Fernández de Puelles et al., 2007). More generally, the Ligurian Sea and the Balearic Sea were suggested to be more clearly linked to large-scale processes, potentially affected by North Atlantic climate variations (Fernández de Puelles et al., 2007; Fernández de Puelles and Molinero, 2008, 2007; Molinero et al., 2005), while the Gulf of Naples (Tyrrhenian Sea) would be more dependent on local conditions (Mazzocchi et al., 2012, 2011; Ribera d'Alcalà et al., 2004).

Furthermore, anthropogenic pressures such as nutrient and heavy metal inputs are strongly suggested to alter zooplankton assemblages and abundances (Berline et al., 2012; Mazzocchi et al., 2007; Ribera d'Alcalà et al., 2004; Siokou-Frangou and Papathanassiou, 1991; Solic et al., 1997; Uriarte and Villate, 2004), which can also be mediated by the alteration of the primary production (Berline et al., 2012; Giani et al., 2012; Marasović et al., 2005). Accordingly, indicators of good environmental status and associated thresholds based on zooplankton data have been proposed for the Bay of Toulon (Serranito et al., 2016). In Corsica (Ligurian Sea, northwestern Mediterranean), the Bay of Calvi is considered as a "pristine area" where environmental disturbance due to anthropogenic pressures is very limited (Gobert et al., 2009; Leduc et al., 2018; Lopez y Royo et al., 2011, 2010; Richir and Gobert, 2014). Monitoring such environment therefore enables to better discriminate impacts of climate change from the effects of local anthropogenic activities. The bay has been studied since the seventies by the marine research station STARESO ("STAtion de REcherches Sous-marines et Océanographiques") through the monitoring of chemical, physical and biological parameters, including phyto- and zooplankton (Gobert et al., 2010). The historical data recording has led the bay to be defined as a "workshop site" for the northwestern Mediterranean Sea and hosts since 2012 the integrative research program STARECAPMED (STAtion of Reference and rEsearch on Change of local and global Anthropogenic Pressures on Mediterranean Ecosystems Drifts) (Richir et al., 2015).

The aim of the present study is to describe the structure and the dynamics of the epipelagic mesozooplankton community in the Bay of Calvi, an oligotrophic area representative of a "pristine" system. Zooplankton data (2004–2016) were analysed through image analysis and machine learning-based classification enabling low-cost, accelerated and standardized time series construction. More precisely, specific objectives are: (i) to describe the seasonality of the zooplankton community; (ii) to characterize a typical year highlighting the community structure succession; (iii) to provide an overview on the seasonal and interannual variability of the zooplankton community; and (iv) to explore the underlying mechanisms likely to shape the dynamics of the zooplankton community.

2. Material and methods

2.1. Study area and zooplankton sampling

Zooplankton sampling was carried out by the marine research station STARESO (42° 35′N 44° 8′45′E), in the Bay of Calvi (northwestern coast of Corsica, France) (Fig. 1). The Bay of Calvi has an area of about 22 km^2 and a narrow continental shelf of about 6 km. It opens to the Ligurian Sea on the northeast and connects to the deep sea by a canyon
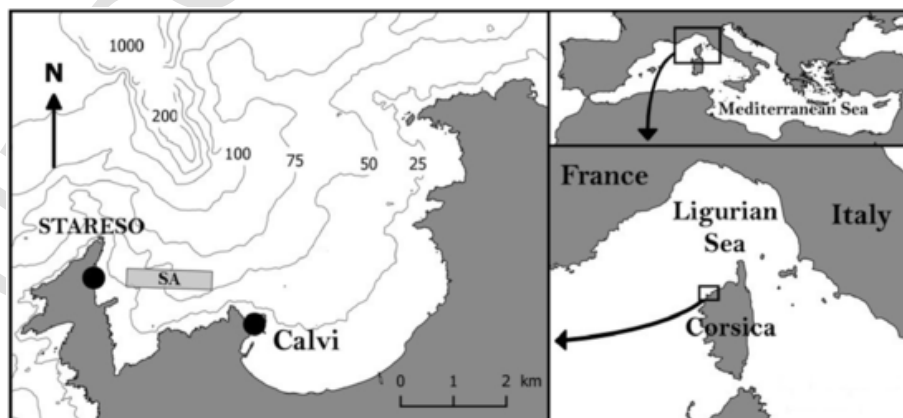

Fig. 1. Location of the sampling area (SA) in the Bay of Calvi (Corsica, France). Black dots locate the marine research station STARESO and the city of Calvi. Grey lines represent the 25 m isobaths.

(~1000 m deep) (Richir et al., 2015). Subsurface (2–3 m depth) horizontal hauls of zooplankton sampling were performed between 7:00 a.m. and 9:00 a.m. (local time) using a WP2 net of 200 μm mesh size with a 60 cm opening diameter, towed at 2 knots during 20 min. Depth of the sampled area ranges between 30 m and 50 m (Fig. 1). The sampled volume of 188 m³ was estimated from the horizontal towed distance and the opening surface (0.28 m²). With few exceptions, samples were collected weekly since 2004. Concentrated samples were preserved in 4% buffered formaldehyde solution and stored in 200 mL polyethylene terephthalate vials.

2.2. Digital imaging

Zooplankton samples were scanned on a fortnightly basis, with some extra weekly samples being scanned during zooplankton peak abundance periods. Samples were digitized with the open source Zoo/PhytoImage imaging software (Grosjean and Denis, 2007, 2014). The applied digitizing procedure is based on the previously established protocol of Grosjean and Denis (2007). Samples were size fractioned (1 mm, 500 μm, 200 μm) to prevent both underestimation of large rare objects and aggregation of small particles on larger particles. Aliquots of each size fraction were scanned using a high resolution flatbed scanning device (Epson V750pro) with the VueScan 8.1 Professional software and polystyrene optically transparent cells (Nunc® Omnitray, 25 cL) to produce 16 bits grey level images at 2400 dpi resolution (pixel size of 10.58 μm). Altogether, 32 different measurements were considered for the image analysis. The resulting time series covering the 2004–2016 period included 318 samples and contained a total of about 760,000 classified item subimages (so-called vignettes).

2.3. Automatic classification system and validation method

A training set containing 11,255 vignettes (images of one digitized particle) was elaborated. Vignettes were distributed into 22 categories (six of non-living particles, one of phytoplankton and 15 of zooplankton including two that were merged together to form a single group of appendicularians) to most completely represent the encountered elements. After running the automated classification on all the vignettes, only the final 14 zooplankton groups were analysed for the present study (Fig. 2). Abundances were calculated for each zooplankton category in each digitized sample and are expressed in number of individuals per cubic meter. The zooplankton categories considered for this study represent the principal taxa described in the Bay of Calvi (Dauby, 1982, 1980) and are hereinafter referred to as "groups". Only few organisms (estimated to represent less than 3% of average total abundance) were not considered in this study due to their scarcity such as annelids, amphipods, isopods, *Creseis* sp., rare copepods such as *Sapphirina* sp., *Copilia* sp. or *Euterpina* sp. Copepods were gathered into 3 groups for best trade-off between meaningfulness of information and automatic classification efficiency. The group of siphonophores is limited to calycophorans and is constituted by the anterior nectophore and gonophore items representing both stages of non-larval development cycle, polygastric and monogastric respectively (Collignon, 2014). As many appendicularians had their "head" torn apart from the tail probably during the collection with the net, an extra category comprised of appendicularians tails was created and added to the complete individuals to limit bias in abundance. Finally the group comprising "other crustaceans" included mainly decapod larvae besides mysids and euphausids and will therefore be referred to as "decapod larvae". While we acknowledge that some groups including small copepods (e.g.,
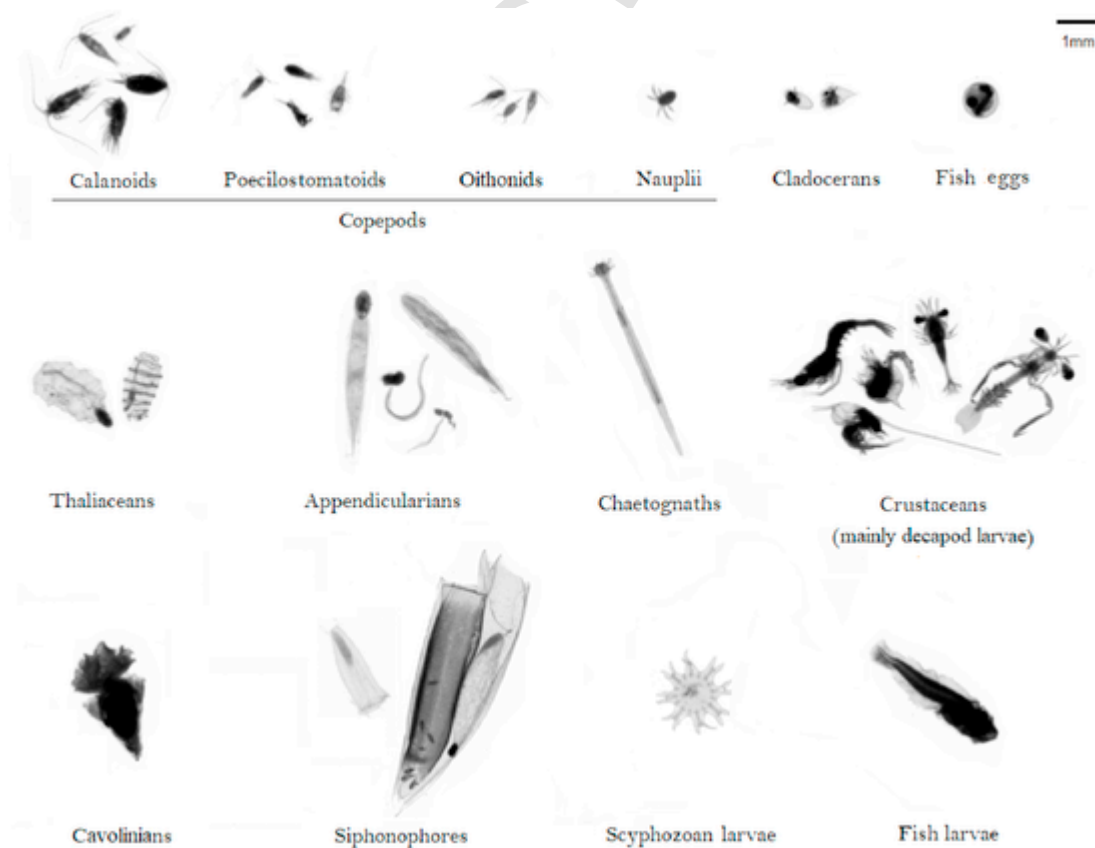

Fig. 2. The 14 zooplankton groups with their respective examples of vignettes issued from the Zoo/PhytoImage analysis.

oithonids) and copepod nauplii may be underestimated owing to the mesh size (Calbet, 2001; Turner, 2004), the multi-annual data collection (13 years) and the constancy of the sampling over the years allows identifying both seasonal patterns and interannual variability.

To reach best performance, the training set was refined considering performances of the classifier by means of ten-fold cross-validation confusion matrix results (Hand, 2009). The Random Forest algorithm (Breiman, 2001) was selected to build a classifier according to Grosjean et al. (2004). For a given sample, after automatic classification on all its objects, a correction was performed by manually validating the most suspect items as identified by a function available in the zooimage R package v. 5.4 (https://github.com/SciViews/zooimage). It was verified that the manual correction of the most suspect vignettes was enough to get a classification of the entire sample with a minimal amount of error in all groups (see recall and precision values in Table 1 and comparison with manual counting for copepods in Fig. A2).

2.4. Classification performance

The classification accuracy applied on the training set and estimated from a ten-fold cross-validation ranged from 96% (fish eggs) to 76% (cavolinians). As an example, 92% of "true" oithonid copepods were successfully classified (recall), although 10% (1-precision) of objects classified as oithonids corresponded to contamination (i.e., objects from other categories misclassified as oithonids). Details regarding the differ-

ent biological groups and their estimated classification accuracy metrics are given in Table 1.

2.5. Environmental parameters

The considered environmental variables were wind gusts (km h^{-1}), subsurface water temperature (°C), nitrate (μmol L^{-1}) and chlorophyll-*a* (μg L^{-1}). Data were partly extracted from the RACE database (Rapid Assessment of the Marine Coastal Environment) of the University of Liège, Belgium (Binard, 2017). Wind gusts correspond to the maximum wind speed in any direction measured over a week period at the Calvi airport by Méteo France, the French national weather organization.

Subsurface water temperature is continuously recorded at 3 m depth in STARESO harbour, generally with a 20 min step frequency. Since 2004, different successive intercalibrated models of probes and loggers (e.g., Hobo UA20, Neotek Pt100) were used over time. For nitrate and chlorophyll-*a*, near-surface water samples (2–3 m depth) were collected weekly to fortnightly close to shore (<200 m) with 2.5 L Niskin bottles around 7:00 a.m. (local time). Twenty mL HCl soaked polyethylene flasks were filled with water samples for nitrate analysis and stored at −28 °C. Nitrate was determined using a Technicon Auto-Analyser II (SEAL Analytical, Inc.) according to working procedures of Tréguer and Le Corre (1975) and with a SAN-Skalar according to the method described by Strickland and Parsons (1972) for an automatic system (Grasshoff et al., 1999) adapted for oligotrophic envi-

Table 1
Description of each zooplankton group and classification performances.

Group	% abd	Description of content	Dominant diet/Trophic group	Recall	1 - precision
Copepods – Calanoids	71.8	Mainly *Clausocalanus arcuicornis, Acartia clausi, Centropages typicus* and *Paracalanus parvus* group (23 species identified in 1978–1979) [a]	herbivores/omnivores	0.91	0.13
Copepods – Oithonids	9.0	Mainly *Oithona nana* and *Oithona similis* [a]	omnivores [b]	0.92	0.10
Cladocerans	8.4	Mainly *Evadne spinifer* [a]	herbivores	0.94	0.08
Copepods – Poecilostomatoids	4.1	Oncaeidae and Corycaeidae	omnivores/detritivores [c] and carnivores [d], respectively	0.83	0.15
Appendicularians	2.8	Both complete organisms and tails (trunkless individuals) Oikopleuridae and Fritillariidae (*Oikopleura dioica, Fritillaria borealis*…)	filter-feeders	(complete) 0.88 (tails only) 0.82	(complete) 0.13 (tails only) 0.12
Other crustaceans (referred to as "Decapod larvae")	1.3	Zoéas, protozoéas and metazoéas mostly of crabs; some euphausiids and Mysidacea	omnivores	0.88	0.20
Copepod nauplii	1.2	Naupliar stages of copepods	Early stages are nonfeeding, late stages are herbivores	0.82	0.07
Fish eggs	0.400	Teleosts [e]	/	0.96	0.03
Thaliaceans	0.040	Doliolidae and Salpidae	filter-feeders	0.83	0.17
Siphonophores	0.014	Calycophora: anterior nectophores and gonophores Mainly *Chelophyes appendiculata* [f]	carnivores	0.81	0.16
Chaetognaths	0.013	Sagittoidae	carnivores	0.87	0.07
Scyphozoan larvae	0.014	Ephyra stage larvae only Mainly *Pelagia noctiluca*	carnivores	0.95	0.07
Fish larvae	0.006	Teleosts	carnivores	0.75	0.13
Cavolinians	0.004	Mainly *Cavolinia inflexa*	filter-feeders/suspensivores	0.76	0.15

Detailed description of each zooplankton group ordered depending on their average relative abundance (% abd), with representative taxa or species (description of content), trophic aspects and classification performances with recall values (proportion of objects well recognized among all objects belonging to a certain category; the highest, the best) and 1-precision values (proportion of objects wrongly assigned to a certain category; the lowest, the best) calculated from ten-fold cross-validation.

[a] Dauby (1980).
[b] Lampitt and Gamble (1982).
[c] (Ohtsuka et al., 1996).
[d] Landry et al. (1985).
[e] (Rodríguez et al., 2017).
[f] Collignon (2014).

ronments. Nitrate data were available only over the period 2006–2016. Chlorophyll-*a* was determined by HPLC (Zapata et al., 2000) after methanol extraction.

2.6. Data analysis

Graphs and analysis were done using R version 3.5.3 (R Core Team, 2018). All datasets were weekly regularized in order to obtain 48 data per year (four per month) using the pastecs R package ("regul" function) and applying a linear method (https://github.com/phgrosjean/pastecs). Average abundances over different time periods (year, month, week) were estimated along with standard deviation ($\pm$).

Seasonal dynamics were described by integrating the time series over one year using boxplot diagrams in order to observe median, first and third quartiles, least values and outliers (described as data point standing 1.5 times outside the interquartile range above the upper quartile and below the lower quartile). Zooplankton seasonal dynamics of each group were further explored by computing the smoothed annual variation of the median, 10th and 90th percentiles of log10 transformed abundances, which allows to highlight both annual and interannual variability. Smoothing was performed using the "lowess" R function which uses locally-weighted polynomial regressions (Cleveland, 1981). Further on, cumulative relative abundances were computed over an average year in order to observe the average annual variation of the community structure.

In order to describe the succession of the peaks of absolute or relative abundance of each group over an average year, a "typical" annual pattern was defined by performing a cluster analysis on zooplankton samples based on the complete linkage method using Bray-Curtis dissimilarity (vegan R package; Dray et al., 2007). Samples were grouped depending on both abundance and general composition similarities. A cut at a distance of 0.81 in the resulting dendrogram allowed to consider eight clusters, each resulting cluster suggesting a different "community state". These eight community states were labelled A to H. A recursive partitioning using the rpart R package (Strobl et al., 2009) was then applied. The analysis used as criteria of classification both absolute and relative abundances of each zooplankton group, including the total. Each decision node of the resulting classification tree corresponded to a condition to which zooplankton samples might respond positively or not. From node to node, all zooplankton samples were classified in one of the eight community states. The succession of the main community states could then be observed over a "typical year".

A Multiple Factor Analysis (MFA) enables an integrative analysis of all parameters including factors and was performed to extract the main modes of relationships between community states, months, zooplankton and environmental time series. Cube root transformation was applied on zooplankton data in order to dampen the influence of highly abundant groups, whilst other variables were standardized to zero mean and scaled to unit variance.

The interannual variability of the zooplankton community structure was explored by depicting the succession of the community states over the 13-year time series, along with the variation of annual anomalies of total zooplankton abundance as well as the weekly anomalies of water temperature.

Finally, in order to further explore the underlying dynamics shaping the zooplankton community, particular emphasis was placed on the spring peak event, since it was found to be a major aspect characterizing the zooplankton annual variation in the Bay of Calvi (Dauby, 1980). Therefore we considered the abundance of the group responsible for the "spring peak", i.e., calanoids, over the peak occurring period (from the first week of March to the third week of May). The 0.80 quantile values were computed to minimize the influence of extreme values and better represent the overall bell shape of the spring peak. To explore potential link between each of the environmental variables with the spring peak magnitude, temporal windows (between October and April) ranging from two to seven months were tested using Spearman's rank correlation coefficient. Relationships with the most correlated temporal windows were then modelled using linear or cubic spline regressions. Similarly, the relationship between spring peak magnitude and the winter North Atlantic Oscillation (NAO) index (downloaded from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based) was also investigated.

3. Results

3.1. Seasonal dynamics

Seasonal variation of wind gusts showed an increase from September onwards until reaching annual maximal values in January (Fig. 3). Subsurface water temperature was lowest from January to April whilst maximal annual variability occurred in July–August and December. Nitrate and chlorophyll-*a* showed an annual peak period with one month lag extending from December to March and January to April, respectively.

Seasonal variation of total zooplankton abundance showed a peak spreading from late March to the end of April (Fig. 4), hereinafter referred to as "spring peak". Increase in total abundance was highest (median > 2500 ind. m^{-3}) during April, with maximal abundance being observed on the 3rd week of April (median = 4850 ind. m^{-3}). Also, important interannual variations of weekly total abundances were observed during this peak period (min = 231 ind. m^{-3} in 2007, max = 17,821 ind. m^{-3} in 2005). From early June until the end of February, total abundance remained relatively stable with the exception of a slight increase in September (average abundance of 820 $\pm$ 375 ind. m^{-3} in September against average abundance of 720 $\pm$ 412 ind. m^{-3} and 690 $\pm$ 366 ind. m^{-3} from July to August and from October to November, respectively). Zooplankton abundances are on average of 1282 $\pm$ 1555 ind. m^{-3} over the whole period, with the most abundant years being 2009 (1768 $\pm$ 1754 ind. m^{-3}) and 2006 (1605 $\pm$ 2138 ind. m^{-3}) and less abundant years being 2007 (574 $\pm$ 518 ind. m^{-3}) and 2015 (721 $\pm$ 526 ind. m^{-3}).

Average annual cycles of copepod nauplii, calanoids, oithonids, decapod larvae, cladocerans, fish larvae, scyphozoan larvae and chaetognaths (in the order of their annual occurrence) showed a clear seasonal peak at different moments of the year (Fig. 5). Calanoid copepods were responsible for the "spring peak" (Fig. 4), as well as oithonid copepods, yet to a lesser extent. While cavolinians, thaliaceans, fish eggs and siphonophores showed several periods of occurrence during the year, abundances of appendicularians and poecilostomatoids remained relatively constant throughout the year.

The 10th to 90th percentile interval gives an insight for each group on their interannual variability at a given period of the year over the 13-year time series. As an example the interpercentile interval of oithonid copepods and cladocerans was relatively homogenous throughout the year indicating little interannual variation, whereas the magnitude of seasonal maximums of fish eggs and thaliaceans was, on the contrary, very irregular (Fig. A1).

The weekly relative abundances of the groups highlight their contribution to the overall annual dynamic of the community (Fig. 6). Over an average year, copepods represented 54%–98% of the total zooplankton abundance. Calanoid copepods, the most abundant group all year round, showed average proportions ranging from 48% to 87%, and in some years, peaking up to 97% in spring periods or dropping down to 16% in summer periods (Fig. 6a). While oithonids also displayed smallest contribution during summer periods, poecilostomatoids were mostly contributing from summer to early winter, coinciding more or
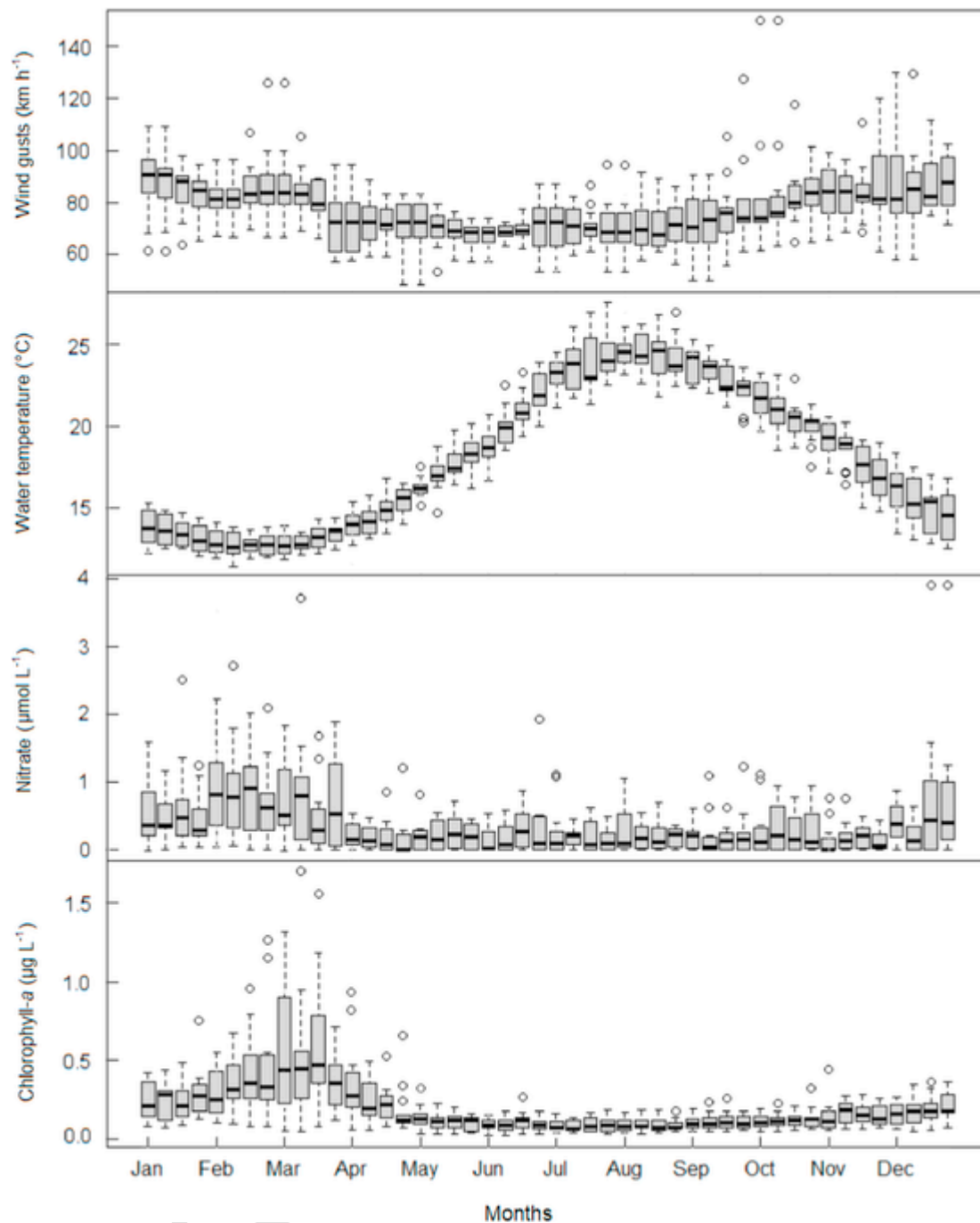
Fig. 3. Average annual cycle of environmental variables for the period 2004–2016, with median, first and third quartiles (boxes), least values (dotted bars) and outliers (dots).

less with appendicularians. After copepods, cladocerans displayed the highest proportional abundance, reaching up to 33% during summer time and, together with copepods, they constituted the core components of the zooplankton community. Regarding the rest of the groups, only copepod nauplii and fish eggs were most contributing during late winter. While most of the carnivorous groups (fish larvae, siphonophores and scyphozoan larvae) coincided with the period of lowest copepods relative abundance, chaetognaths relative abundance increased with decreasing cladocerans relative abundances. Overall, decreasing contribution of copepods after the spring peak gave place to increasing contributions of several trophic groups, whether herbivores (appendicularians, thaliaceans and cladocerans), omnivores (decapod

larvae) and later on carnivores (siphonophores, scyphozoan larvae, fish larvae and chaetognaths) (Fig. 6b).

3.2. Seasonal and interannual dynamics of the community states

The dendrogram resulting from the cluster analysis on zooplankton data showed that the zooplankton community can be differentiated into eight "community states" (A to H). Seeking for rules to easily discriminate these different community states, recursive partitioning analysis revealed five criteria discriminating them more or less successfully (Fig. 7): absolute abundances of calanoids, poecilostomatoids, copepods (i.e., the cumulated three copepod groups), cladocerans and total abundance. To most completely describe each community state, we
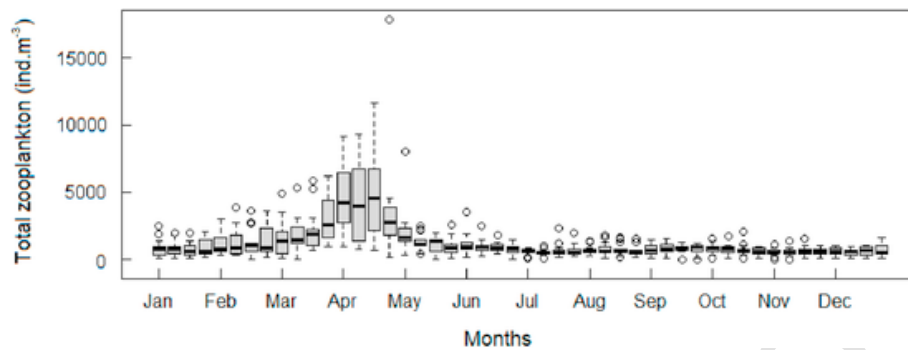
Fig. 4. Average annual cycle of total zooplankton abundance for the period 2004–2016, with median, first and third quartiles (boxes), least values (dotted bars) and outliers (dots).
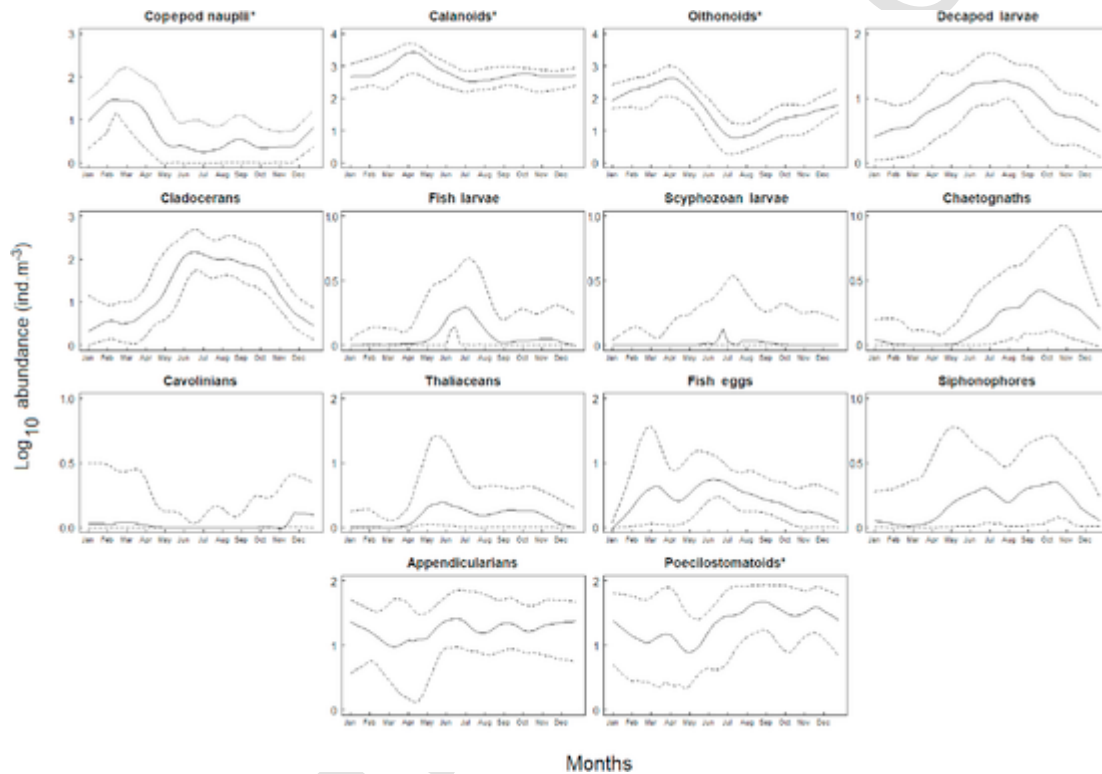

Fig. 5. Smoothed seasonal variation of median abundances of each zooplankton group (full line) and the 10th and 90th percentiles (dotted lines). Copepod groups are highlighted by *. Note that log10 abundance scales differ. The first eight groups (copepod nauplii to chaetognaths) showed relatively clear seasonal peaks in comparison to the other groups and were therefore ordered according to their annual occurrence.

also considered their year-to-year recurrence, and for this, zooplankton community structures were distributed over one year depending on their state (Fig. 8). Most recurrent community states over the year were A, D, B, in decreasing order. They are connected to each other on Fig. 8 by a full line, and together they encompass 56% of all observations. In other words, Fig. 8 characterizes the most usual pattern of zooplankton community change over time, forming a "typical year". When looking at the average annual variation (Fig. 5), calanoids showed a maximal peak of abundance around April (state C), with periods of pre- and post-peak (state B). Periods characterized by state B and C comprised on average 48% and 25% and for some years up to 70% and 39% of the total annual abundance, respectively. State D corresponded to the summer period and was characterized by an increase of cladocerans (Fig. 5). The rest of the year was most frequently characterized as state A, displaying close to average abundances for most of each group. State H revealed a community structure with greater abundance of oithonids than calanoids, appearing only before the spring

peak period. Finally states E, F and G, represented community structures with lowest total abundances, in decreasing order.

We outlined two periods within the zooplankton time series, the former (2004–2010) characterized by rather positive annual abundance anomalies (average abundance of 1412 ± 1876 ind. m^{-3}), and the latter (2011–2016) characterized by rather negative anomalies (average abundance of 1130 ± 1049 ind. m^{-3}, despite lowest abundance occurring in 2007 (Fig. 9a). Such change of annual abundance was also observed for some groups especially calanoids, but also cladocerans, appendicularians and decapod larvae (Fig. A3). When comparing with the previously described typical annual succession of the community states (Fig. 8), years of lowest annual abundance were characterized by particularly different community state successions, especially because they presented very little (2007, 2015 and 2012 with state B only) or short-lived (2011 and 2014 with state C) spring peaks (Fig. 9b). Furthermore, years characterized by lowest presence of state D occurred during years of low spring peak (2007 and 2012) but low spring peak did not always lead to low presence of state D (2015). In terms of timing
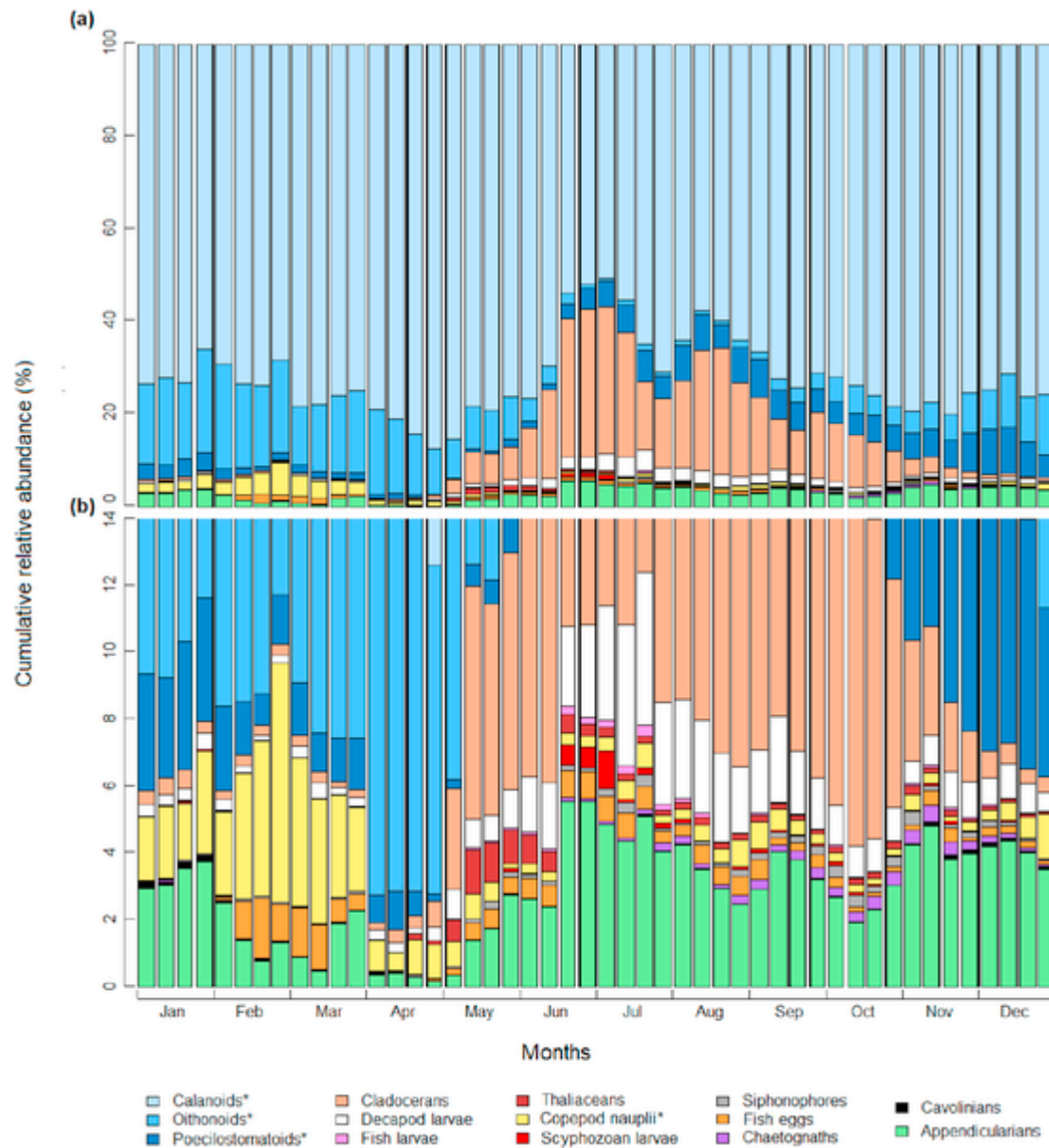
Fig. 6. Mean weekly values of cumulative relative abundances of the 14 zooplankton groups, (a) for the whole community and (b) for groups accounting for less than 8% of the total abundance (i.e., all excluding copepods and cladocerans). Copepods groups are highlighted by *. We remind that some groups, especially copepod nauplii might not be quantitatively sampled, as only the fraction greater than 200 μm is considered. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and duration, spring peak maxima (state C) was short and relatively regular in time (late March to end of April) over the whole series, except for 2004 with an earlier appearance in February. On the contrary, the summer community (state D) was prolonged and its presence could be either continuous (2004 or 2016) or not (2005 and 2015). Water temperature anomalies showed an opposite pattern to that of total annual zooplankton anomalies, with particularly warm periods occurring in 2007 (for half of the year) and later again from 2012 to 2016 (Fig. 9c).

3.3. Relationships between spring peak and environmental conditions

Regarding relationships between the spring peak and the different time windows of environmental parameters, most correlated time windows corresponded to the October–January higher wind gust frequency, to the January–March temperature minima and to the December–March annual peak of nitrate described in Fig. 3. These potential causal relationships between the environmental conditions including winter NAO index and the peak intensity are modelled in Fig. 10. Even though no significant correlation was found between chlorophyll-*a* and the spring peak, the highest correlation was observed considering the February–April temporal window, which corresponds to the phytoplankton bloom period.

Two groups of years could be differentiated depending on their spring peak intensity: below 3000 ind. m^{-3} for years 2007, 2011, 2012, 2014, 2015, 2016; above 3000 ind. m^{-3} for years 2004, 2005, 2006, 2008, 2009, 2010, 2013. Years of weakest spring peak were characterized by low nitrate concentrations (<0.7 μmol L^{-1}) (Fig. 10c), high temperature (>13.6 °C, except for 2011) (Fig. 10b) and high winter NAO index value (except for 2011 as well) (Fig. 10d). Regarding temperature, spline regression fitting showed that greatest spring peak abundances were reached within a limited range of subsurface water
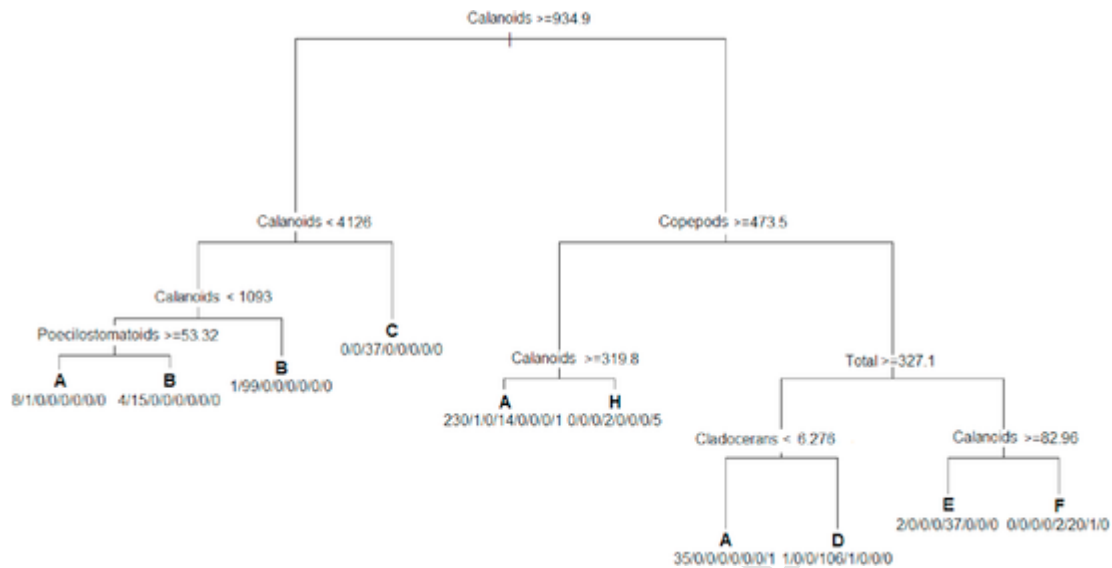
Fig. 7. Decision tree generated through recursive partitioning classification into the eight clusters, highlighting rules that best discriminate these clusters. The decision tree contains all 318 zooplankton samples. The eight clusters, labelled A to H, were identified on a dendrogram resulting from hierarchical clustering analysis. Each node corresponds to a condition to which each individual zooplankton sample may respond positively or not. If the response of the sample to that criterion is positive, then the classification of the sample follows the branch to the left; if not, the classification of the sample goes to the right. As an example, if one sample from cluster A to H contains more than 935 calanoids, then it may be subject to the next decision node for which calanoids can be above or below 4126. If that abundance of calanoids is above 4126, then the sample is classified as cluster C. Otherwise it is redirected to the other nodes at left. The numbers under each ending branch correspond to the number of samples classified in each cluster A/B/C/D/E/F/G/H, respectively. Taking the example of cluster C, 0/0/37/0/0/0/0/0 indicates that 37 samples were all classified as cluster C, with no false positives in any of the other clusters. Overall, states C, D, E, F, H were successfully discriminated, A and B with lesser success, and G not at all.
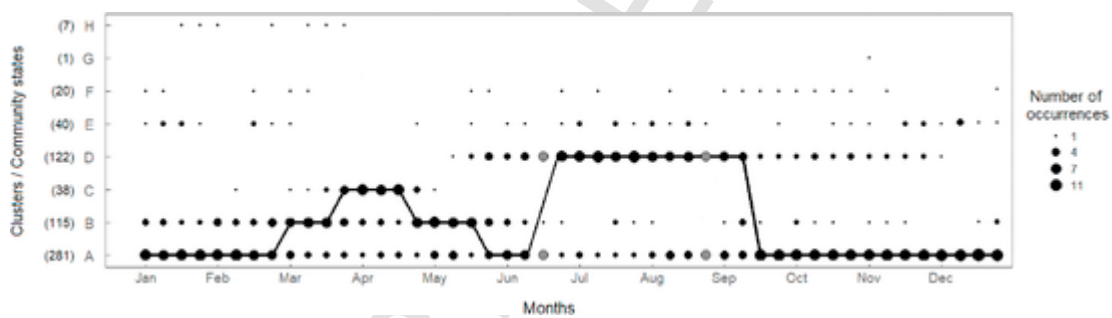

Fig. 8. Weekly succession of the most frequently occurring zooplankton community states out of the eight different clusters labelled A to H identified on a dendrogram resulting from cluster analysis and defined as "community states". The number of observations contained in each cluster is indicated next to it. At a given week averaged over the 13-year time series, dot size corresponds to the year-to-year recurrence of each state. The solid line links the biggest dots, here represented by states A, B, C and D. In case of a tie, dots were colored in grey.

temperature between 12.1 °C and 13.4 °C during the January to March period. Regarding wind gusts, periods from October to January characterized by average gusts greater than 87 km h^{-1} were consistently followed by greater spring peaks (2006, 2010, 2009, 2004) (Fig. 10a). In particular, year 2007 that displayed the lowest spring peak and annual total abundance (Fig. 9a) was characterized by extreme values for all environmental parameters during the October–April period (high values for temperature and winter NAO, low values for wind gusts, nitrate and chlorophyll-*a*).

Subsurface temperature over the whole period (2004–2016) was characterized by a warming trend of 0.08 °C yr^{-1} ($p = 0.016$) (Table 2). Yet, seasonal averages showed a significant increase since 2010 (0.30 °C yr^{-1}, $p = 0.005$) and only for the winter season (January–March), which coincided with the period of lower total zooplankton abundance (Fig. 9a).

4. Discussion

4.1. Seasonal dynamics

The dynamics of the zooplankton community structure over the course of the year was characterized by specific periods of appearance

for most of the groups. On the one hand, we observed a well-defined period of annual highest abundance for about half of the considered groups (copepod nauplii, calanoid and oithonid copepods, decapod larvae, cladocerans, fish larvae and chaetognaths). On the other hand, the rest of the groups displayed either less clear seasonal patterns (e.g., fish eggs, thaliaceans, cavolinians, siphonophores) or no cyclic pattern at all (e.g., appendicularians and poecilostomatoids), partly because these groups might include species with different typical seasons (Licandro and Ibanez, 2000). Annual dynamics of the epipelagic zooplankton of the Bay of Calvi at species level were previously described using traditional methods (manual enumeration and identification) over one year in 1978–1979 (Dauby, 1982, 1980), during spring 1986 (Brohée et al., 1989) and from 2003 to 2012 for calycophores only (Collignon, 2014). In these works, described periods of annual occurrence of total copepods, calanoids, oithonids, copepod nauplii, cladocerans, decapod larvae, siphonophores and fish larvae matched those in our results. Similarities were particularly accurate regarding the spring peak seasonality, spreading from March to mid-May and peaking in April (Brohée et al., 1989). This suggests that the yearly community succession remained fairly stable over time in terms of seasonality for the considered groups, which is also confirmed by the strong seasonal sig-
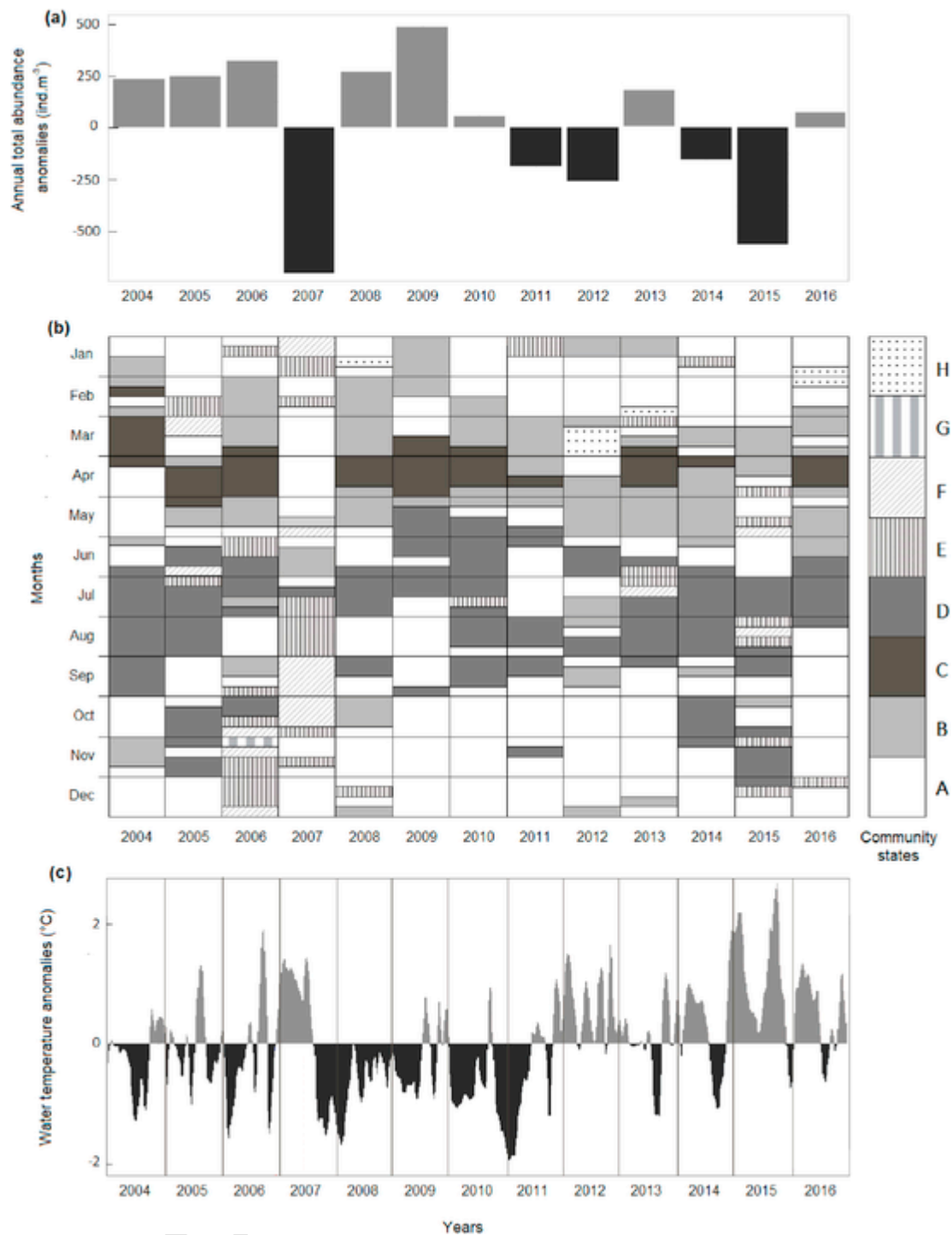
Fig. 9. Variability of zooplankton and water temperature with (a) annual anomalies of total zooplankton abundance, (b) weekly succession of the eight community states (most common states are in plain color (A to D) and less common are represented by patterns (E to H)), and (c) water temperature anomalies.

nature revealed with the MFA sample distribution (Fig. A4). Furthermore, we found that timing of maximal seasonal peak of phytoplankton (through chlorophyll-*a*), (total) copepods, cladocerans and chaetognaths matched (with a lag of 0–2 months) all six coastal Mediterranean zooplankton time series studied by Berline et al. (2012) except for chaetognaths in the eastern basin. Seasonal succession and timing of these broad groups may therefore be considered as a common feature to most studied coastal Mediterranean areas.

On a global scale, it is usually supported that seasonal timing of several functional marine groups including copepods shift with warmer

temperatures (De Senerpont Domis et al., 2013; Edwards and Richardson, 2004; Ekvall and Hansson, 2012; Greve et al., 2001; Mackas et al., 2012; Villarino et al., 2015). Although the timing of the annual maximum of phytoplankton was previously found to change with years in the Bay of Calvi (Goffart et al., 2015), such phenological change was not obvious regarding zooplankton spring peak in our case. It may be linked to the fact that dominant grazers in oligotrophic areas seem to be microzooplankton (<200 μm) (Jackson, 1980), thus probably loosening the trophic relationship between phytoplankton and mesozooplankton. Also, impacts on some zooplankton species might be
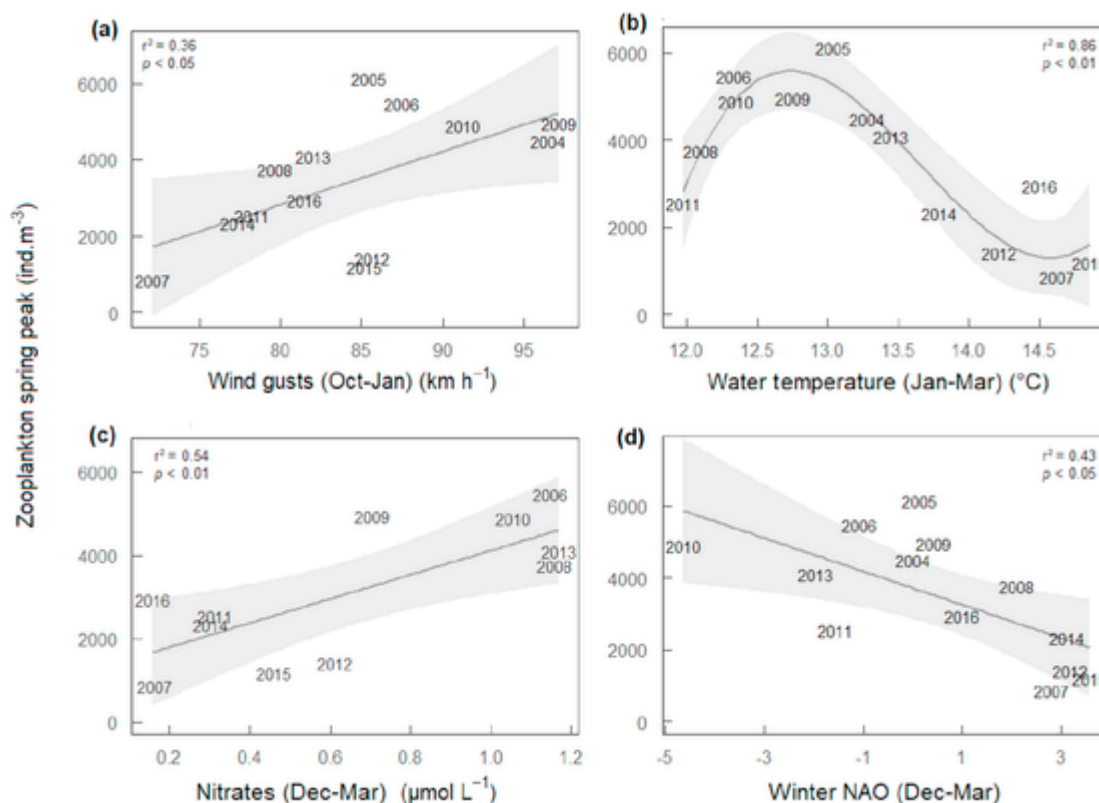
Fig. 10. Relationships between zooplankton annual spring peak abundance and seasonal means of (a) (b) (c) environmental variables and (d) the winter NAO index. Data were fitted with (a) (c) (d) linear regression or (b) spline models, using temporal windows of environmental variables (wind gusts, water temperature and nitrates) that best correlated with the zooplankton sprink peak. The 0.95 confidence envelope of models was added in grey.

Table 2
Sea surface temperature trends.

Time series fraction	Overall	Winter	Spring	Summer	Fall
2004–2016	0.08 ****	0.08 NS	0.07 NS	0.09 NS	0.12 NS
2010–2016	0.23 ****	0.30 **	0.13 NS	0.14 NS	0.34 NS

Trends (°C y^{-1}) were determined through linear regression. NS: not significant, **: $p < 0.01$, ****: $p < 0.0001$.

compensated at community level by other species (even within one of the 14 groups) with overlapping niches and functions (Frost et al., 1995; Hooper et al., 2005; Mouillot et al., 2013), thus enabling the community to adapt to fluctuating environments (Mackas et al., 2012; Mazzocchi and Ribera d'Alcalà, 1995; Mazzocchi et al., 2012).

The seasonal spring peak was a major feature of the seasonal dynamics since it concentrated on average (over the month of April) 25% of the total annual zooplankton abundance. It was composed on average by 85% by calanoids. When comparing with the annual cycle of total zooplankton abundance described in other zooplankton time series of coastal Mediterranean areas (Berline et al., 2012; Christou, 1998; Fernandez de Puelles et al., 2003; Fernández de Puelles et al., 2007; Mazzocchi and Ribera d'Alcalà, 1995; Mazzocchi et al., 2012; O'Brien et al., 2013; Ouba et al., 2016; Ribera d'Alcalà et al., 2004; Siokou-Frangou, 1996; Vandromme et al., 2011) the zooplanktonic system of the Bay of Calvi seems to be annually characterized by a particularly intense single annual peak of total abundance.

The variability over time of calanoid spring peak magnitude strongly affected the year-to-year fluctuation of total zooplankton abundance. Dauby (1980) reported a greater spring peak abundance in 1979 for the Bay of Calvi than in our results. Indeed, over the 2004–2016 period, spring peak was on average 2.16 (range: 1.34 to 3.06) times more abundant than the annual zooplankton mean abundance, against 3.15 for 1979. In order to rule out a potential bias linked to the methodology, semi-automatic classification and traditional manual counting methods were compared based on copepod abundance results; counts did not significantly differ between both methods (5% confident interval, slope = 0.97) and showed a close linear fit ($r^2 = 0.83$, $n = 30$, $p < 0.01$) (Fig. A2). Thus the spring peak of 1978–1979 might have been particularly intense, being even more important than the greatest spring peak of the present study. This could further suggest that, while the timing of appearance of the spring peak did not seem to have shifted in time, a decrease of the intensity might have occurred.

Finally, we highlighted an annual community succession shaped by core structuring taxa (calanoids and cladocerans) and more sporadically appearing groups, built around the spring peak (state B and C) period and the summer period (state D). The community structure underwent a net transition following the spring peak event whereby a taxa association mainly dominated by adult copepod and copepod nauplii was giving place to a much more diversified community in terms of both taxonomical and trophic groups. Purely carnivorous groups (siphonophores, scyphozoan larvae, fish larvae and chaetognaths) occurred solely in summer and fall, suggesting predation by zooplankton to take place mainly at that time of the year.

4.2. Interannual variability

The zooplankton community displayed major variabilities over the 2004–2016 time series. The year 2007 appeared as very particular, in which extreme zooplankton abundances and environmental winter conditions were observed. This same year, particularly low metabolic rates were measured over the *Posidonia oceanica* seagrass meadow (dominant

coastal benthic biotopes of the Bay of Calvi) (Champenois and Borges, 2019), suggesting that such extreme winter conditions probably affected a large variety of ecological compartments of the bay.

Late winter and spring conditions were previously investigated in the Bay of Calvi: strong dominant (North-East) winds lead to vertical mixing of the water column and upwelling of colder water from the canyon, enriched with nutrients. This dynamic can induce phytoplankton blooms (Goffart et al., 2015; Skliris et al., 2001), eventually followed by a zooplankton biomass increase (Brohée et al., 1989). Also, a modeling study carried out in the Bay of Villefranche (Ligurian Sea) showed that interannual variability of winter nutrient contents in the euphotic layer, induced by winter mixing, would control spring primary production and thus annual mesozooplankton biomass (Auger et al., 2014). Our results are partly coherent with such cascading processes, with zooplankton spring peak being positively correlated to the intensity of wind gusts occurring from mid-fall to mid-winter and to nitrate concentrations increasing subsequently from December onwards. However zooplankton spring abundance varied greatly in years with gusts of average intensity, implying either that other parameters might be more decisive under medium strength winds or that their impact depends on their average direction during the late winter-spring period (here not investigated), as previously suggested (Skliris et al., 2001).

Moreover, while low zooplankton spring peaks were consistently preceded by periods of lower nitrate concentrations, no relationship was found as regards to phytoplankton bloom intensity, no matter the considered temporal window. The absence of relationship between zooplankton abundance and availability of food (phytoplankton) was previously reported for other Ligurian bays (Rossi and Jamet, 2009). Food quality or availability of microzooplanktonic preys (such as ciliates) might prevail over chlorophyll-*a* concentration (Ambler, 1986; Broglio et al., 2004), which could explain situations of high chlorophyll-*a* concentrations with low subsequent copepod abundances. Situations of "top-down" control of phytoplankton spring bloom by zooplankton (e.g., Fuchs and Franks, 2010; Prowe et al., 2012; Sommer and Lewandowska, 2011; Sommer and Sommer, 2006) was strongly suggested to occur in the Bay of Villefranche (Auger et al., 2014; Vandromme et al., 2011) and could explain conditions of low phytoplankton yet high zooplankton outbursts (2004, 2006, 2008).

Water temperature anomalies and zooplankton community dynamics varied consistently over time. Years with weakest spring peak and consequently lowest total annual zooplankton abundances (2007, 2012 and 2015) were all characterized by warmer than average subsurface water temperature over the winter (January to March) period. On the contrary, greatest spring peak and annual total abundances were observed in years of colder winter water temperature, in particular when average temperatures were comprised between 12.1 °C and 13.4 °C. On the one hand, cold water could be related to deep winter mixing, supplying nutrients to the euphotic layer and consequently allowing phytoplankton blooms. Indeed, it was previously reported in the Bay of Calvi that the chlorophyll-*a* concentration during phytoplankton bloom period could abruptly drop under stable winter conditions of the water column, when subsurface water temperature exceeded 13.5 °C (Goffart et al., 2015). On the other hand, the bell-shaped relationship between spring peak and subsurface temperature could reflect direct thermal regulation processes. It is often considered that zooplankton population dynamics are tightly linked to water temperature (Hays et al., 2005; Richardson, 2008) and a direct role (as opposed to solely being an indicator of circulation change or deep water mixing) is not excluded (Calbet, 2001; Conversi et al., 2009; Dippner et al., 2000; Fernández de Puelles et al., 2007, 2004; Molinero et al., 2008; Richardson, 2008). Temperature can potentially impact copepod abundance via temperature-dependent feeding preferences (Gusha et al., 2019), enhanced degree of food limitation with increasing temper-

atures (Hirst and Bunker, 2003; Kamykowski and Zentara, 2005) and altered reproductive success (Holste and Peck, 2006; Kiørboe et al., 1988). Accordingly, the existence of species-specific thermal niches (Bonnet et al., 2005; Jiang et al., 2008; Molinero et al., 2009; Peralba et al., 2017; Peralba and Mazzocchi, 2004) was, along with local warming velocity, identified as key to rearranging copepod community composition in coastal ecosystems (Batistić et al., 2014; Villarino et al., 2020). Back in the late 1970s, *Clausocalanus arcuicornis* was identified as responsible for the mesozooplankton spring peak in the Bay of Calvi, composing 85% of the copepod community at that season (Dauby, 1982, 1980). Interestingly, it was shown in the Gulf of Naples that *C. arcuicornis* attained peak abundance in the upper layer during spring and avoided surface layers in the summer when surface temperatures were close to 20 °C or exceeded 20 °C (Mazzocchi et al., 2012; Peralba and Mazzocchi, 2004). The hypothesis of a temperature-induced migration to deeper (unsampled) layers contradicts a comparative analysis between vertical (30 hauls of sampling from 100 m depth to surface) and horizontal mesozooplankton samples in the Bay of Calvi, concluding that the relative abundances of calanoids were not significantly different from one sampling methodology to the other, including for spring periods (Quivy, Unpublished results). While our results could potentially support the previously expressed idea that *Clausocalanus* species may be considered as good indicators of changes in ecosystem structure due to climate change (Peralba et al., 2017), we acknowedge that our zooplankton data should undergo species-level identification and be completed with multi-depth sampling campaigns in order to better understand the impacts of local warming on the zooplankton population dynamics of the Bay of Calvi.

Literature on the zooplanktonic system in the Ligurian Sea suggests a quasi-decadal cycle. This hypothesis follows from the observation of significant zooplankton abundance increase during the 80s (Molinero et al., 2008), decrease in the early 90s and again increase in early 2000s (García-Comas et al., 2011; Vandromme et al., 2011). We suggest that our results could fit into such quasi-decadal fluctuations, with overall greater zooplankton abundances over the 2000–2010 period, followed by a decade of lower abundances. While we found zooplankton spring peak to be negatively correlated to winter NAO index, a study analyzing six mesozooplankton time series of the Mediterranean Sea between years 1957 and 2006 did not find any correlation between NAO and temperature or zooplankton abundance (Berline et al., 2012). Authors suggested that the strength of the correlation could vary in time, with previous correlations (e.g., Molinero et al., 2008; Piontkovski et al., 2006) being no longer significant when considering data of the twenty-first century. In contrast, in the Balearic Sea, copepod abundances were found to be negatively correlated to winter NAO over the 1994–2003 period (Fernández de Puelles et al., 2007, 2004), which is consistent with our results. Potential mechanisms linking the North Atlantic climate to zooplankton variability have been proposed for both the Ligurian Sea (Molinero et al., 2008, 2005) and the Balearic Sea (Fernández de Puelles and Molinero, 2008, 2007). The authors described a relationship driven by a chain of events from the large-scale atmospheric forcing down to the regional and local meteorological and hydrological conditions. It was highlighted that this relationship was most dynamic during winter, and that negative anomalies of the North Atlantic climate were associated to colder winters and more intense water column mixing (Fernández de Puelles and Molinero, 2008). This is coherent with our findings, as positive winter NAO index anomalies were associated to warmer winters and lower zooplankton abundances. A study using 10-m-deep measurements near our sampling area reported a similar seawater warming trend (0.07 °C yr^{-1}) and also positively correlated the water temperature increase to the sustained more positive winter NAO index values (Champenois and Borges, 2019). Our results therefore strongly suggest large-scale

processes to influence the zooplankton dynamics in the Bay of Calvi, whereby water temperature may play a key role in the underlying connecting mechanisms.

5. Conclusion

Our results indicate that the zooplankton community in the Bay of Calvi is marked by an important seasonality with specific periods of occurrence for many zooplankton groups, and a single major annual peak concentrating during April 25% of the total annual zooplankton abundance. Important interannual variabilities in total abundance outlined by particular years were associated to environmental changes, which suggests a highly sensitive zooplankton - especially copepod - community characterized by a limited resilience compared to other coastal communities (Mazzocchi and Ribera d'Alcalà, 1995; Mazzocchi et al., 2012; Villarino et al., 2020). Late fall and winter emerged as a critical time window during which a tight link between the North Atlantic climate variability, wind, water temperature, nutrient replenishment and zooplankton changes is evident in the Bay of Calvi. While our findings contrast with previous results suggesting that the correlation between NAO and zooplankton abundance was no longer significant for data of the twenty-first century, the main processes by which large-scale climate fluctuations might affect changes in the abundance of zooplankton are coherent with those described for the Balearic Sea (Fernández de Puelles and Molinero, 2008). Furthermore, we suggest a direct impact of water temperature on zooplankton through the identification of an optimum temperature range associated to high spring abundance. Predominantly lower abundances since 2010 could be explained by intensified winter warming or/and weakened winter mixing, and the relative importance of each hypothesis should be verified via specific target studies. Within the current context of increasing environmental pressures and global change, it seems particularly relevant to monitor zooplankton given both its attributes as a sensitive beacon of climate change and its central function within the trophic chain and the biogeochemical processes of the water column. The approach of establishing a "typical year" could also be useful for providing a baseline regarding a zooplankton-based indicator of environmental disturbance (Uusitalo et al., 2016). The rapid changes occurring nowadays and those expected in the upcoming century might imply profound changes and challenge potential adaptive response mechanisms that deserve to be studied.

CRediT authorship contribution statement

Lovina Fullgrabe: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing - original draft. **Philippe Grosjean:** Funding acquisition, Conceptualization, Methodology, Software, Resources, Formal analysis, Writing - review & editing. **Sylvie Gobert:** Funding acquisition, Data curation, Conceptualization, Resources, Writing - review & editing. **Pierre Lejeune:** Funding acquisition, Data curation, Resources, Writing - review & editing. **Michèle Leduc:** Data curation, Writing - review & editing. **Guyliann Engels:** Formal analysis, Writing - review & editing. **Patrick Dauby:** Validation, Data curation, Writing - review & editing. **Pierre Boissery:** Funding acquisition, Data curation, Writing - review & editing. **Jonathan Richir:** Data curation, Formal analysis, Supervision, Validation, Writing - original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2020.104962.

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