Inter-annual climate variability and zooplankton: applying teleconnection indices to two deep subalpine lakes in Italy

Marina MANCA,[1*] Michela ROGORA,[1] Nico SALMASO[2]

[1]CNR - Institute of Ecosystem Study, Largo Tonolli 50, 28922 Verbania Pallanza; [2]Sustainable Agro-ecosystems and Bioresources Department, IASMA Research and Innovation Centre, Istituto Agrario di S. Michele all'Adige, Fondazione E. Mach, via E. Mach 1, 38010 S. Michele all'Adige, Trento, Italy
*Corresponding author: m.manca@ise.cnr.it

ABSTRACT

Investigating relation between meteo-climatic indices and between-year variation in Daphnia *population density and phenology is crucial for* e.g. *predicting impact of climate change on lake ecosystem structure and functioning. We tested whether and how two teleconnection indices calculated for the winter period, namely the East Atlantic pattern (EA$_{DJF}$) and the Eastern Mediterranean Pattern (EMP$_{DJF}$) were correlated with* Daphnia *population growth in two Italian subalpine lakes, Garda and Maggiore. We investigated between-lake temporal coherence in: i) water temperature within the water layer in which* Daphnia *is distributed; ii) timing of* Daphnia *initial and spring maximum population density peak and iii) the level of* Daphnia *spring maximum population density peak over an eleven-year period (1998-2008) of unchanged predation pressure by fish and invertebrates, and of common oligotrophy. Between-lake temporal coherence was high for an earlier start, and earlier, and lower,* Daphnia *population spring density peak after milder winters. Peak density level was coherently, positively correlated with soluble reactive phosphorus (SRP) concentration. We hypothesized that* Daphnia *peak densities were related to atmospheric modes of variability in winter and to the degree of late winter mixing promoting replenishment of algal nutrients into upper water layers and phytoplankton growth, enhancing food availability and* Daphnia *fecundity, promoting and* Daphnia *peak.*

Key words: Climate change, population phenology, Daphnia *fecundity, SRP, phytoplankton.*

Received: May 2014. Accepted: August 2014.

INTRODUCTION

Climate has increasingly been regarded as a major driver of changes in population phenology, directly and indirectly influencing between-year variability of seasonal cycles in terrestrial, marine and freshwater organisms (Winder and Schindler, 2004; Visser and Both 2005; Menzel *et al.*, 2006; Richardson, 2006; Vadadi-Fülöp and Hufnagel, 2014).

The growing interest is also consequent to the awareness that we are facing a dramatic increase in ambient temperatures. The average increase in the observed annual mean temperature across Europe for the last century was 0.8°C (Dokulil *et al.,* 2010). Temperature increase for the year 2035 is estimated as 2.0-3.5°C, depending on the scenario and whether or not the damping by aerosols is considered (Kromp-Kolb, 2001). Temporal (between seasons) and spatial (between regions) variability of precipitations are also estimated to increase, with Northern Europe experiencing an increase in annual precipitations between 10-40% and increased risk of droughts in central and southern Europe. Ambient temperature changes and range of seasonal variations have been found to directly and indirectly influence timing and rates at which plants and heterotherms grow and reproduce along the season (Walther *et al.,* 2002). By taxa- and population-specific responses, changes in ambient temperature also promote temporary changes in biotic interactions and predator-prey uncoupling, which ultimately result in changes in diversity and functioning of ecosystems (Moss *et al.,* 2009; Shurin *et al.,* 2010). The search for common responses at local, regional and global scales to changes in temperature has also resulted in increasing attention for possible common meteo-climatic drivers, causing temporal coherence observed at local level. Such effort was particularly important for lakes, regarded as sentinels and integrators of climate change (Adrian *et al.,* 2009), acting as *filters* able to integrate and amplify the local climate (Blenckner, 2005; George, 2010).

An important role in this respect has been played by studies on crustacean zooplankton, because of their key, intermediate role, linking fast-reacting and fast-growing phytoplankton to upper levels of the food web exhibiting a delayed response to changes in climate. Pioneer studies, inspired by evidence from sea plankton (Taylor *et al.,* 1992) and awareness that plankton succession in temperate lakes was strongly influenced by year-to-year variations in the weather (Reynolds, 1987), demonstrated that between-year variations in zooplankton biomass were closely correlated with meteo-climatic indices (namely, the latitude of the north wall of the Gulf Stream; George and Taylor, 1995). Successive research on meteoclimatic drivers of change in zooplankton have been mainly addressed to indices devel-

oped for North America and Central Europe, particularly the North Atlantic Oscillation (NAO) index, calculated for the winter period (Hurrell *et al.,* 2003). Comparison of response patterns to the winter (December-February) NAO$_{DJF}$ index, however, resulted in weak or inconsistent results when applied to lakes in the southern side of the Alps (Salmaso, 2005; Manca and DeMott, 2009; Dokulil *et al.,* 2010). The Alps are indeed a barrier to the mass movement of air and cause the sharp climatic division between Atlantic, Continental and Mediterranean influences. Because of this barrier, lakes located in the southern flank of the Alps are likely somewhat shaded against influences of climatic indices to which lakes in Northern and Central Europe respond. In an attempt to find reliable drivers able to explain changes in phytoplankton taxa composition and nutrient dynamics of Lake Garda, Salmaso (2012) applied two other-than-NAO$_{DJF}$ winter teleconnection indices of climate change, the Eastern Mediterranean Pattern (EMP$_{DJF}$) and the East Atlantic (EA$_{DJF}$) pattern for the winter (December-February) period.

In the present paper, we tested NAO$_{DJF}$, EMP$_{DJF}$ and EA$_{DJF}$ teleconnection indices to investigate temporal coherence in seasonal dynamics of a key cladoceran zooplankter, *Daphnia*, in lakes of the subalpine region. We investigated the two large, deep lakes which are representative of the westernmost and easternmost part of the subalpine region, lakes Maggiore and Garda. At present, both are quite comparable for trophic status, *i.e.* they are characterised by oligotrophic (Lake Maggiore) and oligo-mesotrophic (Lake Garda) conditions (Salmaso *et al.,* 2007; Mosello *et al.,* 2010). Because of their depth, the lakes are olo-oligomictic; long periods of incomplete spring mixing are interrupted by complete overturns promoted by harsh and windy winters (Ambrosetti and Barbanti, 1999). We tested whether between-year changes in *Daphnia* population phenology and maximum density in spring were coherent between lakes, and whether they might be explained by a common response to the same meteoclimatic forcing, expressed by winter teleconnection patterns. We hypothesized that changes in winter water temperature driven by a common climatic forcing acting at a regional scale affected between-year changes in time at start of *Daphnia* population growth. We also hypothesized that timing at start of *Daphnia* population growth was related to timing at *Daphnia* maximum spring density peak. We further hypothesized that the level of *Daphnia* spring population density peak attained each year was not directly consequent to climate change, being mediated by food availability. We based our hypothesis of a food-mediated impact on *Daphnia* maximum population density on the knowledge that a peak in fecundity precedes *Daphnia* spring density peak in Lake Maggiore; that, indeed, *Daphnia* fecundity (as defined in Manca *et al.,* 2008a) can be regarded as an indirect estimate of food availability, the latter being difficult to estimate from field

data (Manca *et al.,* 1994). In Lake Maggiore, over the long-term (1978-present), *Daphnia* year maximum clutch size has been detected after spring phytoplankton Standing Stock Biomass (SSB) peak (Manca *et al.,* 2000a), as also suggested by the so-called *PEG (Plankton Ecology Group)* model of plankton seasonal succession (Sommer *et al.,* 1986; Manca *et al.,* 2008b). This hypothesis is further based on recent observations carried out in Lake Garda and in the other deep lakes south of the Alps which demonstrated a strong impact of the winter EA and EMP on the winter air and spring lake temperatures, spring deep mixing dynamics, replenishment of phosphorus in the epilimnetic layers, and development of phytoplankton during spring and summer (Salmaso, 2012; Salmaso *et al.,* 2013).

METHODS

Sampling, field measurements and laboratory analyses

The data were collected in the framework of the Long Term Ecological Research (LTER-Italy) carried out in Lakes Maggiore and Garda between 1998 and 2008 (Salmaso *et al.,* 2007). This time window was chosen taking into account the availability of data, and because it is long enough to detect common temporal patterns in response to climatic forcing, while allowing for ruling out confounding factors, such as changes in algal nutrient concentrations and in predation pressure by fish and invertebrates (Manca and Ruggiu, 1998; Manca and De-Mott, 2009; Manca, 2011).

Air temperature was recorded in the meteorological stations of Pallanza (CNR-ISE), along the shores of Lake Maggiore, and of Arco, around 5 km away from the northern border of Lake Garda. Water temperatures were measured with multiparameter probes (Garda) or with mercury-filled Celsius thermometers (Maggiore) every month and every two weeks in Garda and Maggiore, respectively. In this work, we will use the temperatures measured in the 0-50 m water layer, which coincides with the layer where zooplankton was traditionally sampled for long-term monitoring of deep lakes (de Bernardi *et al.,* 1990; Salmaso and Naselli-Flores, 1999). The choice of this layer was also justified because our interest was directed towards biological response to common climate drivers, rather than to direct impact of climate on water temperature, traditionally investigated by using lake surface water temperatures (LSWTs; Livingstone and Dokulil, 2001; Dokulil *et al.,* 2010). Soluble reactive phosphorus (SRP) at spring overturn was determined following standard methods (Mosello *et al.,* 1997; Salmaso and Cerasino, 2012), on samples collected in the epilimnetic layers (0-20 m).

The impact of atmospheric modes of circulation on the limnological variables and the populations of *Daphnia* in the two lakes were tested using 3 indices relevant or potentially relevant for the southern subalpine region

(Salmaso, 2012). The winter (December-February) North Atlantic Oscillation (NAO$_{DJF}$) and the winter East Atlantic pattern (EA$_{DJF}$) were computed by the NOAA-CPC (www.cpc.ncep.noaa.gov). The winter Eastern Mediterranen Pattern (EMP$_{DJF}$) was computed following Hatzaki *et al.* (2007). While winter NAO has been successfully applied to lakes in North America and Central Europe, the other two teleconnection indices have been increasingly used to explain temporally coherent changes in air and water temperature in lakes from the southern slide of the subalpine region (Salmaso and Cerasino, 2012). The EA pattern is defined by a center located near 55°N, 20°-35° W and an opposite one over North Africa and the Mediterranean Sea (25°-35° N, 0°-10° W). Compared with the nodal lines of the NAO, the two anomaly centres of the EA pattern are displaced southeast ward. For this reason the EA pattern is often interpreted as a *southward shifted* NAO pattern. In its negative state, the EA$_{DJF}$ pattern is characterised by intense high pressure over the West Atlantic, causing a north-easterly airflow, which brings cold air from continental Europe over the full Mediterranean basin. Cold winters over the Mediterranean area are, instead, associated with positive values of the EMP$_{DJF}$.

In lakes Maggiore and Garda zooplankton was sampled around every two weeks and every month, respectively. In both lakes, zooplankton was collected by vertical tows from 50 m to the surface. Details on samplings and population density estimations were reported in Manca and Ruggiu (1998) and Salmaso and Naselli-Flores (1999). The temporal dynamics of *Daphnia* in relation with the climatic fluctuations and water temperatures were evaluated based on different descriptors. The *Daphnia* start of population density increase (D$_{start}$) was assessed taking the Julian day at which *Daphnia* population density level reached at least 400 ind·m^{-3} and 500 ind·m^{-3} in Lake Maggiore and Lake Garda, respectively. The choice of these two threshold density levels was based on analyses of *Daphnia* pluriannual seasonal dynamics over the time period selected for the two lakes. It was justified by the fact that in some years *Daphnia* persisted all over the year, therefore making it difficult to define an initial state of density increase above zero. The timing of *Daphnia* population density peak was also investigated in the two lakes, *i.e.* the Julian date of *Daphnia* spring peak (between May and June; D$_{peak1}$;D=day). We also analysed temporal coherence of *Daphnia* spring density peak in the two lakes (defined as the maximum population density peak recorded between May and June; P$_{peak1}$; P=population density).

Data analysis

The three teleconnection indices (NAO$_{DJF}$, EA$_{DJF}$ and EMP$_{DJF}$) were related to selected limnological variables describing the physical and chemical characteristics of the water column during and after the period of maximum spring overturn (between March and April), and to the variables describing the temporal dynamics of *Daphnia*. The environmental variables include the mean winter air temperatures computed in the period from December to February (Tair$_{DJF}$), the spring water temperatures between 0 and 50 m (T$_{0-50S}$), and the maximum concentrations of epilimnetic (0-20 m) SRP at spring overturn (SRP$_{epiS}$). The relationships between different explanatory (EV) and response variables (RV) were evaluated using Generalised Least Squares models (GLS). In every model, GLS was applied including *lake* as a categorical variable; single limnological or biological variables as continuous explanatory variables (EV); and a lake-EV interaction term:

$$RV_{ij}=\alpha_j+\beta_j \times EV_{ij}+\varepsilon_{ij}$$

where *i* and *j* are indices for the observations of the two lakes, respectively; and ε is the residual errors (Zuur *et al.,* 2009; Tab. 1). Selection of models was evaluated based on the small sample Akaike Information Criterion (AICc), which includes a correction for finite sample sizes (Burnham and Anderson, 2004). AIC is known for inadequate penalization of complex models, therefore the selection process was confirmed also computing BIC (Bayesian Information Criterion). BIC is more conservative, *i.e.* the number of parameters have a higher penalty than in the AIC (Zuur *et al.,* 2009; Hastie *et al.,* 2009). Different intercepts and slopes were included only if significant (at least P<0.05). Independence of residuals was confirmed in all the tested models by computing the Breusch-Godfrey test (P always >0.05). Statistical analyses and statistical graphs were calculated in R 3.0.0 (R Core Team, 2013).

Taking into account the strict correlation between EA and EMP (see below), the graphs will report only the relationships between EA and the environmental variables. Complete statistical results (including EMP) have been reported in Tab. 1.

RESULTS

The winter NAO (NAO$_{DJF}$) did not have any impact (P>0.1) on the winter air temperatures (Tair$_{DJF}$) measured in lakes Maggiore and Garda. Similarly, the relationships between the minimum winter water temperatures (T$_{0-50S}$) and NAO$_{DJF}$ was non significant in both lakes. In the same way, NAO$_{DJF}$ did not show any significant relationship with the other response variables considered in this work (P>0.10). Air temperatures measured in Lake Garda were lower than those measured in Lake Maggiore. The meteorological station in Lake Garda is located in the northern part of the lake, where air temperature is by far lower than in the southern part of the lake basin (Neteler *et al.,* 2011). The strict correlation between the winter EA pattern (EA$_{DJF}$) and the winter Eastern Mediterranean Pattern (EMP$_{DJF}$) (Salmaso,

2012) was confirmed also in this dataset (1998-2008; r=-0.92; P<0.001). EA_{DJF} and EMP_{DJF} strictly controlled (P<0.05) the interannual temporal development of the winter air temperatures ($Tair_{DJF}$) (Tab. 1; Fig. 1a). Based on the AICc values, the final models did not include different slopes and intercepts. Spring water temperatures showed a strong dependence on EA_{DJF} and EMP_{DJF} (Tab. 1; Fig. 1b). Contrary to air temperature, the spring water temperatures showed significant different intercepts, indicating that mean winter temperatures in Lake Maggiore were 1.6°C lower than those measured in the same years in Lake Garda.

The time at start of *Daphnia* populations (D_{start}) showed a significant (P<0.05) negative coupling with EA_{DJF} (Fig. 2a). The computations did not include an outlier highlighted in the figure. D_{start} did not differ between the two lakes for slope of the curve, suggesting that it

might be driven by a common meteoclimatic forcing. The same considerations could apply to the relationships between D_{start} and EMP_{DJF} (Tab. 1). Nevertheless, in this case, the value of the slope was not significant (P=0.10). The relationships between the two teleconnection indices and D_{start} were mediated by water temperature at spring overturn (Fig. 2b). The time at start of *Daphnia* population growth showed a strong dependence (P<0.01) from the mean water temperatures in winter, *i.e.* in a month preceding *Daphnia* start of seasonal increase. The range of winter temperatures differed for the two lakes, Lake Maggiore spanning between 6.2 and 7.5°C and Lake Garda between 7.5 and 9.4°C. Within the range of variation in T_{0-50S}, *Daphnia* modulated time at start of population growth by ca. 50-60 days in both lakes, although being the two shifted for range of variation, in Lake Maggiore
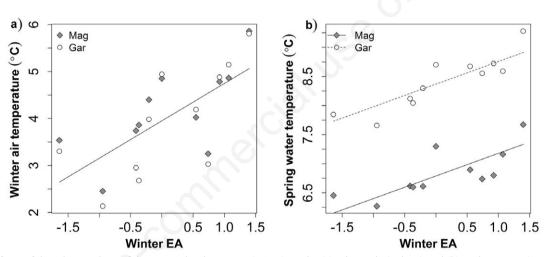
Tab. 1. Effects of the winter East Atlantic pattern (EA_{DJF}) and the winter Eastern Mediterranean Pattern (EMP_{DJF}) on $Tair_{DJF}$ (winter air temperature), T_{0-50S} (spring water temperatures between 0 and 50 m), D_{start} (*Daphnia* start of population density increase), P_{peak1} (spring density peak of *Daphnia*). A selection of other relationships (including SRP_{epiS}, maximum concentrations of epilimnetic SRP at spring overturn) is reported at the bottom of the table. The columns report the parameters of the models selected by the small sample Akaike Information Criterion (AICc) and Bayesian Information Criterion (BIC). Underlined figures indicate the better models (the lower the better).

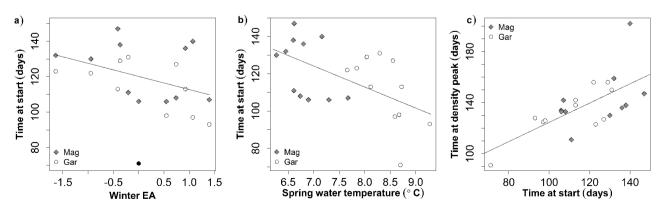| EV (X), RV (Y)	Intercept(s)	Slope (SE); t-values P	RSE; df	AICc° BIC°	AICc# BIC#	AICc§ BIC§	AICc^ BIC^	Figure
EA_{DJF}, $Tair_{DJF}$	3.95	0.796 (0.19); 4.25***	0.777; 20	<u>56.6</u> <u>58.5</u>	59 61	62 63.7	59.2 61.3	Fig. 1a
EA_{DJF}, T_{0-50S}	G, 8.37; M, 6.79	0.39 (0.06); 6.36***	0.254; 19	61.2 63.2	<u>9.2</u> <u>11.3</u>	11.5 13.2	63.6 65.6	Fig. 1b
EA_{DJF}, D_{start}	120.2	-7.39 (3.45); -2.14*	14.32; 19	<u>176.7</u> <u>178.4</u>	177.3 179.0	180.5 181.7	179.2 180.9	Fig. 2a
EA_{DJF}, P_{peak1}	2559.2	-1718 (364); -4.72***	1512; 20	<u>389.8</u> <u>391.7</u>	392.4 394.4	394.8 396.5	392 394	Fig. 3a
EMP_{DJF}, $Tair_{DJF}$	4.2 (0.17) 24.5***	-0.77 (0.18); -4.20***	0.782; 20	<u>56.8</u> <u>58.8</u>	59.3 61.3	62.3 64	59.3 61.3	
EMP_{DJF}, T_{0-50S}	G, 8.49; M, 6.91	-0.37 (0.06); -5.88***	0.267; 19	61.4 63.4	<u>11.5</u> <u>13.5</u>	14.2 15.9	63.8 65.8	
EMP_{DJF}, D_{start}	118	5.99 (3.50); 1.71 ns	14.85; 19	<u>178.2</u> <u>179.9</u>	178.8 180.5	181.3 182.5	181.0 182.7	
EMP_{DJF}, P_{peak1}	1985	1866 (300); 6.21***	1284; 20	<u>382.6</u> <u>384.6</u>	385 387	384.8 386.5	381.5§ 383.6§	
T_{0-50S}, D_{start}	203.1	-11.27 (3.72); -3.03**	15.56; 20	<u>188.4</u> <u>190.4</u>	188.8 190.8	191.9 193.6	189 191	Fig. 2b
D_{start}, D_{peak1}	49.2	0.75 (0.19); 3.91***	16.20; 20	<u>190.2</u> <u>192.2</u>	193.2 195.2	196.6 198.3	193.2 195.2	Fig. 2c
T_{0-50S}, P_{peak1}	G, 29210; M, 23799	-3166 (887); -3.57**	1736; 19	405.3 407.2	<u>397.8</u> <u>399.8</u>	400.9 402.6	398.4 400.4	
SRP_{epiS}, P_{peak1}	31.7	285.0 (68.6); 4.15***	1610; 20	<u>392.6</u> <u>394.5</u>	392.8 394.8	396 397.8	392.9 394.9	Fig. 3b

SE, standard error; RSE, residual standard errors; df, degrees of freedom; °$RV_i=\alpha+\beta \times EV_i+\epsilon_i$, 1 unique regression line; #$RV_{ij}=\alpha_j+\beta \times EV_{ij}+\epsilon_{ij}$, 1 regression line per lake, with equal slopes; §$RV_{ij}=\alpha_j+\beta_j \times EV_{ij}+\epsilon_{ij}$, 1 regression line for each lake (full model); ^$RV_{ij}=\alpha_j+\beta_j \times EV_{ij}+\epsilon_{ij}$, 1 regression line for each lake, with 1 unique intercept (see Zuur et al., *2009);* §*non significant (P>0.10)* β_j *in the fourth model. G, Garda, M, Maggiore;* ***P<0.001; **P<0.01; *P< 0.05; ns, not significant.*

between 100 and 150 days, and in Lake Garda between 70 and 130 Julian days, with difference between the means of 13 days.

The start of *Daphnia* population growth was in turn highly correlated (P<0.01) with the timing of *Daphnia* spring population density peak (D_{peak1}; Fig. 2c; Tab. 1). The complete overlapping of data from the two lakes and the common slope and intercept indicate that, once promoted, population density increase resulted into coherent delay in peak timing of *Daphnia* in the two lakes. Peak timing therefore appears like a simple, linearly delayed consequence of time at start of population growth. *Daphnia* spring population density peak (P_{peak1}) showed a negative relationship with EA_{DJF} (P<0.001; Fig. 3a) and a positive relationship with EMP_{DJF} (P<0.001) (Tab. 1).

Slopes and intercepts of P_{peak1} were not statistically different in the two lakes. Within the range of population density and of teleconnection indices values relative to the time window we analyzed, *Daphnia* tended to reach higher maximum density levels at negative EA values, and positive EMP values (Tab. 1) corresponding in both cases to lower water temperatures. In fact, P_{peak1} in both lakes showed a strong (P<0.01) and negative relationship with spring water temperature, T_{0-50S} (Tab. 1). Interestingly, D_{peak1} values in the two lakes were not correlated (P>0.1) with the spring water temperatures. P_{peak1} was strongly connected (P<0.01) with the epilimnetic spring SRP concentration (SRP_{epiS}) (Fig. 3b). The regression lines best fitting the data of the two lakes did not differ for slope and intercept (Tab. 1). A *ca.* twofold increase in

Fig. 1. Effects of the winter values of the East Atlantic pattern (EA_{DJF}) on the (a) winter air ($Tair_{DJF}$) and (b) spring water (0-50 m depth) temperatures (T_{0-50S}) in lakes Maggiore (Mag) and Garda (Gar) (1998-2008). Statistical analyses are reported in Tab. 1.

Fig. 2. Effects of (a) the winter East Atlantic pattern (EA_{DJF}), and (b) spring water temperature (T_{0-50S}) on time at start of *Daphnia* population growth (D_{start}). c) Effect of D_{start} on time at density peak (D_{peak1}) of *Daphnia* populations in lakes Garda and Maggiore, 1998-2008. Statistical analyses are reported in Tab. 1.

SRP concentration resulted in doubling of D_{peak1} level*,* with an increase in spring density peak of *Daphnia* population of 285 ind. m^{-3} for 1 µg L^{-1} SRP increase.
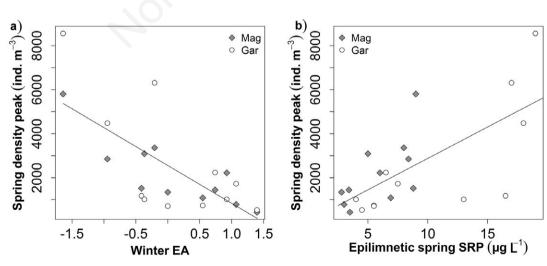
Overall, our results suggest a complex effect of winter water temperatures on the seasonal development of *Daphnia* populations in the two lakes. We summarized these complex interactions in Fig. 4, which will be discussed in the next section.

DISCUSSION

In most studies investigating interactions between climate change and zooplankton spring development, teleconnection indices developed for North and Central Europe and North America were applied, thus reflecting the origin and initial development of these studies. While being able to predict changes in plankton seasonality also in response to duration of the ice cover and melting timing (George *et al.,* 2004), these indices resulted fully inappropriate when applied to the deep lakes in the southern slide of the subalpine region (Salmaso, 2005, 2012; Salmaso *et al.,* 2013). The lower impact of NAO is likely a consequence of a sheltering effect of the Alps on the climate patterns prevailing in Northern and Central Europe. In this work, by using the two lakes representative of the easternmost and westernmost part of the subalpine region, we were able to prove that the influence of the two teleconnection indices (EA and EMP) on the zooplankton dynamics was extended to the entire subalpine region.

Warming is often regarded as a factor able to worsen the effects of eutrophication, resulting in similar patterns of change, although originating from different mechanisms (Schindler, 2001; Winder and Sommer, 2012). Our

data are representative of a time window in which the two lake systems did not show strong changes in the trophic conditions. In the considered period, Lake Maggiore was fully recovered from eutrophication, with well balanced, stable plankton communities. As for Lake Garda, the between-year fluctuations in the availability of nutrients in the same period were far more important compared with the long-term decadal changes (Salmaso, 2012). In addition, as shown in previous works (Salmaso *et al.,* 2013) which analyzed more extended periods and a larger number of lakes, the comparison of the regressions obtained with the de-trended and non de-trended series provide equivalent results. Nevertheless, an effect of other trophy-related changes in *e.g.* fish predation pressure on the analyzed relationship cannot be excluded. Studies on climate impact are commonly restricted to analyses of surface water temperatures, which are much more influenced by daily variations and of biological restricted relevance. The focus on surface water temperature was related to the possibility of applying satellites for detecting temperature change at large scale (Schneider *et al.,* 2009). Owing to our interest in *Daphnia*, we considered winter water temperatures of the water layer where the species was mainly distributed, particularly in spring, *i.e.* the upper 50 m depth. The use of temperature data of this water layer could in turn explain the high degree of temporal coherence of the two lakes.
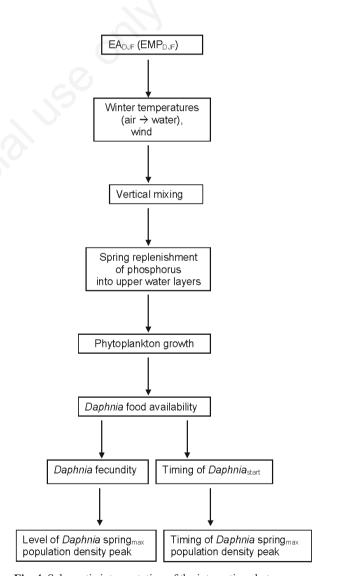
We interpreted temporal coherence of data from the two lakes on *Daphnia* seasonal growth timing (time at onset and time at maximum *Daphnia* population density growth) as consequent to the impact of common atmospheric circulation patterns described by EA and EMP. The

Fig. 3. Effects of the winter values of (a) the East Atlantic pattern (EA$_{DJF}$) on *Daphnia* population spring density peak (P$_{peak1}$) in lakes Maggiore and Garda (1998-2008). (b) Relationship between epilimnetic spring SRP concentration (SRP$_{epiS}$) and P$_{peak1}$ in lakes Maggiore and Garda (1998-2008). Statistical analyses are reported in Tab. 1.

results are therefore consistent with those obtained in Central and Northern Europe, as well as North America, where other teleconnection indices for the winter period were applied (Irigoien *et al.,* 2000; Straile, 2000, 2002; Piontkovski *et al.,* 2006). Similarly to those studies, time at start was in turn correlated with timing at which the major population density peak was attained (Straile *et al.,* 2003; Schalau *et al.,* 2008). Such a correlation was also found for predatory zooplankters, not least *Bythotrephes*, in Lake Maggiore (Manca and DeMott, 2009). Timing at density peak can be therefore regarded as a delayed response to the same common cue which promoted initial population growth, *i.e.* winter temperature. Our results also suggest that time lag between time at start and time at peak in *Daphnia* population density tends to be relatively constant between the two lakes. The high between-lake coherence in delta time at (D_{start}-D_{peak}), suggests that warming rate and rate of increase in food conditions are basically the same in the two lakes, therefore suggesting that the two lakes respond to warming coherently and environmental conditions promoting initial development also promote those causing subsequent development of the population; therefore environmental conditions will be relevant for *Daphnia* to promote initial development, later on being the population somewhat resilient to external perturbations (homeostasis).

In our study, increasing levels of *Daphnia* abundance were, at a high between-lake temporal coherence, inversely correlated to warming-associated modes of variations of both teleconnection indices applied. Negative relationship of *Daphnia* peak densities with milder winters (less phosphorus due to less mixing) was predicted from *e.g.* mesocosm experiments (Berger *et al.,* 2007) and modeling studies (Schalau *et al.,* 2008). Both studies show that algal carrying capacity, experimentally modified by modifying light availability in the mesocosm studies of Berger *et al.* (2007), and tested in different modeling scenarios by Schalau *et al.* (2008) would enhance peak densities of *Daphnia*. Based on the direct, highly between-lake coherent and significant correlation between *Daphnia* population density peak level and SRP concentration, we hypothesize that the level of peak reached by *Daphnia* in spring is indirectly related to winter water temperature, being mediated by the degree of winter mixing, which in turn regulates the algal carrying capacity. Our hypothesis is supported by previous works on Lake Maggiore (Manca *et al.,* 2000a, 2000b) demonstrating that the initial phase of increase in phytoplankton biomass is translated within a certain time lag into a peak in *Daphnia* mean clutch size and fecundity. At a time of the year between *Daphnia* initial growth and *Daphnia* density peak, a relatively low number of ovigerous females within the population carry a high number of eggs/clutch, an expression of increase in fecundity of

Daphnia population related to increase in food availability (Manca *et al.,* 2000a). The level attained on each year is dependent from phytoplankton development, which in turn depends on phosphorus concentration (Salmaso *et al.,* 2013). In fact, spring *Daphnia* clutch size during the mesotrophic phase of Lake Maggiore was found to be double than that measured after the reversal of eutrophication (Manca *et al.,* 2000a). Similarly, as observed in Lake Iseo (Leoni *et al.,* 2014), it was demonstrated how a complete winter mixing event during the oligotrophic phase could promote an increase in *Daphnia* clutch size to values of the mesotrophic phase, as a result of increased phytoplankton biomass and primary productivity (Manca

Fig. 4. Schematic interpretation of the interactions between meteoclimatic forcing and *Daphnia* spring population growth. Control of winter water temperature on *Daphnia* spring population density growth is indirect, *i.e.* mediated by food availability.

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et al., 2000b), consequent to an increase in nutrients. The increase in clutch size and fecundity observed with complete winter overturn also resulted in unusually high *Daphnia* spring population density peak in that year with respect to values measured over the period (Manca *et al.,* 2000b). Similarly, we suggest that temperature indirectly controls the timing of events in the plankton seasonal succession, being mixing depth and phosphorus replenishment for algal growth crucial also in this respect. Laboratory experiments have shown that *Daphnia* can grow, provided that food is not limiting, at the temperatures our study lakes experience in winter (>6°C, >8°C), therefore suggesting that also start of increase in abundance cannot be constrained by temperature alone. An increase in fecundity is also required for triggering recruitment of newborn into the population, necessary to promote initial population growth.

According to our results, we hypothesize that food availability is the major constrain for *Daphnia* spring maximum population density level attained in a given year in the two deep subalpine lakes we investigated. The question is therefore on whether, how, and to what extent, is food availability for *Daphnia* related to meteo-climatic drivers, as suggested by the fact that *Daphnia* peak density is correlated negatively with winter temperature and positively with spring SRP concentration. Correlation between *Daphnia* population density and SRP also confirms the *Daphnia* population density increase during Lake Maggiore eutrophication (Manca *et al.,* 2007). Our hypothesis is that *Daphnia* peak density level is indirectly related to climatic-forcing, *via* the same factors which promote increase in spring food sources (Salmaso and Cerasino, 2012; Salmaso *et al.,* 2013; Fig. 3). In our summarizing scheme (Fig. 4), we therefore hypothesize that the increase of algal nutrients in the trophogenic layers triggered by cold winters and specific patterns in the atmospheric modes of circulation, were directly responsible, *via* an increase in fecundity, of the *Daphnia* spring density peak. Environmental temperature indirectly affected also timing of *Daphnia* growth, by enhanced egg production, in turn related to mixing depth and algal carrying capacity. Ongoing research on other main deep subalpine lakes seems to confirm our hypothesis of food mediated *Daphnia* response to climate forcing.

CONCLUSIONS

This study represents the first application of two teleconnection indices potentially relevant for the Mediterranean area, namely the East Atlantic pattern (EA) and the Eastern Mediterranean Pattern (EMP), to assess the effects of atmospheric modes of variability on *Daphnia* population growth in two lakes south of the Alps (Garda and Maggiore). The results of our analyses highlighted the effects of winter water temperatures on the extent of

the late winter mixing and, indirectly, on the *Daphnia* peak densities. More specifically, our data support the hypothesis that the spring maximum densities of *Daphnia* were related to EA and EMP in winter and, through a linked chain of events, to the degree of late winter mixing, replenishment of algal nutrients into upper water layers, higher phytoplankton growth, enhancing food availability and *Daphnia* fecundity.

This study confirmed the usefulness of meteo-climatic indices as indicators of climate forcings and predictors of the impact of climate change on the functioning of lake ecosystems. The EA and EMP in particular proved to be suitable climatic indices for the assessment of interannual variability and temporal coherence of several limnological variables in the lakes of the southern subalpine area.

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