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# Interannual variations in Adriatic Sea zooplankton mirror shifts in circulation regimes in the Ionian Sea

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ABSTRACT: We investigated potential connections over the past 2 decades between mesoscale circulation regimes in the Ionian Sea and newly observed species and the concurrent rise in sea temperature in the Adriatic Sea. Analyses of plankton samples from 1993 to 2011 in the southern Adriatic revealed marked changes in the non-crustacean zooplankton community. Eleven species were recorded for the first time in the Adriatic, while 3 species reappeared after years of absence. We found that pluriannual changes in the zooplankton community tracked the continuum of circulation regimes in the Northern Ionian Gyre (NIG). The occurrence of Atlantic/Western Mediterranean species coincided with anti-cyclonic circulation in the NIG, probably due to the advection of Modified Atlantic Water into the Adriatic, while the presence of Lessepsian species coincided with the cyclonic pattern, which governs the entry of Eastern Mediterranean waters. The impact has been that newcomers now make a significant contribution to the zooplankton community in the southern Adriatic and, in certain cases, have replaced native species. Our results provide new evidence of the influence of teleconnection processes between the North Atlantic and Eastern Mediterranean on the dynamics of water masses in the southern Adriatic. The synergistic effects of these processes, together with warmer Mediterranean waters, raise concerns over dramatic changes in the marine biodiversity of the Adriatic.

KEY WORDS: North Atlantic climate · Hydroclimatic changes · BiOS · Thermohaline circulation · Zooplankton · Indicator species · Mediterranean · Adriatic



## 1. INTRODUCTION

The Mediterranean Sea is a semi-enclosed marine biodiversity hotspot, and of the mature biomes, it is probably one of the most sensitive to global warming; it is also particularly susceptible to biological invasions (Coll et al. 2010). In addition to the potential for species influx through the Straits of Gibraltar, the construction of the Suez Canal has led to the introduction of a number of tropical and subtropical species from the Red Sea (Por 1978, Pancucci-Papadopoulou et al. 2005, 2012). According to the most recent studies, 680 alien marine multicellular species have been recorded in the Mediterranean (Galil & Goren 2014). As the Mediterranean has warmed, the incidence of tropical and subtropical species has increased throughout the whole of the basin, threatening native diversity and sounding a warning of a potential shift towards the dominance of thermophilic species (Boero et al. 2008, Bianchi & Morri 2000). Alongside these changes, native warmer-water species have extended their range towards colder, fertile northern Mediterranean sub-basins, among them the Adriatic Sea (Azzurro et al. 2011).

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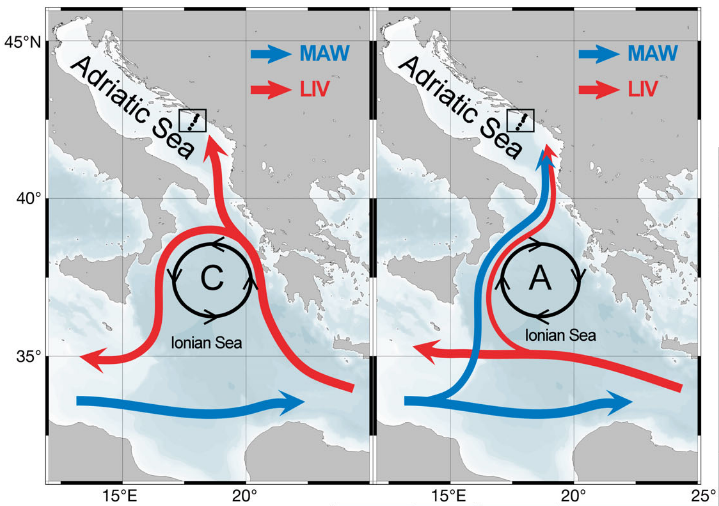
The Adriatic Sea is a semi-enclosed basin that extends southward from the highest latitude (45° 47′ N) in the central Mediterranean (Fig. 1). The deepest part of the southern Adriatic (ca. 1250 m depth) is influenced by Ionian and eastern Levantine waters, and plays an important role as a site for the formation of a body of dense water, the Adriatic Dense Water (AdDW) (Ovchinnikov et al. 1985). On decadal scales, the density of the AdDW varies with incoming Ionian waters. This process is coupled to the Bimodal Oscillating System (BiOS), which drives the continuum of mesoscale circulation regimes in the Ionian Sea, i.e. the alternation of cyclonic and anti-cyclonic patterns on a pluriannual basis (Gačić et al. 2010). While the cyclonic regime brings saltier waters of Levantine origin into the Adriatic, the anti-cyclonic pattern favors the inflow of less saline Ionian waters diluted by the Atlantic Water (Civitarese et al. 2010).

The influence of BiOS on plankton communities and the advection of newcomer zooplankton species has remained largely unknown to date. We addressed this question by analyzing thermohaline data and plankton records collected over the period 1993–2011 off the eastern coast of the southern Adriatic in an area exposed to the main pattern of circulation in the Adriatic. By tracking the incidence of new incoming species, we aimed to depict their potential link with variations in mesoscale circulation and climate-forcing experienced in the southern Adriatic. We hypothesized that, on decadal time-scales, the structure of the zooplankton community in this area mirrors the continuum of circulation changes in the Northern Ionian Gyre (NIG), with species of Atlantic origin and Lessepsian migrants dominating the anti-cyclonic and cyclonic circulation, respectively. In addition, we tested the potential role of incoming zooplankton as a proxy for rising temperatures in the Mediterranean.

## 2. METHODS AND DATA

### 2.1. Biological data

Zooplankton data were collected through a pluriannual survey of the southern Adriatic from 1993 to 2011. A total of 492 samples from fortnightly coastal and open-sea cruises at intervals of 2 mo were examined. Samples were taken off Dubrovnik by means of vertical hauls (average hauling speed 1 m s$^{-1}$) from a depth of 100 m to the surface using 200 and 250 µm Nansen nets at 5 stations of different maximal depths (Fig. 1): P-1200 (1242 m depth; 42° 13′ 01″ N, 17° 42′ 50″ W), P-1000 (1000 m; 42° 20′ 37″ N, 17° 48′ 50″ W), P-300 (300 m; 42° 27′ 32″ N, 17° 56′ 02″ W), P-150 (150 m;, 42° 32′ 55″ N, 17° 57′ 45″ W), P-100 (100 m; 42° 38′



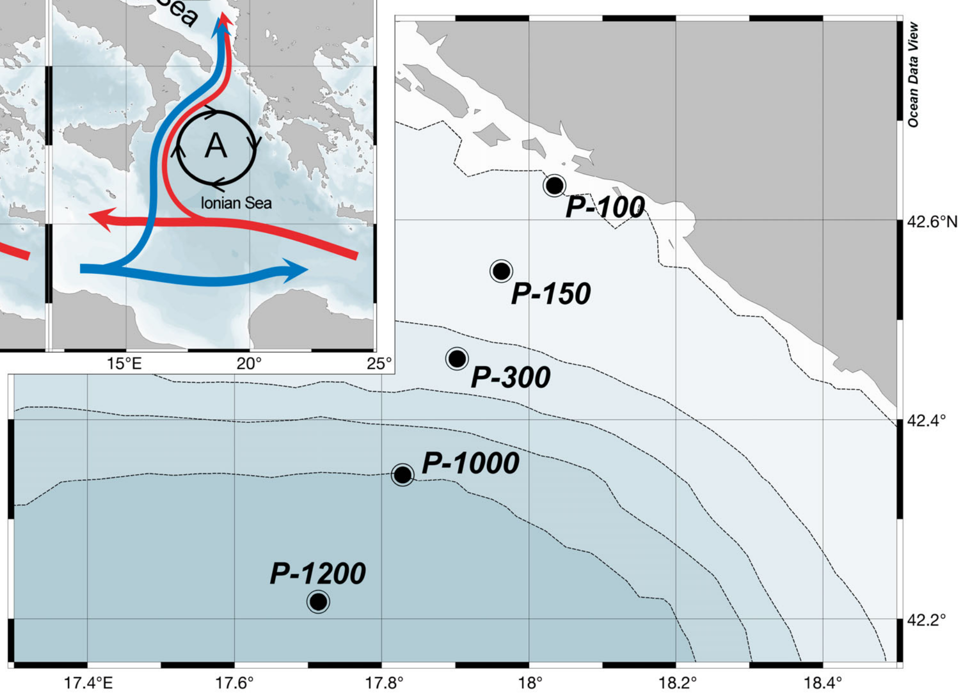




Fig. 1. Top left: Adriatic Sea indicating the study area (black square) and (A) anticyclonic and (C) cyclonic) circulation patterns in the Ionian Sea, after Gačić et al. (2010). MAW: modified Atlantic waters; LIV: Levantine intermediate water. Bottom right: location of sampling stations in water of increasing depth in the southern Adriatic Sea off the coast of Dubrovnik

04″ N, 18° 02′ 05″ W). The location of the area investigated offers an ideal opportunity to assess connections between changes in BiOS thermohaline circulation and incoming plankton species (Fig. 1). Samples were preserved in a 2.5% formalin–seawater solution buffered with $CaCO_3$, and were examined exhaustively to identify taxa and quantify non-crustacean zooplankton. Analyses were done for the following zooplankton taxa: Hydromedusae, Siphonophorae, Ctenophora, Pteropoda, Heteropoda, Polychaeta, Chaetognatha and Thaliacea. In addition, an exhaustive bibliographical search covering the period 1884 to 1993 was performed to track historical records of non-crustacean zooplankton species.

Only those species currently listed in the most updated inventories of Mediterranean alien species (Zenetos et al. 2010) were considered alien.

### 2.2. Climate and hydrographic data

To examine the southern Adriatic climate, we used monthly anomalies in the atmospheric variables of air temperature, sea surface temperature, sea level pressure, 500 hPa geopotential height, precipitation and long-wave radiation over the period 1985–2012. These data were provided by the Climate Diagnostics Center (NCEP/NCAR) reanalysis fields (Kalnay et al. 1996). The selected area extends from 43° to 40° N and from 16° to 19.5° E, and the data used correspond to the closest grid at 2° resolution. We also assessed the relationship between hydroclimatic conditions in the southern Adriatic and large-scale climate drivers influencing the hydrodynamic pattern of the central Adriatic (Grbec et al. 2002). To do so, we used climate proxies for the North Atlantic and Eastern Mediterranean sectors, in the form of the North Atlantic Oscillation (NAO) and the Eastern Mediterranean pattern (EMP) respectively. Temperature and salinity profiles were recorded from surface to bottom (maximum depth 1200 m, Fig.1) with a CTD multiparameter sonde SBE 19plus (Sea-Bird Electronics) and averaged over 1 m intervals. To track thermohaline circulation changes, we extended our dataset back to 1985 by using average salinity values in the 200 to 800 m depth layer from the Medatlas database (MEDAR Group 2002). Temporal changes in salinity were fitted to a 6 degree polynomial curve to capture the interannual trend and to detect years with cyclonic (more saline) and anticyclonic (less saline) circulation in the NIG, as in Civitarese et al. (2010).

### 2.3. Data analysis

To assess temporal changes in regional climate conditions, we followed the procedure used in Molinero et al. (2005, 2008a), which consists of extracting the seasonal trend of monthly meteorological time series and then synthesizing the meteorological information by means of Principal Component Analysis (PCA). PCA was applied on a matrix composed of the seasonal detrended climate variables, i.e. months × climatic variables. The general trend of the regional climate, as indexed by the first principal component (PC1, 58% of total variance), was examined to quantify potential structural changes over the period investigated. The timing of structural changes in the regional climate was detected using the cumulative sum of standardized ordinary least square residuals (OLS-based CUSUM test). This technique allows for computing the probability of significant modifications in a time-series, and is useful in detecting shifts in chronological records (Fernandez de Puelles & Molinero 2013). The test of large-scale climate influence on regional hydroclimatic conditions in the southern Adriatic was done using a General Linear Model (GLM) in a factorial mode, which allowed for the assessment of the individual effects of the climate proxies, the NAO and the EMP, and their interactions.

A proxy for interannual changes in local thermohaline conditions (i.e. temperature and salinity in the upper 100 m depth) was computed as deviations to the mean value recorded over the whole period. Regional climate (PC1) and the hydrological proxy were displayed as traffic-light diagrams to qualitatively assess the dominant conditions concomitant with each mesoscale circulation regime in the Ionian Sea. Traffic-light diagrams display a range color from red (0.90 quantile) to blue (0.10 quantile).

To test the hypothesis that the occurrence of incoming zooplankton in the Adriatic Sea reflects the dominant circulation regimes in the NIG, we used a nonparametric stationary bootstrap method for correlation analysis. The procedure involved a random pairwise sampling with replacement where each time-series was resampled 1000 times. The number of elements in each bootstrap sample equals the number of elements in the original time series. We used a conservative alpha level of 0.01 to minimize the likelihood of committing Type I error when identifying links between climate and newcomers. Data analysis was done using Matlab, with the exception of the structural change analysis, which was performed using the strucchange package in R version 2.7.1.

## 3. RESULTS AND DISCUSSION

### 3.1. Hydroclimate variations and incoming species

GLM results show that around half of the temporal variance in the regional hydroclimate is significantly linked to the North Atlantic climate, although a significant effect can also be ascribed to the synergistic effect of the North Atlantic climate and atmospheric dynamics in the Eastern Mediterranean, as indexed by the NAO and the EMP respectively (Table 1). The parameter estimates revealed a positive role of the NAO (parameter estimate 0.58, SE 0.09), while the climatic influence is enhanced by the combined effect of NAO and EMP (parameter estimate 0.67, SE 0.23). Temporal variations in the advection of Levantine intermediate water (LIW) have previously been shown to relate to atmospheric teleconnections between the North Atlantic and the Eastern Mediterranean (Grbec et al. 2002). Our results extend previous observations (Civitarese et al. 2010) on the decadal dynamics of the NIG, showing that this regional hydrographic feature shapes the origin of newcomers into the Adriatic Sea. In addition, we show that the variability of water-mass dynamics in the southern Adriatic is linked to teleconnection processes mainly driven by the North Atlantic Ocean (Fig. 2). That is, a positive relationship is revealed during the positive phase of the NAO, while an opposite relationship occurred during the negative phase of the NAO. This opens up the possibility of forecasting potential plankton biodiversity changes promoted by the entry of new species into the Adriatic.

During the period investigated, 11 species were recorded for the first time in the Adriatic, while 3 species reappeared after years of absence (Fig. 3c). The periods of first occurrence or reappearance of these species can be divided as follows: 1993–1995, 2001–2007 and after 2008. The first and second period were driven by well-established anticyclonic and cyclonic circulation patterns respectively (Fig. 3b). These results are in line with previous investigations describing the mesoscale current system in the NIG (Gačić et al. 2010). However, by extending the analysis up to 2011 we provide evidence of a further change in the NIG system, which shifted back to the anticyclonic circulation pattern after 2007 (Fig. 3b). Our results reveal that the highest influx of newcomer zooplankton species occurred when a particular circulation pattern in the NIG was well established (Fig. 3b,c). In contrast, a low influx of new species appears linked with transitional periods, i.e. the reversal of the dominant circulation pattern, when the 2 types of circulation weaken each other (Fig. 3b,c). These periods have been referred to vaguely as the 'end of the 1980s' and the 'end of the 1990s' in descriptions of NIG temporal dynamics (Civitarese et al. 2010). The biological records we examined fully matched the timing of advection of different water masses, for example modified Atlantic waters (MAW) or Eastern Mediterranean waters, into the Adriatic Sea and suggest that the dominant circulation in the Ionian Sea is a driving force for newcomer zooplankton species in the Adriatic (Fig. 4a). Indeed, our results show that the occurrence of newcomers mirrors the dominant circulation regime in the NIG ($r = 0.68$; $p < 0.001$).

Table 1. General Linear Model (GLM) results of the effects of North Atlantic Oscillation (NAO) and Eastern Mediterranean pattern (EMP) on regional hydroclimate in the southern Adriatic Sea

| R | SS | df | MS | *F* | p |
|---|---|---|---|---|---|
| 0.47 | 28.96 | 3 | 9.65 | 21.68 | <0.001 |

| Parameter estimates | Param. | SE | *t* | p |
|---|---|---|---|---|
| Intercept | 0.04 | 0.04 | 1.15 | 0.25 |
| NAO | 0.58 | 0.09 | 6.31 | <0.001 |
| EMP | 0.04 | 0.09 | 0.45 | 0.65 |
| NAO × EMP | 0.67 | 0.23 | 2.89 | <0.001 |

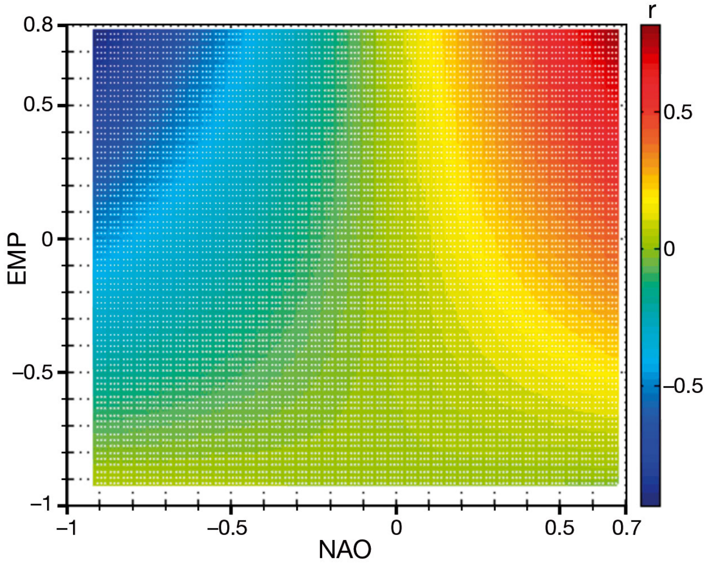



Fig. 2. Response surface depicting the joint effects of climate teleconnections from the North Atlantic Oscillation (NAO) and Eastern Mediterranean pattern (EMP) on standardized regional climate variability in the southern Adriatic Sea during the period 1985–2011

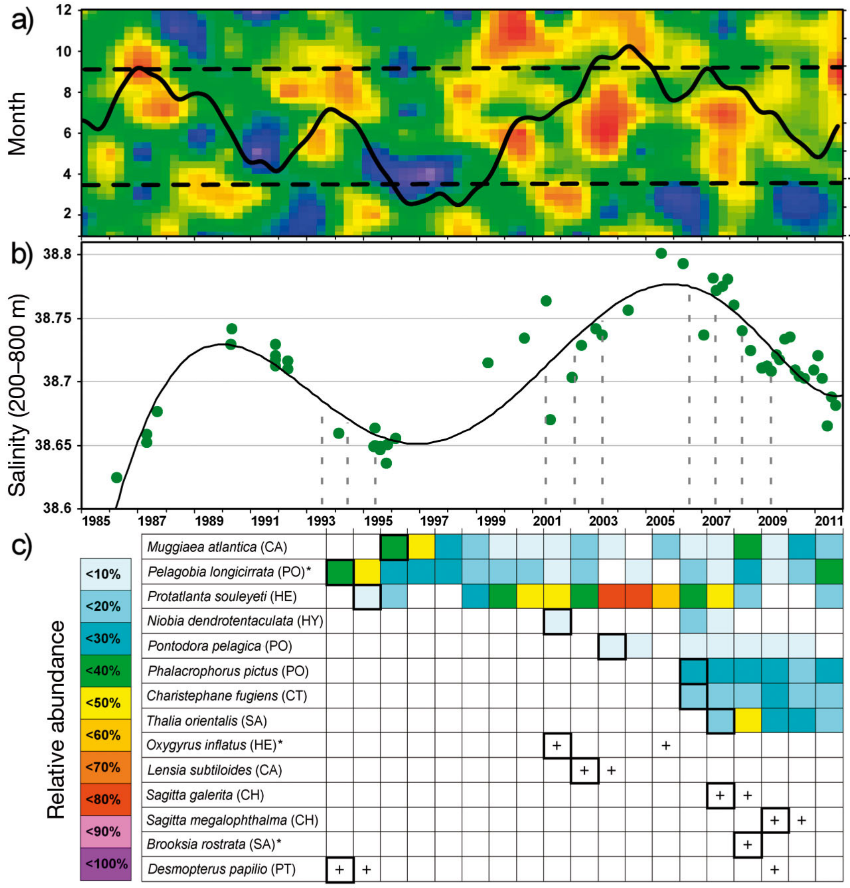



Fig. 3. (a) Seasonal and interannual variability of regional climate conditions in the southern Adriatic Sea experienced over the period 1985–2011. The color gradient, from blue through green and yellow to red, codes for negative to positive anomalies. The bold line denotes structural changes uncovered by the cumulated sums of standard ordinary least square residuals (OLS-based CUSUM test) of the monthly variability of south Adriatic climate. Horizontal dashed lines: confidence interval ($\alpha = 0.05$). efp: empirical fluctuation process. The timing of significant temporal changes is detected when the cumulative sums (bold line) cross the confidence interval (dashed lines). (b) Interannual variability of average salinity in the 200 to 800 m depth layer (green spots). Higher and lower saline conditions indicate the occurrence of cyclonic and anti-cyclonic circulation, respectively, in the Northern Ionian Gyre (NIG). The trend was obtained by fitting a 6 degree polynomial curve, as in Civitarese et al. (2010). Vertical dashed lines: year of first occurrence of the species in the table. (c) Records over the period 1993–2011 of 11 newly recorded non-crustacean zooplankton species in the Adriatic Sea (black frames: first record of the species; (+): sporadic occurrence), and 3 species that re-appeared after several years of absence (*), and their relative abundance (%) in their respective groups: Calycophorae (CA), Polychaeta (PO), Pteropoda (PT), Heteropoda (HE), Hydromedusae (HY), Ctenophora (CT), Salpida (SA), Chaetognatha (CH)

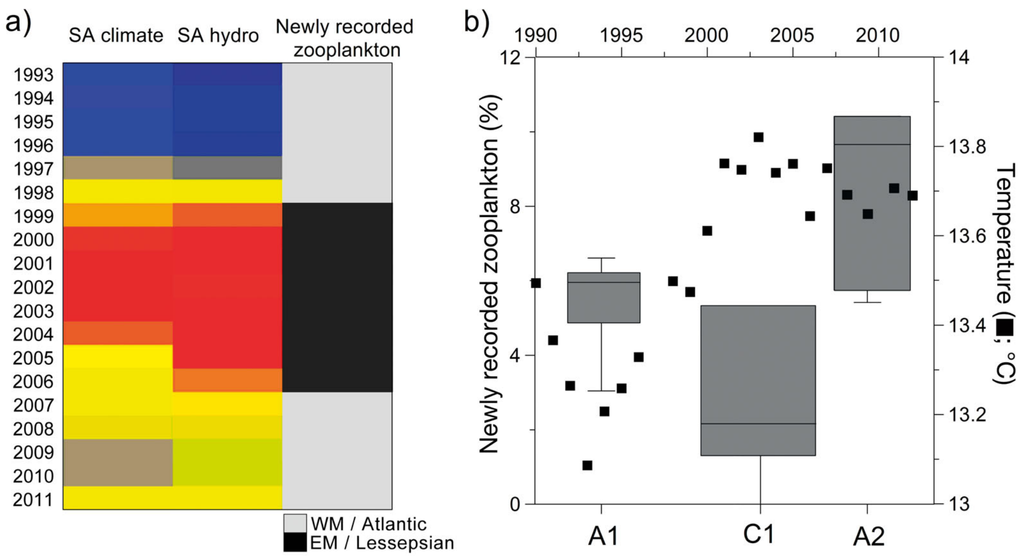



Fig. 4. Interannual variability of climate, local thermohaline conditions and incoming zooplankton species in the Adriatic Sea. (a) Traffic-light diagram of southern Adriatic climate (SA climate) and local thermohaline conditions (SA hydro). The diagram displays a color range from red to blue, where the quantiles 0.90, 0.50 and 0.10 correspond to the colors red, yellow and blue, respectively. The grey scale indicates the timing of dominance of West Mediterranean (WM)/Atlantic (light grey) and East Mediterranean (EM)/Lessepsian (dark grey) newly recorded zooplankton species. (b) Box-and-whisker plots showing the relative contribution of the newcomers to total non-crustacean species in (A1, A2) anti-cyclonic and (C1) cyclonic periods. The plot was generated by putting together the relative abundance of newcomers with respect to the total non-crustacean zooplankton during the years included in each period, A1 (1993–1995), C1 (2001–2007) and A2 (2008–2011). Bold horizontal lines: median values; whiskers: maximum and minimum values; box length: 25th and 75th percentiles. (■) Average temperature in the 200 to 800 m depth layer

### 3.2. The continuum of species arrival

From 1993 to 1995, 3 species new to the Adriatic Sea were recorded: calycophoran *Muggiaea atlantica*, pteropod *Desmopterus papilio,* and heteropod *Protatlanta souleyeti* (Batistić 1999, Kršinić & Njire 2001, Batistić et al. 2004). In addition, the pelagic polychaete *Pelagobia longicirrata*, registered for the first time in 1967 (Požar 1972), reappeared in the Adriatic in 1993 (Batistić et al. 2004) (Fig. 3c). These species are common in the Atlantic Ocean and have been recorded in the Western Mediterranean over past decades (Furnestin 1960, Di Geronimo 1970, Rampal 1975, Pleijel & Dales 1991, Pinca & Dallot 1995). Their first occurrence or reappearance in the Adriatic was associated with the inflow of colder and less saline MAW driven by anti-cyclonic circulation in the NIG. While generally lower temperatures enabled the entry of 2 cold-temperate species, *M. atlantica* and *P. longicirrata*, 2 warm-temperate species, *D. papilio* and *P. souleyeti*, were also recorded (Batistić et al. 2004). However, the latter 2 species were associated with warmer years (Fig. 3a,c) influenced by higher than average winter temperatures (Fig. 3a), which probably permitted their survival.

From 1993 to 1995 changes also occurred in the microzooplankton community of the southern Adriatic. Rare oceanic species, the tintinids *Protorhabdonella curta, Ascampbelliela armilla* and *Rhabdonella amor*, appeared in the open waters of the southern Adriatic in relatively high number, while the tintinid *Acanthostomella lata* was registered for the first time (Kršinić 2010).

A contrasting pattern was observed over the period 2001–2007. These years were characterized mainly by the presence of warm/warm-temperate species, which benefited from the shift to cyclonic circulation in the NIG and with it from the flow of a greater volume of warmer and saltier Levantine waters into the Adriatic (Gačić et al. 2010, Civitarese et al. 2010).

Species found in the southern Adriatic during the period 2001–2007 include *Niobia dendrotentaculata* (Hydromedusae), *Lensia subtiloides* (Calycophorae), *Oxygyrus inflatus* (Heteropoda), *Pontodora pelagica* (Polychaeta), *Phalocrophorus pictus* (Polychaeta), *Ferosagitta galerita* (Chaetognatha), *Thalia orientalis* (Thaliacea), and *Charistephane fugiens* (Ctenophora). All of these species were observed for the first time in the Adriatic, with the exception of *O. inflatus*, which had previously been reported in 1952 (Gamulin 1979). Among these species, the alien *Ferosagitta galerita* has its origins exclusively in the Indo-Pacific and the Red Sea, and probably entered the Eastern Mediterranean as a Lessepsian migrant. *F. galerita* is common in the Indian Ocean, and was reported for the first time in the Eastern Mediterranean in 2003, in relative abundance in the northeast Levantine Sea (Terbiyik et al. 2007). The arrival and establishment of Lessepsian migrants in the Eastern Mediterranean, followed by their spread throughout the entire Mediterranean basin, including the Adriatic, has accelerated (Boero et al. 2008, Pancucci-Papadopoulou et al. 2012). *L. subtiloides* is also an Indo-Pacific species. Although there are records of it in the Atlantic Ocean, these are considered to be cases of mistakenly identified *Lensia leloupi* (Pugh 1999). With the exception of *C. fugiens*, the remaining species found during this period have a circum-(sub) tropical distribution. They have previously been found in the Indian Ocean, Red Sea and Levantine Basin (Alvariño 1974, Day 1975, Lakkis & Zeidane 2010), which suggests that they too may be Lessepsian migrants. During the same period, the warm-water tintinnid species *Amplectella colaria* and *A. tricollaria*, considered indicators of LIW (Kršinić & Grbec 2002), were recorded in the southern Adriatic (Kršinić 2010). In addition, the tintinnid *Undella hadai*, a new immigrant from the Red Sea, was found in the southern Adriatic in 2004 and 2007 (Kršinić 2010).

During the period 2008–2011, hydrographic conditions displayed a decrease in salinity, indicating a shift back to anticyclonic circulation in the NIG. This change yielded a similar dominant circulation to that of the years 1993–1998 (Fig. 3b). In 2009, we recorded the chaetognath *Sagitta megalophthalma* for the first time in the southern Adriatic, (Fig. 3c), a species reported so far only in the deep waters of the Western Mediterranean and in the Atlantic Ocean (Dallot & Ducret 1969, Michel 1984). The pteropod *Desmopterus papilio*, recorded for the first time during the anticyclonic period in the 1990s, reappeared in the southern Adriatic in 2009 in the course of the same circulation regime (Fig. 3c). The thaliacean *Brooksia rostrata* was also recorded during this period. This species inhabits warmer oceanic areas and is frequently found in the Western Mediterranean (Van Soest 1975), although only a single record of it in the Adriatic Sea exists, dating from the early twentieth century (Sigl 1912).

Our results depict an overall increase in zooplankton newcomers in the southern Adriatic. Indeed, superimposed on the cyclical pattern of incoming species, we observed an overall upward trend that has translated into a noticeably larger contribution of these species to the non-crustacean Adriatic zooplankton community (Fig. 4b).

From an ecological perspective, specifically that of source-sink dynamics theory (Pulliam 1988), these changes point to a potentially dramatic ongoing process, related to rising temperatures in northern Mediterranean areas, whereby the function of the Adriatic Sea as a sink to newcomer warm-water zooplankton may be lost over time. The sink area, according to source-sink dynamics theory, represents an environment which prevents species establishment. In the present case, warm-water species are still being supplied to the Adriatic from either the Eastern or Western Mediterranean and cannot form lasting populations (Fig. 3c). This hypothesis, however, needs to be tested using field observations spanning longer periods.

### 3.3. Fate of newly recorded species

Fig. 3b shows how the relative abundance of newly arrived species in their respective groups varied over the period 1993–2011. The low temperatures experienced in the southern Adriatic during the years 1995–1998 (Fig. 3a) favored the arrival and establishment of the cold-temperate calycophoran *M. atlantica* (Fig. 3c). The progressive dominance of this species over the native *M. kochi* was quantified from 1995 to 1997 (Kršinić & Njire 2001, Batistić et al. 2007) during anticyclonic circulation in the NIG (Fig. 3b,c). From 1999 to 2007, temperature and salinity increased owing to the greater influence of Eastern Mediterranean waters, and the relative abundance of *M. atlantica* dropped dramatically (Fig. 3a–c). From 2008 onwards, however, the growing influence of MAW stimulated large peaks in *M. atlantica*, which reached 33 % of the total annual calycophoran abundance (Fig. 3c).

The anticyclonic circulation in the NIG also appeared favorable to the polychaete *Pelagobia longicirrata*. The higher abundance and dominance of this species within the planktonic polychaete community were related to cold and low salinity conditions (Fig. 3a,c). In contrast, the increased contribution to the heteropod community of *Protatlanta souleyeti*, which has been observed in the southern Adriatic continually since 1994, was related to warm and high salinity conditions during the cyclonic circulation (Fig. 3a,c).

The warm-temperate hydromedusa *Niobia dendrotentaculata* was recorded sporadically from 2001 to 2003, but a noticeable increase in abundance was observed in 2006 (Fig. 3c), when it made an annual contribution of 16 % to the total hydromedusan community. It reached peak abundance in August 2006, with a contribution of 44 % to the total hydromedusan community. In 2007, however, this species appeared in low numbers, and it disappeared afterwards. This species is characterized by a peculiar growth and budding involving the development of young medusae on each marginal tentacle bulb. Asexual reproduction in jellyfish from tentacle bulbs may be explained as a polyembryonic strategy to boost population increase rapidly when abundant food and optimal environmental envelopes are available (Boero et al. 2002). This is probably the mechanism underlying the unusually high abundance recorded during cyclonic circulation in 2006. *N. dendrotentaculata* is not, however, established in the Adriatic Sea, and its incidence appears driven by intrusions of warmer waters.

The warm-temperate thaliacean *Thalia orientalis*, common in the northern Levantine Basin (Weikert & Godeaux 2008), was observed for the first time in the Adriatic Sea in 2007. In 2008, the annual contribution of *T. orientalis* to total Salpida abundance in the southern Adriatic increased markedly (Fig. 3c). This species took the place of the formerly dominant congener *Thalia democratica* with 55 % of total Salpida abundance in January. Similarly, the ctenophore *Charistephane fugiens* and the planktonic polychaete *Phalocrophorus pictus* became established after their first occurrence in the Adriatic, and since then have been continually recorded in relatively high abundance within their taxonomic group (Fig. 3c). These 3 species appeared and established themselves in the Adriatic at the end of the cyclonic period, although a longer survey is needed to show possible variations in their abundance relative to the BiOS. The species *Pontodora pelagica* has been present from 2003 onwards without any obvious abundance pattern relative to the BiOS.

Three species associated with warmer waters, *Desmopterus papilio* (Pteropoda), *Oxygyrus inflatus* (Heteropoda) and *Ferosagitta galerita* (Chaetognatha), entered the Adriatic Sea in different years. *D. papilio* entered during anticyclonic circulation in the NIG, but the overall low temperature conditions are likely to have hampered its establishment (Fig. 3a,c). *O. inflatus* and *F. galerita*, which inhabit tropical waters, arrived in the Adriatic with warmer waters associated with cyclonic circulation in the NIG, but no evidence exists as to their establishment in the area. Future monitoring will indicate the fate of the recently recorded species *Sagitta megalophthalma* (Chaetognatha) and *Brooksia rostrata* (Thaliacea).

Thermal changes in the Mediterranean Sea are critical to the fate of new incoming organisms, as temperature plays a central role in reproductive success and phenology (Coll et al. 2010, Edwards & Richardson 2004, Oguz et al. 2008). Rising temperatures can also affect the phenology of native species, and with it food web interactions (Sommer et al. 2012). For instance, abundance shifts in northern Adriatic zooplankton assemblages over the past 3 decades have been related to rising temperatures (Kamburska & Fonda-Umani 2009, Conversi et al. 2010). Similarly, warmer conditions in the Mediterranean have been linked to changes in the phenology of copepods (Molinero et al. 2005), a decrease in cold-water ctenophores (Molinero et al. 2008a) and an increase in the recurrence of high jellyfish blooms (Molinero et al. 2008b). In this way, the trend over recent decades towards rising temperatures in the Adriatic Sea (see Fig. 4b) sounds a warning about the potential spread of favorable conditions for thermophilic species. At the same time, 2 cold-temperate species have also expanded their geographical range in the Adriatic over the past 2 decades. It seems that temperature increase in the Adriatic is still not a limiting factor for these Atlantic species, whose arrival was likely brought about by circulation shifts. In view of ongoing climatic changes, we can expect the Atlantic to become a more frequent source of warm-temperate species for the Western Mediterranean and the Adriatic. This is in accordance with the trend towards rising temperatures over the past 60 yr in the Northeast Atlantic (IPCC 2007), which promotes the spread of warmer-water species while curbing the abundance of colder-water species (Beaugrand et al. 2009).

## 4. CONCLUSIONS

We provide a compelling understanding of how circulation patterns in the NIG shape the origin of incoming zooplankton in the Adriatic Sea. The species in question may be used as proxies for the flow of water masses, for example Western Mediterranean/ Atlantic or Eastern Mediterranean waters, into the Adriatic Sea, since the timing of their first appearance and their temporal patterns reflect mesoscale hydrodynamics in the NIG. Hydrographic dynamics also influence the probability of establishment and population dynamics of newcomers.

Although the Mediterranean Sea experiences marked natural variations related to the North Atlantic and subtropical atmospheric systems, overall there is a discernible trend towards increasing temperature over the last 60 yr (IPCC 2007). Our results indicate that the prevalence of warm-temperate newcomer zooplankton species in the Adriatic Sea over the past 2 decades echoes this temperature increase. They further sound a warning that rising temperatures in the Adriatic may amplify the effect of the continuous arrival of new zooplankton species by opening favorable thermal windows for thermophilic species, likely enabling their establishment. In this scenario, the Adriatic may no longer represent a sink for warmer affinity species. These changes may ultimately enhance the risks posed by tropicalization to the already-threatened biodiversity of the Adriatic Sea.

We stress the importance of reliable plankton surveys at species level as a critical tool for tracking changes in biodiversity hotspots such as the Mediterranean basin. Long-term surveys and high taxonomic resolution are essential to understanding marine ecosystem responses to environmental variations.

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