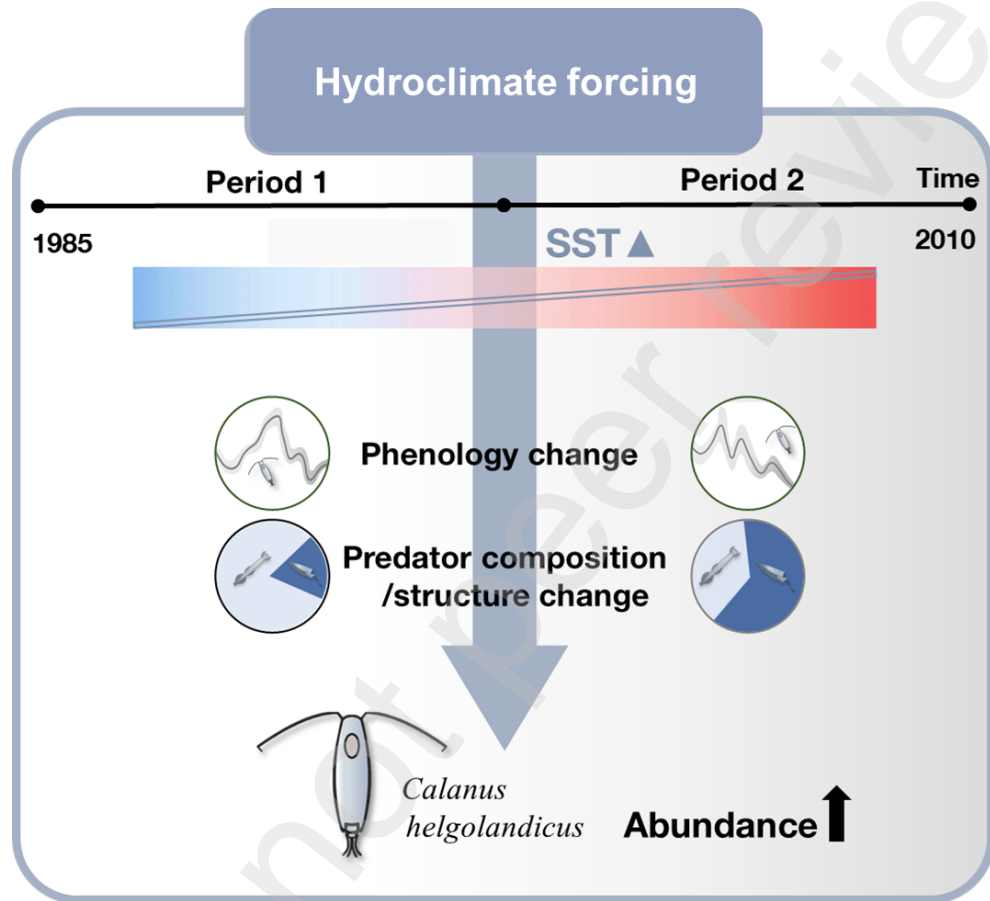


Graphical abstract



Graphical abstract. Climate warming triggered cascading effects on zooplankton dynamics of the Marine protected area of Mljet Island, Croatia, including an abundance decline of the main copepods predator, *Parasagitta setosa*, which favored enhanced abundance and phenological changes of *Calanus helgolandicus*.

Compound effects of warming and predation shaped decadal changes of *Calanus helgolandicus* in the marine protected area of Mljet Island, South Adriatic Sea

Juan Carlos Molinero^{1*}, Eduardo Ramirez-Romero², Mirna Batistić³, Delphine Bonnet¹, Sun-Hee Lee¹, Davor Lučić³, Marijana Hure³

¹ MARBEC – Marine Biodiversity, Exploitation and Conservation.

IRD/CNRS/IFREMER/Université de Montpellier, Sète Cedex, France.

² Instituto de Ciencias Marinas de Andalucía (ICMAN)-Consejo Superior de

Investigaciones Científicas (CSIC), C/ República Saharaui,4, 11519

Puerto Real, Cádiz, Spain.

³ Institute for Marine and Coastal Research, University of Dubrovnik, D. Jude 12, 20000

Dubrovnik, Croatia.

*Corresponding author:

E-mail: juan-carlos.molinero@ird.fr

Abstract

Calanus species are perhaps the most investigated planktonic copepods due to their pivotal role supporting pelagic food webs in temperate and cold shelf ecosystems. In the Adriatic Sea, *C. helgolandicus* is a prominent species of the seasonal bulk of copepods biomass. We here examined temporal changes of *C. helgolandicus* over the period 1985-2010 in the marine protected area of Mljet Island, south Adriatic Sea. Our results showed close connection between regional and local hydrographic variability, which cascaded down shifting the local environment towards warmer conditions after 1997. *C. helgolandicus* displayed marked year-to-year variations from the middle 1980s until the late 1990s, followed by a sustained abundance increase in the 2000s, which was concurrent with warmer environmental conditions. The temperature increased further altered the phenology of the species, where the timing of seasonal peak shifted forward ca. two months under higher temperatures. Partitioning effects of forcing factors highlighted a leading role of temperature favoring *C. helgolandicus*, while negatively affecting chaetognaths abundance, the main copepod predator in the system. These results illustrate a climate-driven top-down control released, which combined with favorable environmental conditions, lead the abundance observed abundance increase of *C. helgolandicus* in the first decade of 2000s. Sheltered from anthropogenic disturbances, marine protected areas appear as natural laboratories to assess plankton food web responses to changing climate.

1. Introduction

Long term field observations of zooplankton abundance have proven essential to track climate-related marine ecosystem changes (Edwards and Richardson, 2004). This is due partly to the zooplankton generally short life cycle that favors rapid responses to environmental change, and partly to the pivotal role these organisms play in marine ecosystems, linking environmental variability, primary production, and fish recruitment (Hays et al., 2005). *Calanus* species are perhaps the most investigated planktonic copepods, as they play a prominent role supporting pelagic food webs, thus influencing the pace of carbon cycle in shelf ecosystems (Conover et al., 1995; Lindeque et al., 2004). In the North Atlantic and adjacent seas, long term changes in biogeographic patterns of *Calanus* species have been widely documented in recent decades (Planque and Fromentin, 1996; Reygondeau and Beaugrand, 2011; Chust et al., 2014). Among the reported abundance and spatial changes in *Calanus* species, the warm-temperate species *C. helgolandicus* has displayed a conspicuous abundance increase (Helaouët et al., 2013), concurrently with a widened spatial distribution ascribed to the pace of warming in the North Atlantic (Chust et al., 2014). By contrast to the well-known changes in northern latitudes, little is known on temporal patterns in southern locations of the species' geographic distribution, e.g., the Mediterranean Sea, where *C. helgolandicus* is an important component of copepods community in productive sites (Bonnet et al., 2005).

In the Mediterranean basin, *C. helgolandicus* inhabits productive rich areas of Alboran Sea, Gulf of Lion, Ligurian Sea, Adriatic Sea, and northern Aegean Sea (Bonnet et al., 2005; Mazzocchi et al., 2014 and references therein). The species markedly drop and is only seasonally present off Tunisia and in the most oligotrophic region of the Mediterranean basin, the Levantine Sea (Yebra et al., 2011), whereas in southern coasts of the eastern Mediterranean it is absent (Weikert et al., 2001). As other congeners, *C. helgolandicus* displays a seasonal vertical migration, which in the Mediterranean Sea occurs likely to avoid high temperatures. During late summer-autumn, the species descends to intermediate and deep layers, as deep as 1500 m (Scotto di Carlo et al., 1991) and ascends to epipelagic waters in late winter-spring (Mazzocchi et al., 2014, and references therein). Such seasonal pattern has been observed in the northwestern Mediterranean, northern Adriatic Sea, and Aegean

Sea, where the main seasonal peak is concurrent with the species presence in epipelagic waters (Weikert et al., 2001).

In the Adriatic Sea, *C. helgolandicus* is among one of the most abundant large copepods (> 2 mm), and part of the diet of large planktivorous fish, e.g., basking shark (Soldo et al., 2008). The Adriatic Sea also harbors hotspots of *C. helgolandicus*, i.e., sites with recurrent high densities, such as the marine lakes in the marine protected area of Mljet Island, southern Adriatic Sea. These bodies of seawater surrounded by land and connected to the sea through channels offer unique ecological settings. The Mljet National Park embodies the Veliko Lake, a stratified water body that supports high zooplankton richness, including a native population of *C. helgolandicus* (Miloslavica, 2012). Although the lake is connected to the open sea, genetic and morphological analyses of *C. helgolandicus* have shown significant differences between the population inhabiting Veliko Lake and populations from other European seas (Yebra et al., 2011). Moreover, this lake shelter genetically isolated assemblages of the moon jelly *Aurelia* sp. (Benovic et al., 2000, Schroth et al., 2002) and the chaetognath *Parasagitta setosa* (K. Peijnenburg and M. Batistic unpubl. data).

Understanding the impact of changing climate on *C. helgolandicus*, the interannual variability and mechanisms through which the species respond to changing environments is essential due to the prominent role it plays in pelagic food webs and carbon cycling. We here examine pluriannual field records spanning over two decades to examine underlying environmental and ecological forces shaping long term patterns of *C. helgolandicus*. The Marine protected area of Mljet Island is not affected by anthropogenic stress, e.g., pollution and fishing, and therefore offers an ideal framework to investigate plankton responses to natural forcing.

2. Methods

2.1 Data collection

Biological data were collected over the period 1985 to 2010 mainly on a monthly or bimonthly basis, although several gaps exist. For instance, no samples were taken in 1987, as well as during the period 1991 to 1995, and in the years 2002, 2005 and 2007. Samples were taken by vertical net hauls during daylight at the deepest location in the lake (42°771'N, 17°370'E ca. 46 m depth and fixed immediately with buffered formalin (5 % final

concentration). The plankton mesh size used was 125 μm , excepting in 1985 and 1986 when a mesh size of 250 μm was used. Taxonomic determination was performed consistently at the species level and zooplankton quantification was done using a stereomicroscope. We used predators' abundance, chaetognaths and siphonophores, to assess the predation pressure on *C. helgolandicus*. Chaetognaths were dominated by *Parasagitta setosa*, while siphonophores were mainly composed by *Muggiaea atlantica*. For siphonophores we counted both, asexual (nectophores) and sexual (eudoxids) stages to estimate the total abundance of feeding individuals. We acknowledge that the mesh size used does not provide an accurate abundance estimate of *C. helgolandicus*, however the consistency of samples treatment throughout the whole period makes these observations comparable among them, thus useful to assess interannual patterns over the period investigated.

Physical data used cover regional and local scales to assess potential links between hydroclimate variability in the south Adriatic and local hydrological conditions in the Veliko Lake. At the regional scale, we used average salinity values in the 200-800 m depth layer to track thermohaline changes in the south Adriatic. These data were obtained from the Medatlas database over the period 1985-2010 and have proved useful to capture low frequency salinity changes in the south Adriatic (Batistic et al., 2014). Also, we used monthly anomalies of hydroclimate variables (air temperature, sea surface temperature, sea level pressure, 500 hPa geopotential height, precipitation and long-wave radiation over the period). These data were downloaded from the Climate Diagnostics Center (NCEP/NCAR) reanalysis, which combines past observations with models to generate consistent time series of multiple climate variables (Kalnay et al., 1996). Downloaded data correspond to the nearest grid point (42°9'N, 16°9'E) to the sampling station (42°77'N, 17°36'E). In addition, local hydrological variations were assessed by means of integrated field records of temperature and salinity taken from bottom (~40m) to surface concurrently with plankton samples.

2.2 Statistical Analysis

Temporal changes in the south Adriatic climate were assessed following the procedure used in Molinero et al. (2005, 2008). This consists of extracting the seasonal trend of atmospheric variables and summarizing the climate signal by means of Principal Component Analysis

(PCA). PCA was applied on a matrix composed of the seasonal detrended climate variables, i.e., months \times climatic variables. The general trend of south Adriatic climate, as indexed by the first principal component (PC1, 58% of total variance), was used as proxy of the regional climate variability.

The temporal variations of water temperature records in Veliko Lake and SST data in the south Adriatic obtained from the Climate Diagnostics Center (NCEP/NCAR) were assessed by plotting the cumulative sum of standardized values over time. The method consists of plotting the cumulative sum of standardized values over time. Each data point, Y_t , corresponding to time t (t from 1 to n) was added to the preceding data point according to the equation: $S_t = \sum_{t=1}^n Y_t$. A constant deviation from the mean of the time series shows a constant slope (Molinero *et al.*, 2008). The cumulative sum allowed identifying shifts in temperature records at regional and local scales over the last decades. A bootstrapped t -test was performed to assess whether periods identified were statistically different. In addition, environmental conditions in Veliko Lake were also assessed by computing the mean seasonal pattern of temperature and salinity displayed in each period identified by the cumulative sum method.

The responses of *C. helgolandicus* to changing climate are manifested in temporal abundance trends and variations in the timing of life history events. Thus, we computed seasonal patterns of *C. helgolandicus* adult abundance to track potential phenological variations, i.e., modifications in the timing of seasonal peaks and interannual changes in the mean population size. The former was computed according to the identified temperature regimes. To avoid artifacts in the assessment of seasonal changes, only years where data covered all months was considered ($n=12$). Seasonal patterns were computed as monthly average. In addition, to explore the influence of temperature on the timing of *C. helgolandicus* seasonal peak, we used the median of the month (e.g., day 15) in which the annual abundance peak was observed. Thus, if the annual peak occurred in May, the corresponding day of year was day 135. Subsequently, the interannual variations in the timing of major peak were regressed against temperature.

The observed temporal pattern of *C. helgolandicus* was assessed regarding hydrological variations and *Parasagitta setosa* abundance. By doing this, we simultaneously assessed bottom-up and top-down controls. Hydrological changes have broad implications

as they directly impact autotroph communities (Edwards *et al.*, 2001), while chaetognaths abundance allows estimate potential changes in top-down pressure on *C. helgolandicus* population. To assess partitioning effects of external forces on the long-term variability of *C. helgolandicus* we used structural equation modeling (SEM). This technique allows identifying direct and indirect effects, as well as their relative importance. The strength and sign of links and the quantification of the overall model were determined by simple and partial multivariate regression and Monte Carlo permutation tests (1000 replicates), while Chi-square values were used to assess robustness and fit of the overall path model (Alsterberg *et al.*, 2013). Individual path coefficients (i.e., partial regression coefficients) indicate the strength of the relationship between causal and response variables.

Predation pressure by the chaetognath *P. setosa* was assessed by means of clearance rates (Cl_{Sa}) reported in the literature (Kjørboe and Hirst 2013; 2014): $Cl_{Sa} = 5.16 \pm 1.64 \text{ mL ind}^{-1} \text{ h}^{-1}$ (n=5; at 15°C). A temperature regulation via Q_{10} was included, with $Q_{10} = 2.44$ (Martinussen and Båmstedt (2011):

$$Cl_T (\text{mL ind}^{-1} \text{ h}^{-1}) = Cl_{Sa} * Q_{10}^{(Temp-15)/10} \quad (\text{eq. 1})$$

The volume-specific population clearance rate of predators (Cl_{pop}) and half-life ($t_{1/2}$) of the copepods derived from chaetognaths predation were assessed using the following equations (eq. 2 and 3)(e.g. Hansson *et al.*, 2005; Riisgård *et al.*, 2010), using the chaetognaths abundances (N_c , individual m^{-3}):

$$m(d^{-1}) = Cl_T * N_c; \quad (\text{eq. 2})$$

$$t_{1/2}(d) = \ln 2 / m \quad (\text{eq. 3})$$

3. Results

Interannual variations of regional climate and oceanographic features in the south Adriatic Sea displayed synchronous low frequency changes of averaged salinity patterns in the 200-800 m depth layer over the period 1985-2010 (Fig. 1a). Likewise, SST in the south Adriatic Sea showed marked variations and predominant negative anomalies from the 1980s to the middle 1990s. Negative anomalies denoted values lower than the temperature average of the period 1985-2010. The observed pattern shifted ca. 1997 towards a dominance of positive anomalies lasting until the end of the period investigated, except for 2005, 2006 and 2010 where negative values were observed (Fig. 1b). The temporal variability of SST in the south

Adriatic Sea was closely related to local temperature records in the Lake Veliko, showing a correlation coefficient of $r = 0.90$ ($p < 0.01$).

Environmental conditions showed marked changes in the average annual patterns mainly driven by temperature conditions prior and after 1997 (Fig. 2). The average annual cycle of temperature showed a sharp seasonality described by low values from December to April, ranging between 10.7 to 13.3 °C. Temperature increased afterwards reaching the warmest values in August (19 °C), high values lasted until autumn followed by a decline in temperature. The main change in temperature before and after 1997 was observed in February and March, however significant differences were only found in March with 1°C warmer after 1997 (Fig. 2a). In turn, the annual pattern of salinity showed slight variations between 37.3 and 38.2, while no clear seasonality was observed. Regarding the average annual pattern before and after 1997, we found that prior to 1997, salinity showed high values in June and from October to December, and low values were observed in May and July, August, and September. In contrast, the average annual pattern of salinity showed consistent high values around 38 (Fig. 2b).

Interannual changes in *C. helgolandicus* abundance showed relatively large variations prior to the temperature shift in 1997. Overall, the species abundance was low excepting in 1989, when it reached annual average values of 84 adults m⁻³. Note that the survey was not performed in 1987 and from 1991 to 1995. After the temperature shift in 1997, no records were done in the years 2002, 2005 and 2007. *C. helgolandicus* abundance was low during the late 1990s, however a sustained increase was observed during the 2000s, when the species showed high abundances, with an annual average of 70 adults m⁻³, while by the end of the period investigated the species reached an annual average of 138 adults m⁻³ in 2009 (Fig. 3a). Conversely, the abundance of predators (chaetognaths and siphonophores) showed high abundances in the late 1980s and 1990, with an annual average of 62 ind.m⁻³. High values were observed as well in the years 1997-1998 with an average of 47 ind.m⁻³ and sporadic peaks reaching 100 ind.m⁻³. Afterwards, however, their population size declined and remained relatively low. Chaetognaths were dominated by the genus *Parasagitta*, while siphonophores were mainly composed by *Muggiaea atlantica*. *Parasagitta* decreased after the middle 1990s and low abundances lasted throughout the first decade of the 2000s, while

M. atlantica showed a strong increase ca. 1997, although their abundance declined afterwards (Fig. 3b).

Along with these interannual changes, the annual pattern of *C. helgolandicus* showed clear modifications after 1997. During the low temperature regime, 1985-1996, the annual pattern was characterized by a major peak in June-July, and two minor peaks in September and December-January. During this period, the average population abundance was 40 ± 22.3 adults m^{-3} (Fig. 4a). By contrast, after the temperature shift, major abundances were clustered in the first half of the year. High values were noticed in January and a major peak in April, which was followed by less intense peaks in June and September. The average abundance after 1997 was 66 ± 31.3 adults m^{-3} (Fig. 4a). These changes were at least partly driven by temperature, as shown by the regression model of the timing of the seasonal peak versus temperature (Fig. 4b), where the seasonal timing was described as follows: $\text{timing} \sim -49.17 * \text{temp} + 706.24$ ($r = -0.74$, $p < 0.05$).

Results from the structural equation model unveiled a combined effect of changes in hydrology, driven by temperature, along with a decrease of top-down control ascribed to chaetognaths predation, as leading drivers of the overall pattern of *C. helgolandicus* variability (Fig. 5). Indeed, temperature showed both direct and indirect effects on the copepod by influencing positively the copepod abundance (path coefficient: 0.49), while impacting negatively on chaetognaths abundance (path coefficient: -0.40), which were negatively linked with *C. helgolandicus* (path coefficient: -0.53). Salinity appeared only indirectly linked with the copepod through its negative effect on chaetognaths (path coefficient: -0.51), while the model did not show any significant influence by siphonophores (*M. atlantica*) (Fig. 5).

The negative link between chaetognaths and *C. helgolandicus* depicted by the SEM is supported by computation of $t_{1/2}$ estimates derived from chaetognath predation on *C. helgolandicus* (eq. 1-3). For instance, during the cold years 1985-1996, the abundance of chaetognaths (average 48 ind. m^{-3} , maximum 130 ind. m^{-3}) likely nurtured high predation pressure on *C. helgolandicus*, as shown by the low $t_{1/2}$ values, which dropped to a minimum of 32 d under maximum densities of chaetognaths (Fig. 6a). Conversely, in the warmer period 1997-2010, chaetognaths abundance decreased (average 23 ind. m^{-3} , maximum value 28 ind. m^{-3}), while the $t_{1/2}$ values rose up to 200-500 d (Fig. 6b).

4. Discussion

We have examined field records of *C. helgolandicus* in the Lake Veliko ecosystem, marine protected area of Mljet Island, south Adriatic Sea. The period assessed, 1985-2010, displayed marked hydroclimate changes that pointed out two environmental regimes shaping the long-term patterns of plankton.

4.1 Regional hydroclimate variability

The water-mass dynamics in the southern Adriatic Sea has been related with atmospheric variability in the North Atlantic; in particular, with the pressure difference between the North Atlantic and the Southeast Mediterranean, which shapes low frequency changes of the water-mass inflow into the Adriatic Sea (Grbec et al., 2002). A positive pressure difference occurs during the positive phase of the North Atlantic Oscillation (NAO). These conditions are favorable for the formation of the Levantine Intermediate water (LIW), a warm salty water formed in the eastern Mediterranean. LIW promotes the inflow of more saline water masses into the Adriatic Sea that ultimately drive the Adriatic thermohaline circulation (Grbec et al., 2002). Our results point out that the influence promoted by the North Atlantic – Mediterranean teleconnection on the dynamics of water masses in the southern Adriatic also influence hydrographic conditions in the Lake Veliko over decadal scales, as suggested by the close correlation between water temperature in the south Adriatic and local temperature records in the lake. Our findings further support recent observations on the coupled low frequency changes of plankton taxa and hydroclimate in the south Adriatic (Batistic et al., 2016).

4.2 *Calanus helgolandicus* interannual and phenological changes

Our results show a close relationship between *C. helgolandicus* and changes in hydrological conditions, e.g., enhanced warmer and saltier waters, noticed after the late 1990s, which modified the seasonal dynamics of the species, promoted an earlier spring peak, ca. two months earlier, and larger abundance. Similar results on positive links between temperature and *C. helgolandicus* have been shown in the North Atlantic, where high temperature appears as leading driver of the species abundance expansion from its population centres (Chust et

al., 2014). The observed phenological changes of *C. helgolandicus* after the temperature shift in 1997 agree with the temperature influence on the species and reports of earlier zooplankton abundance peaks in warming environmental conditions. For instance, an overview of biological and ecological features of the species showed a close link between the pattern of Northern Hemisphere Temperature and *C. helgolandicus* abundance in the last 50 years (Bonnet et al., 2005). In line with this, the higher temperatures in winter and summer noticed in the last decades have favored a strong positive abundance deviation in the North Sea (Lindley and Reid, 2002; Helaouët et al., 2013). The Mediterranean Sea has experienced similar patterns of warming during the same period. Our results pointed out that significant differences in temperature annual patterns between the two periods, 1985-1996 and 1997-2010, occurred mainly during February and March. Higher temperatures during this period might yield favorable conditions for the onset of population growth. In line with this, population dynamics models have shown that relatively small variations (i.e., larger starting population density) greatly increase the development of the seasonal population growth in copepods (Ji et al., 2013). It is therefore ecologically plausible that one of the processes driving the abundance increase might be related to a larger overwintering population density, favored by warmer temperatures in late winter.

4.3 Effects of biotic and abiotic factors on *Calanus helgolandicus*

Along with the rising temperatures, the Adriatic Sea pelagic ecosystem has experienced substantial changes in structure and functioning, including enhanced occurrence of warmer-affinity alien species (Batistic et al. 2014), decrease of cold-water species, decline of diatoms blooms and phytoplankton biomass, as well as a decline in biomass of target demersal and small pelagic fish (CIESM, 2008; Giani et al., 2012). Such modifications in the marine habitat raise the possibility of ecological factors behind the increase of *C. helgolandicus*.

The use of SEM allowed testing this hypothesis by partition direct from indirect effects and deciphering the strength of paths linking *C. helgolandicus* with the environment. SEM results unveiled a compound effect of temperature and predation by chaetognaths behind the overall pattern of *C. helgolandicus* changes. Previous reports assessing the role of chaetognaths in zooplankton communities have shown a marked top-down control on copepod populations and standing stocks in different environments (Williams and Collins,

1985), suggesting these predators are an important vector transferring most of the energy to biomass from copepods to higher trophic levels (Feigenbaum, 1991). Predation by *Parasagitta* on zooplankton taxa appears as a major driver of the zooplankton long-term dynamics in the coastal central-west North Sea (Clark et al., 2003), as well as in the western English Channel, where chaetognaths structure temporal patterns of *C. helgolandicus* (Bonnet et al., 2010). In Lake Veliko, the dominant chaetognath species, *P. setosa*, occupies depth strata similar to *C. helgolandicus* and is the main predation force on this copepod (Miloslavić et al., 2015). Hence, the observed decline in chaetognaths abundance after 1997 suggests a release of top-down control. *P. setosa* is a temperate species that has also shown an abundance drop under high temperature conditions in the northwestern Mediterranean (Molinero et al., 2008). The governing hydrological conditions observed after the late 1990s, warmer and saltier, have likely negatively affected this species. Other carnivore zooplankton inhabiting this ecosystem, i.e., *Aurelia* sp., seem not having a significant impact on *C. helgolandicus*, as suggested by former stomach content analysis and feeding experiments (Malej et al., 2007).

We acknowledge that zooplanktivorous fish can play a major role shaping the copepod population size. In Lake Veliko, the majority of the reported 53 fish species are seagrass or reef associated species, among them only 5 are considered zooplanktivorous, e.g., *Atherina boyeri*, *Spicara maena*, *Liza aurata*, *Boops boops* and *Spondyliosoma cantharus* (Graham et al., 2009), however little is known on their potential impact on *C. helgolandicus* abundance in this ecosystem. Notwithstanding this caveat, our results provide evidence of the interconnections between temperature changes and release of one of the main predators as leading drivers of the long-term pattern of *C. helgolandicus*.

The temporal variations here reported provide insights on the *C. helgolandicus* responses to the changing Mediterranean marine environment, thereby suggesting structural changes in this pelagic ecosystem due to the role of this species in pelagic food webs. Our study further stresses the importance of sustained field surveys in marine protected areas to understand plankton responses to changing climate. Semi-enclosed marine lakes and lagoons are in essence large natural laboratories that allow exploring ecological complexity of marine ecosystems that are logistically difficult to survey in open locations. The pelagic ecosystem of Lake Veliko is unique in its temperate marine setting and geographic semi-isolation, which

offers an ideal framework to examine the sensitivity of prominent zooplankton taxa to warming Mediterranean conditions.

Acknowledgments

This work is dedicated to the memory of our friend and colleague Professor Adam Benović who devoted his efforts to the conservation of the marine protected area of Mljet Island as a natural laboratory for marine research. We are grateful to Zoran Jurić and Marko Žarić for assistance during zooplankton sampling and to authorities of the National Park Mljet for facilities and support during plankton surveys. Funding by the Ministry of Science Education and Sport of the Republic of Croatia is gratefully acknowledged.

References

- Alsterberg, C., Eklöf, J.S., Gamfeldt, L. *et al.*, 2013. Consumers mediate the effects of experimental ocean acidification and warming on primary producers. *Proc. Natl. Acad. Sci. U.S.A.*, 110, 8603-8608.
- Batistić, M., Garić, R. and Molinero, J.C., 2014. Alien zooplankton in the Adriatic Sea track thermohaline circulation changes in the Eastern Mediterranean Interannual variations in Adriatic Sea zooplankton mirror shifts in circulation regimes in the Ionian Sea. *Clim. Res.*, 61, 231-240.
- Benovic, A. Lučić, S., Onofri, V. *et al.*, 2000. Ecological characteristics of the Mljet Island seawater lakes (South Adriatic Sea) with special reference to their resident populations of medusae. *Sci. Mar.*, 64, 197–206.
- Bonnet, D., Lindeque P. and Harris R. P., 2010. *Sagitta setosa* predation on *Calanus helgolandicus* in the English Channel. *J. Plankton Res.*, 32, 725-737.
- Bonnet, D., Richardson, A., Harris, R. *et al.*, 2005. An overview of *Calanus helgolandicus* ecology in European waters. *Prog. Oceanogr.*, 65, 1-53.
- CIESM, 2008. Climate warming and related changes in Mediterranean marine biota. N° 35 in CIESM Workshop Monographs [F. Briand, Ed.], 152 pages, Monaco.
- Conover, R.J., Wilson, S., Harding, G.C.H. *et al.*, 1995. Climate, copepods and cod: some thoughts on the long-range prospects for a sustainable northern cod fishery. *Clim. Res.*, 5, 69-82.
- Chust, G., Castellani, C., Licandro, P. *et al.*, 2014. Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach. *ICES J. Mar. Sci.*, 71, 241–253.
- Clark R. A., Frid C. L. J. and Nicholas K. R., 2003. Long-term predation based control of a central-west North Sea zooplankton community. *ICES J. Mar. Sci.*, 60, 187-197.
- Edwards, M., Reid, P. C. and Planque, B., 2001. Long-term and regional variability of phytoplankton biomass in the north-east Atlantic (1960-1995). *ICES J. Mar. Sci.*, 58, 39-49.
- Edwards, M. and Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, 430, 881–884.
- Giani, M., Djakovac, T., Degobbis, D. *et al.*, 2012. Recent changes in the marine ecosystems of the northern Adriatic Sea. *Est. Coast. Shelf Sci.*, 115, 1-13.

- Graham, W.M, Chiaverano, L., D'Ambra, I. *et al.*, 2009. Fish and jellyfish: using the isolated marine lakes of Mljet Island, Croatia, to explore larger marine ecosystem complexities and ecosystem-based management approaches. *Annales Ser. hist. nat.*, 19, 39-48.
- Grbec, B., Dulcic J, and Morovic, M., 2002. Long-term changes in landings of small pelagic fish in the Eastern Adriatic – possible influence of climate oscillations over the Northern Hemisphere, *Clim. Res.*, 20, 241–252.
- Hansson, L. *et al.*, 2005. Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). *Mar. Ecol. Prog. Ser.*, 304, 117–131.
- Hays, G. C., Richardson A. J. and Robinson C., 2005. Climate change and marine plankton. *Trends Ecol. Evol.*, 20, 337-344.
- Helaouët, P., Beaugrand, G. and Edwards, M., 2013. Understanding Long-Term Changes in Species Abundance Using a Niche-Based Approach. *PLoS ONE*, 8, e79186.
- Hure, J. and Kršinić, F., 1998. Planktonic copepods of the Adriatic Sea. *Nat. Croat.*, 7, 1-135.
- Ji, R., Stegert, C., and Davis, C., 2013. Sensitivity of copepod populations to bottom-up and top-down forcing: a modeling study in the Gulf of Maine region. *J. Plankton Res.*, 35, 66-79.
- Kjørboe T., Hirst, A.G., 2013. Data compilation of respiration, feeding, and growth rates of marine pelagic organisms. PANGAEA, doi.org/10.1594/PANGAEA.819857.
- Kjørboe T., Hirst, A.G., 2014. Shifts in mass-scaling of respiration, feeding, and growth rates across life-form transitions in marine pelagic organisms. *The American Naturalist*, 183, E118–E130.
- Lindeque, P., Harris, R., Jones, M. *et al.*. 2004. Distribution of *Calanus* spp. as determined using a genetic identification system. *Sci. Mar.*, 68, 121-128.
- Lindley, J. A, and Reid, P. C., 2002. Variations in the abundance of *Centropages typicus* and *Calanus helgolandicus* in the North Sea: deviations from close relationships with temperature. *Mar. Biol.*, 141, 153-165.
- Martinussen, M. and Bamstedt, U. 2001. Digestion Rate in Relation to Temperature of Two Gelatinous Planktonic Predators. *Sarsia*, 86, 21-35.

- Mazzocchi, M. G., Siokou, I., Tirelli, V., *et al.*, 2014. Regional and seasonal characteristics of epipelagic mesozooplankton in the Mediterranean Sea based on an artificial neural network analysis. *J. Mar. Syst.*, 135, 64–80
- Malej, A., Turk, V., Lučić, D. *et al.*, 2007. Direct and indirect trophic interactions of *Aurelia* sp. (Scyphozoa) in a stratified marine environment (Mljet lakes, Adriatic Sea). *Mar. Biol.*, 151, 827 – 841.
- Miloslavić, M., 2012. Zooplankton dynamics in an enclosed marine ecosystem (Mljet Lakes, NP "Mljet"): seasonal and long-term changes. PhD thesis, University of Split.
- Miloslavić, M., Lučić, D., Žarić, M. *et al.*, 2015. The importance of vertical habitat gradients on zooplankton distribution in an enclosed marine environment (South Adriatic Sea). *Mar. Biol. Res.*, 11, 462-474.
- Molinero JC, F Ibanez, E Buecher, S Souissi, P Nival, 2005. The North Atlantic climate and the North-western Mediterranean plankton variability. *Limnol. Oceanogr.*, 50, 1213-1220.
- Molinero, J.C., Ibanez, F., Souissi, S. *et al.*, 2008. Climate control on the long-term anomalous changes of zooplankton communities in the Northwestern Mediterranean. *Global Change Biol.*, 14, 11-26.
- Planque, B. and Fromentin, J. M., 1996. *Calanus* and environment in the eastern North Atlantic. I. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. *Mar. Ecol. Prog. Ser.*, 134, 101-109.
- Reygondeau, G. and Beaugrand G., 2011. Future climate-driven shifts in distribution of *Calanus finmarchicus*. *Global Change Biol.*, 17, 756–766.
- Riisgård, H. U. *et al.*, 2010. High abundance of the jellyfish *Aurelia aurita* excludes the invasive ctenophore *Mnemiopsis leidyi* to establish in a shallow cove (Kertinge Nor, Denmark). *Aquat. Invasions*, 5, 347–356.
- Scotto di Carlo B., Ianora A. Mazzocchi M.G., Scardi M., 1991. Atlantis II Cruise. Uniformity of deep assemblages in the Mediterranean Sea. *J. Plankton Res.*, 13, 263-277.
- Soldo, A., Lučić, D. and Jardas, I., 2008, Basking shark (*Cetorhinus maximus*) occurrence in relation to zooplankton abundance in the eastern Adriatic Sea. *Cybium*, 32, 103-109.

- Schroth, W., Jarms, G., Streit, B. et al., 2002. Speciation and phylogeography in the cosmopolitan marine moon jelly, *Aurelia* sp. *BMC Evol. Biol.*, 2, 1–10.
- Vučetić, T. (1966) Prilog poznavanju biologije kopepoda *Calanus helgolandicus* (CLAUS) iz Velikog jezera na otoku Mljetu. *Acta Adriat.*, 6, 91pp.
- Weikert, H., Koppelman R., Wiegratz S., 2001. Evidence of episodic changes in deep-sea mesozooplankton abundance and composition in the Levantine Sea (Eastern Mediterranean). *J. Mar. Syst.*, 30, 221-239.
- Williams, R. and Collins, N.R., 1985. Chaetognaths and ctenophores in the holoplankton of the Bristol Channel. *Mar. Biol.*, 85, 97-102.
- Yebra, L., Bonnet, D., Harris, R.P. *et al.*, 2011. Barriers in the pelagic: population structuring of *Calanus helgolandicus* and *C. euxinus* in European waters. *Mar. Ecol. Prog. Ser.*, 428, 135-149.

Figure Caption

Figure 1. Interannual variations of regional climate and oceanographic features in the south Adriatic Sea and water temperature in Veliko Lake. (a) Regional climate (PC1, 58% of total variance) and average salinity in the 200-800 m depth layer (dots) over the period 1985-2010. The trend of salinity was obtained by fitting a 6-degree polynomial curve; (b) Interannual variability of sea surface temperature (SST) in the south Adriatic (bars). Lines show the cumulative sums of SST in the south Adriatic (continuous line) and the average water column temperature in the lake (dotted line). The cumulative sum highlights a shift ca. 1997, in both the south Adriatic Sea and Veliko Lake.

Figure 2. Hydrological variability recorded in Veliko Lake over the period 1985-2010. Mean annual pattern of (a) temperature and (b) salinity. Annual patterns represent monthly average conditions of the water column before (grey lines) and after (black lines) 1997. Significant differences were noticed in March temperature after 1997.

Figure 3. (a) *Calanus helgolandicus* annual abundance; (b) Predator field; annual abundance of chaetognaths (*Parasagitta*, light bars) and siphonophores (*Muggiaea*, dark bars).

Figure 4. Seasonal abundance distribution of *Calanus helgolandicus*. (a) The average annual pattern in the low temperature regime, 1985-1996, and high temperature regime, 1997-2010, are denoted by grey and black lines, respectively. The latter displayed an earlier seasonal peak advanced ca. two months. (b) Timing of the seasonal peak in relation to temperature ($r = -0.74$, $p < 0.05$; $n=12$).

Figure 5. Path diagram showing partitioning effects of external forces shaping *Calanus helgolandicus* abundance. Solid paths are statistically significant ($P < 0.05$) whereas the dashed lines are not. At each significant path the standardized coefficients are represented.

Figure 6. Estimated *Parasagitta* induced half life-time ($t_{1/2,d}$) on *Calanus helgolandicus* during the periods 1985-1996 (a) and 1997-2010 (b).

Figure 1

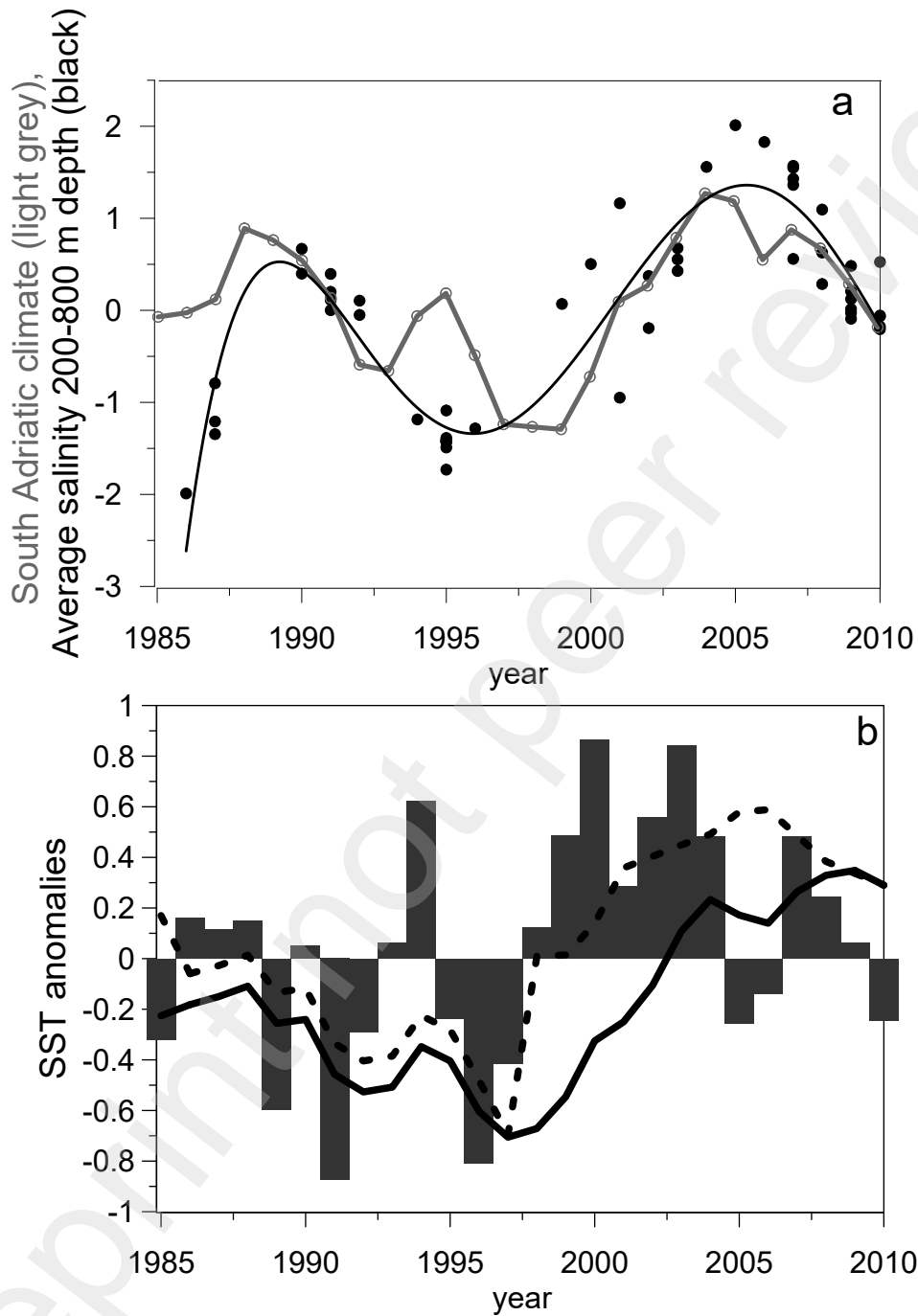


Figure 2

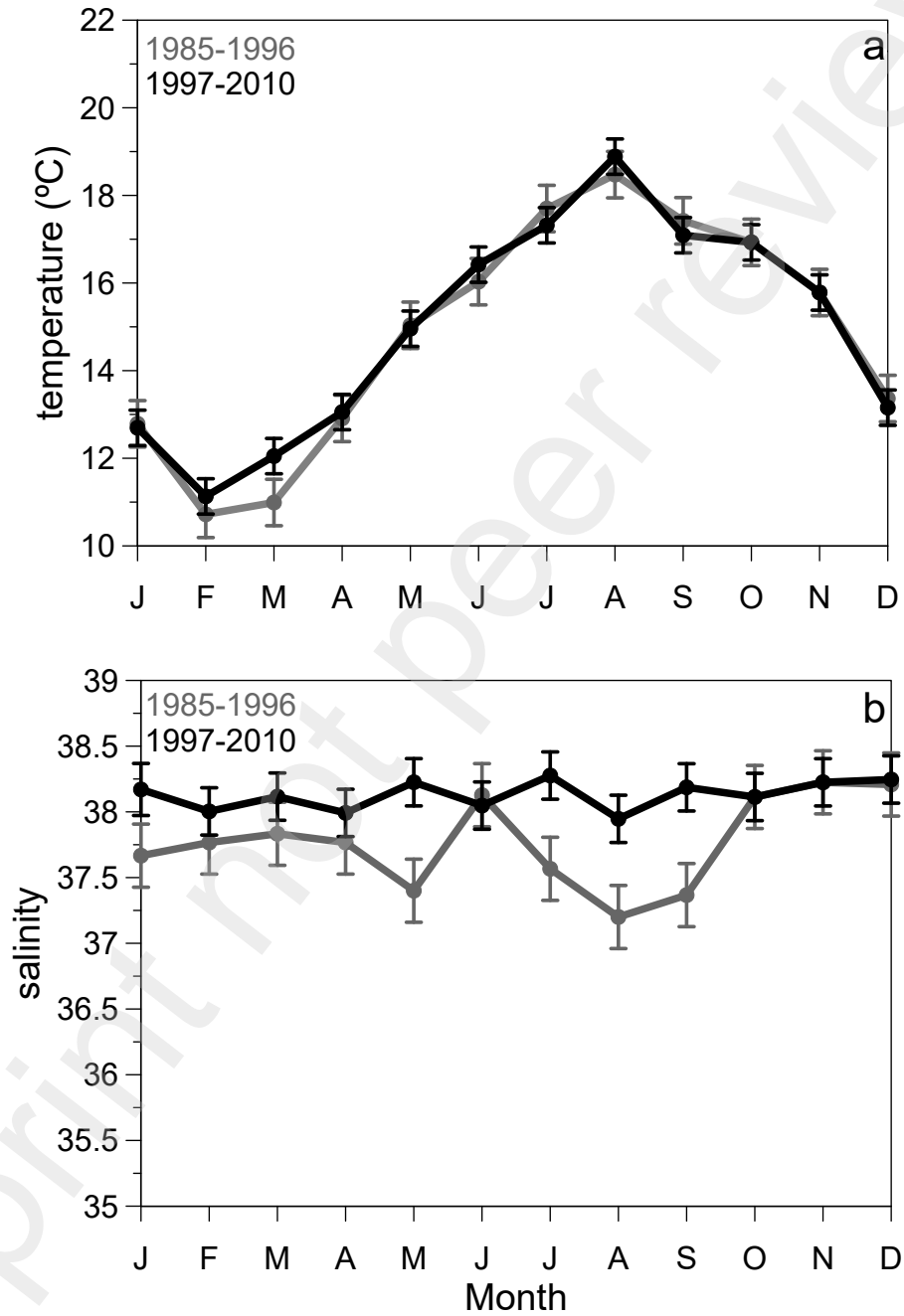


Figure 3

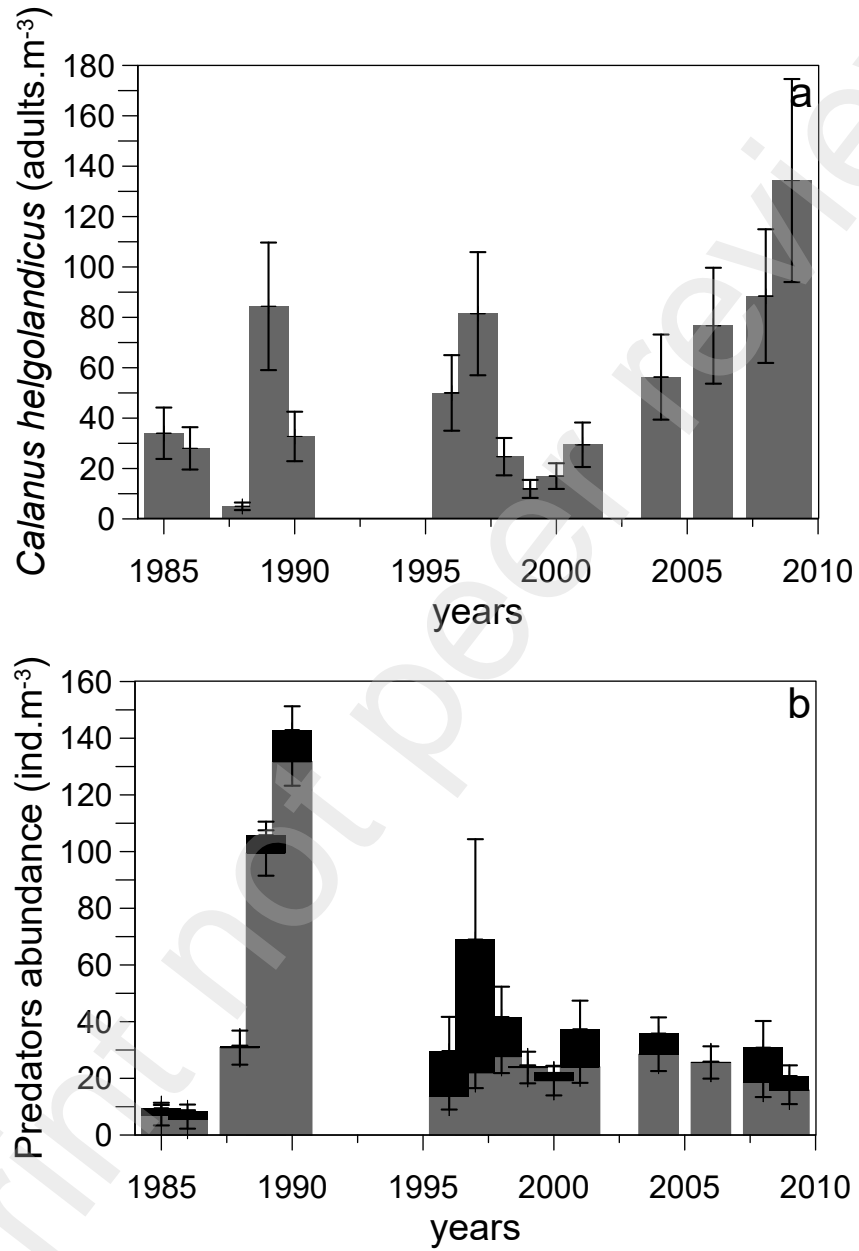


Figure 4

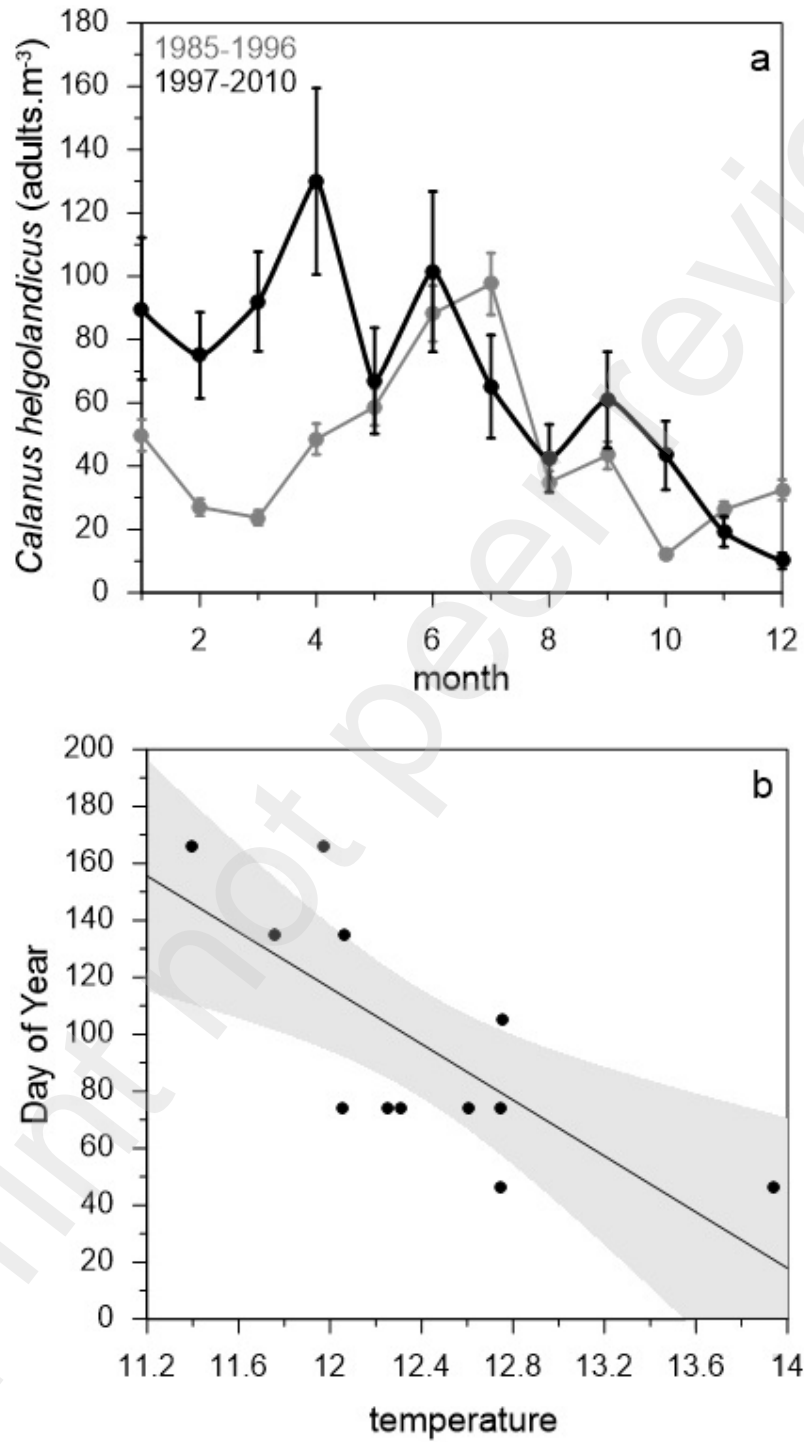


Figure 5

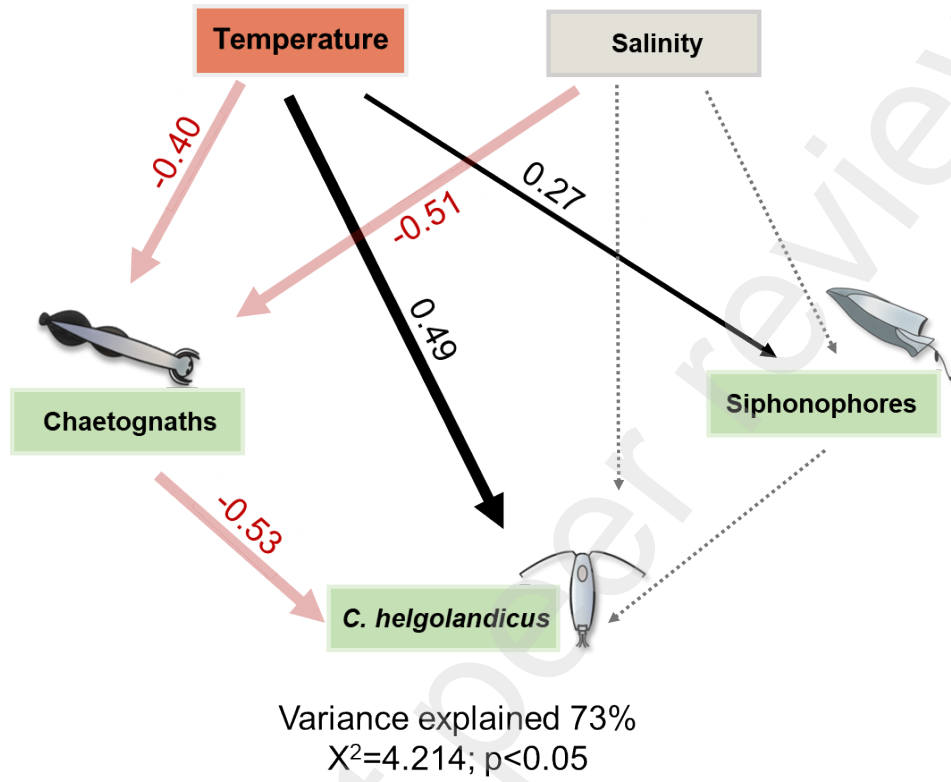


Figure 6

