Contribution to the Themed Section: 'The Role of Zooplankton in Marine Biogeochemical Cycles: From Fine Scale to Global Theories'

Oithona similis likes it cool: evidence from two long-term time series

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We compare the long-term and seasonal patterns of abundance and phenology of the cyclopoid copepod *Oithona similis* at the L4 site (1988–2013) in the North Atlantic and at the LTER-MC site (1984–2013) in the Mediterranean Sea to investigate whether high temperature limits the occurrence of this species with latitudinal cline. The two sites are well suited to testing this hypothesis as they are characterized by similar chlorophyll *a* concentration (Chl *a*) but different temperature [sea surface temperature (SST)]. The abundance of *O. similis* at L4 was ∼10 times higher than at LTER-MC. Moreover, this species had several peaks of abundance during the year at L4 but a single peak in spring at LTER-MC. The main mode of temporal variability in abundance was seasonal at both sites. The abundance of *O. similis* was negatively correlated with SST only at LTER-MC, whereas it was positively correlated with Chl *a* at both sites. *Oithona similis* had a temperature optimum between 15 and 20°C reaching maximum abundance at ∼16.5°C at LTER-MC, but showed no Chl *a* optimum at either site. We conclude that the abundance of *O. similis* increases with prey availability up to 16.5°C and that temperature >20°C represents the main limiting factor for population persistence.

KEYWORDS: time series; copepod; *Oithona similis*; temperature; Atlantic; Mediterranean

INTRODUCTION

The small cyclopoid copepod *Oithona similis* is considered one of the most abundant and ubiquitous metazoan species in the marine environment with a distribution ranging from coastal to oceanic regions and from tropical to temperate and polar waters (Paffenhöfer, 1993; McKinnon and Klumpp, 1998). Despite its reported widespread occurrence, published literature suggests that *O. similis* thrives in boreo-arctic localities (Nielsen and Sabatini, 1996; Gislason and Astthorsson, 2004; Castellani *et al.*, 2007; Blachowiak-Samolyk *et al.*, 2008) whereas

evidence of its presence in tropical areas is more sparse and in some case doubtful (Nishida, 1985; Razouls et al., 2005–2015; Hwang et al., 2007).

The seasonal and geographical distribution of a species is determined by biotic and abiotic environmental conditions with ambient temperature, food availability and predation mortality being among the most important parameters (Ussing, 1938; Carlotti and Slagstad, 1997). To date, information on the environmental factors determining the seasonal and spatial distribution of the abundance of O. similis is still limited due to lack of concomitant measurements on ambient parameters, in addition to difficulty with the taxonomic identification of this species (Nishida, 1985; Calbet et al., 2001; Gislason, 2003; Gislason and Astthorsson, 2004; Hwang et al., 2007).

Published studies have attributed the ubiquity and high abundance of O. similis mainly to its ability to withstand a relatively wide temperature range (Castellani et al., 2005a), to exploit oligotrophic environments (Nielsen and Sabatini, 1996), and to its low energy requirement (Castellani et al., 2005a) and to its low predation mortality (Logerwell and Ohman, 1999; Eiane and Ohman, 2004) compared with other copepod species. However, reports that O. similis peaks in eutrophic conditions (Castellani et al., 2007; Mazzocchi et al., 2014) suggest that low food availability may limit the abundance and distribution of this species in more oligotrophic areas.

Temperature can play an important role in limiting abundance of Oithona, especially in polar oligotrophic waters. Seasonal studies on reproductive characteristics of Oithona spp. at high latitudes have reported low temperature as an important factor limiting fecundity (Metz, 1995; Ward and Hirst, 2007; Dvoretsky and Dvoretsky, 2009). However, no information is available on the effect of tropical temperatures on the ecology of this species. Since O. similis is either not abundant or not reported at tropical latitudes (Deevey, 1971; Deevey and Brooks, 1977; Paffenhöfer and Mazzocchi, 2003), we hypothesize that temperatures ≥20°C can limit the geographical distribution and the seasonal abundance of this species.

We test this hypothesis by comparing the seasonal and multiannual variability in the abundance of O. similis at two latitudinally distinct sites, in the North Atlantic Ocean and in the Mediterranean Sea, characterized by a very different range in ambient temperatures but similar Chl a and comparable sampling and analytical methods.

METHOD

Plankton sampling and environmental data

L4 station, English Channel, North-East Atlantic

Since 1988, zooplankton samples have been collected weekly at station L4 (50° 15′ N, 4° 13′ W), a coastal site located ∼7.5 nautical miles (∼13.9 km) south-west of Plymouth. Zooplankton were sampled by vertical net hauls from the sea floor (∼55 m) to the surface using a WP2 net with a mesh size of 200 μm and a mouth area of 0.25 m². Two hauls were successively taken at approximately mid-morning and the samples were concentrated on a 200 μm sieve and preserved in a 5% formaldehyde–sea water solution. For the analysis, a concentrated zooplankton sample was diluted and sub-sampled using a Folsom splitter and a Stempel pipette to count and identify between 200 and 400 organisms under a dissecting microscope. The abundance of adults and late copepodite stages (CIII–CV) was calculated from the volume sampled and expressed as total numbers of organisms per cubic meter (Ind. m^{-3}). The morphological microscopic analysis of the specimens in the samples revealed that O. similis was the only species of the genus Oithona found at L4 during the present study.

Temperature and chlorophyll a concentration (Chl a, μgL^{-1}) were measured at the surface from the water collected by a Niskin bottle. Between 1988 and 1992, sea surface temperature (SST, °C) was measured using a mercury-in-glass thermometer immersed in a stainless steel bucket of surface water. Since 1992, SST and Chl a concentration have been measured from a depth of 0–2 m using a 10-L Niskin bottle. In addition, since 1988 the temperature profile of the water column has been measured using a CTD and a SeaBird SBE19+ (Smyth et al., 2010). Chl a was determined by filtering 100 mL of seawater through 25 mm GF/F filters in triplicate and extracted in 90% acetone overnight at 4°C and samples analyzed fluorometrically with a Turner fluorometer according to Welschmeyer (Welschmeyer, 1994). For further information on physical and biological variables measured at L4, see reviews by Smyth et al. (Smyth et al., 2010), Eloire et al. (Eloire et al., 2010) and Widdicombe et al. (Widdicombe et al., 2010).

LTER-MC station, Gulf of Naples, western Mediterranean Sea

The sampling site station LTER-MC (40°48.5′N, 14°15′E) is located in the inner Gulf of Naples close to the 75 m isobath, two nautical miles from the coast. Physical and chemical variables and plankton communities have been monitored since January 1984, with a major interruption from 1991 through February 1995. The sampling frequency was biweekly until 1990 and has been weekly since 1995 (see Ribera d'Alcalà et al., 2004 for details). Zooplankton samples were collected by vertical tows in the upper 50 m with a Nansen net (200 μm mesh, 1.13 m mouth diameter, i.e. ∼1 m² mouth area) and fixed with buffered formaldehyde (2–4% final concentration). Aliquots ranging from 1/4 to 1/32, according to sample density, were taken with a large-bore pipette. As

for L4, the abundance of *O. similis* is reported as Ind. m^{-3} and includes adult females and males and the late copepodite stages (CIII−CV).

Temperature of the water column was recorded using Niskin bottles equipped with reversing thermometers between 1984 and 1990 and on a few occasions between 1995 and 2000. Since 1995, CTD and fluorescence profiles were obtained with a SBE911 mounted on a Rosette sampler equipped with 10 12-L Niskin bottles. Samples for Chl *a* were collected at discrete depths with the Niskin bottles. Chl *a* concentration was determined with a spectrophotometer (Strickland and Parsons, 1972) until 1990 and with a spectrofluorometer (Holm-Hansen *et al.*, 1965; Neveux and Panouse, 1987) from 1995 onward. Further details on analytical procedures are reported in Ribera d'Alcalà *et al.* (Ribera d'Alcalà *et al.*, 2004). Only the surface (0−2 m) values of temperature and Chl *a* have been analyzed for the present study.

Data analysis

Eigen-Vector filtering

To extract the main patterns of *O. similis* variability at the two sites, first two matrices were composed comprising fortnightly log$_{10}$ transformed mean abundance (Ind. m^{-3}). The data spanned over the period 1988−2013 for L4 and 1984−2013 for LTER-MC series, in which a gap of 4 years between 1991 and 1994 was eliminated. The principal modes of variability of *O. similis* were extracted by the Eigen-Vector Filtering method (EVF; Ibanez and Etienne, 1992) separately for LTER-MC and the L4 datasets.

The EVF procedure corresponds to a principal component analysis (PCA) calculated on an auto-covariance matrix based on the original time series X_t lagged with itself N times, where N is the lag at which the auto-correlation function of X_t goes to zero. The first and second axes extracted by the PCA, i.e. the filtered variables F_1 and F_2, represent the main modes of variability, generally corresponding to the inter-annual and seasonal cycle, respectively. Ibañez and Etienne (Ibanez and Etienne, 1992) showed that the filtered variables F_i (with $i = 1$ to N) can be equally estimated by a weighted moving average on the original series of order $r − 1$, containing $2(r − 1) + 1$ terms. Here, $r = 13$ was chosen considering that plankton species usually have some degree of auto-correlation at the annual scale. Before using the EVF, missing values in the original series (i.e. $m = 37$ in L4 and $m = 67$ in LTER-MC) were predicted by an iterative approach that consisted in replacing the m values with the main filtered variables (accounting for at least 80% of the total variance) obtained by performing several iterations of EVF, the first of which occurs while retaining the missing data (Ibanez and Conversi, 2002).

To identify the periodicities that primarily characterized the temporal fluctuations of *O. similis* at the two sites, harmonic analysis (Kendall, 1976; Legendre and Legendre, 1998) was applied to F_1 and F_2 and the significant harmonics, together with their associated percentage of variance, were extracted (Anderson, 1971). In order to investigate the influence of environmental changes on *O. similis* variability, at each site the log$_{10}$ transformed F_1 and F_2 of the species were correlated with the log$_{10}$ transformed F_1 and F_2 of SST and Chl *a*, correcting the number of degrees of freedom for temporal auto-correlation according to Pyper and Peterman (Pyper and Peterman, 1998).

Environmental preferences

The environmental preferences of *O. similis* with respect of SST and Chl *a* concentration were determined for each site based on the methodology proposed by Perry and Smith (Perry and Smith, 1994). This method consists in a pairwise comparison of the cumulative distributions of *O. similis* abundance $g(t)$ and the cumulative distribution of environmental parameters $f(t)$ over the range of the ambient parameter, where the null hypothesis (H_0) tested is that no particular association exists between these two. It can be assumed that if there was no association between *O. similis* and the environmental factor, $g(t)$ and $f(t)$ would be almost identical, whereas the greater their difference (D) the stronger the association. Therefore, D maxima were calculated and tested statistically against H_0, using a Monte Carlo randomization test with 10 000 permutations to estimate the significance level.

Phenology

The inter-annual variability of *O. similis* phenology at L4 and LTER-MC was investigated using the method of Greve *et al.* (Greve *et al.*, 2005). This method uses the cumulative sum of the abundance of a species to calculate the day of the year when the population reaches 25% (i.e. the start of the season), 50% (i.e. the middle of the season) and 75% (i.e. the end of the season) of the total abundance over its annual cycle. These three phenophases were calculated from weekly abundance data for each of the two sites. The duration of the annual cycle of *O. similis* (i.e. the "duration of the season") was calculated as the difference between the end and the start of the season.

The annual anomalies of the duration of the season and SST were calculated for L4 and LTER-MC between 1988 and 2013. The average of the annual means was subtracted from each annual mean and the differences (anomalies) were normalized by the standard deviation of the annual means.

The presence of significant trends in SST over the course of the time series during each month of the year

and their relationship with the abundance of *O. similis* was also investigated for the two sites using correlation analysis.

RESULTS

Long-term changes

The mean and maximum annual abundances of *O. similis* adults and late copepodite stages at L4 (mean $\pm$ SE, 369 ± 14 Ind. m^{-3}; range, 0–4791 Ind. m^{-3}) were higher than at LTER-MC (mean $\pm$ SE, 35 ± 3 Ind. m^{-3}; range, 0–1624 Ind. m^{-3}) (Fig. 1, Table I). Moreover, the mean ($\pm$ SE) annual percentage contribution of this species to total copepod abundance was four times higher at L4 (i.e. $17.1 \pm 0.4\%$) than at LTER-MC (i.e. $3.7 \pm 0.2\%$) (Table I).

The harmonic analysis on the F_1 revealed that the temporal variability of *O. similis* abundance was mainly associated with a 12-month period harmonic (i.e. 26 fortnights) at both sites (Table II). This harmonic explained 67% of the variance at LTER-MC and 25% at L4, indicating that the English Channel site is a more variable system characterized by recurrent pulses in abundance compared with the Gulf of Naples. It is worth noting that, although explaining only 3–4% of the F_1 variability, both time series were characterized by a significant periodicity of 13 years (i.e. 338 fortnights) and by a significant

long-term trend, which was positive at L4 and negative at LTER-MC (Table II).

The regression analysis of the SST data versus time showed that the L4 site experienced an overall warming trend between April and August ($r = 0.45$, $P = 0.04$, df $= 26$). Nevertheless, the abundance of *O. similis* was not correlated with SST increases during any part of the year ($P > 0.05$). The regression analysis of the SST data versus time at LTER-MC showed that between 1984 and 2013 temperature has cooled between January and March, although the relationship is only significant for the month of February (i.e. range 13.7–15.2°C, df $= 19$; $r = -0.43$; $P = 0.05$). Moreover, temperature at this site has increased during the last 2 weeks of April (i.e. range 13.3–16.7°C, df $= 22$; $r = 0.59$; $P = 0.003$), during the whole of May (i.e. range 14.1–21.7°C, df $= 20$; $r = 0.54$; $P = 0.012$) and during the last 2 weeks of June (i.e. range 21.4–26.9°C, df $= 21$; $r = 0.64$; $P < 0.001$). The abundance of *O. similis* at the LTER-MC has decreased significantly (df $= 25$; $r = -0.45$; $P = 0.023$) during June and this decline was significantly inversely correlated (df $= 23$; $r = -0.45$; $P = 0.027$) with the increase in SST recorded in May.

Seasonal changes

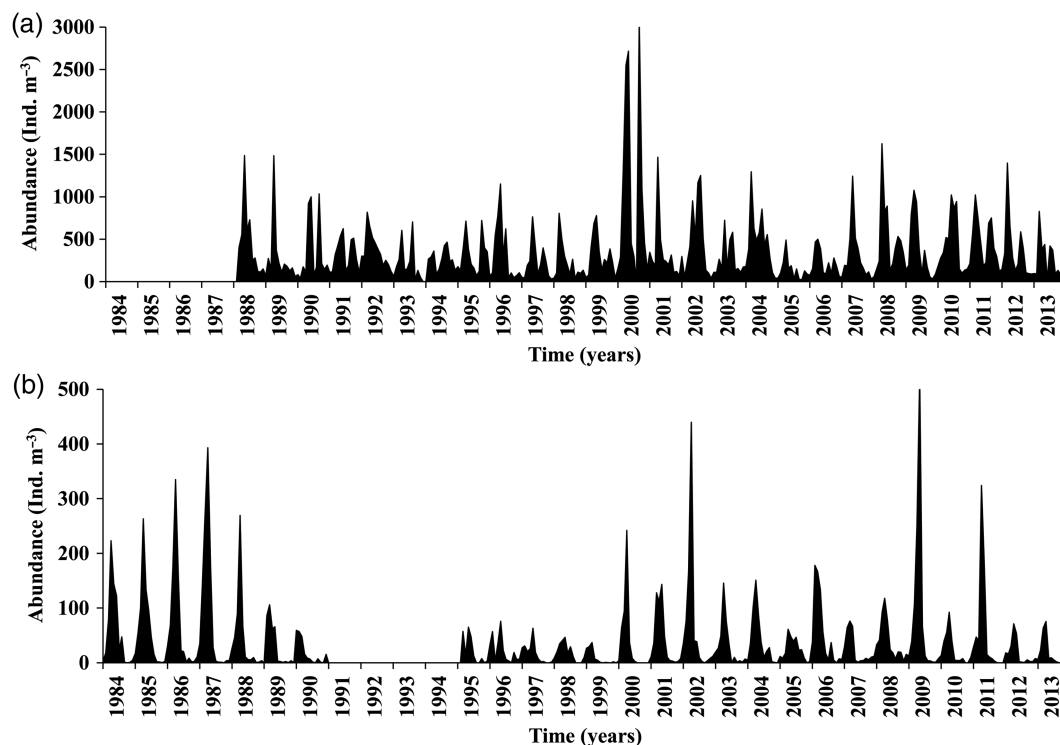The annual range of SST monthly means ($\pm$ SE) between 1988 and 2013 was lower and narrower at L4 (mean range

Fig. 1. *Oithona similis* monthly mean abundance (Ind. m^{-3}) at (**a**) L4 between 1988 and 2013 and at (**b**) LTER-MC between 1984 and 2013.

Table I: Summary of Oithona similis annual mean and absolute range (min−max) of abundance (Ind. m^{-3}) and relative contribution (%) to total copepods at L4 and LTER-MC between 1988 and 2013

Site	Total number of samples N	Annual mean Ind. m^{-3}	SE	Min Ind. m^{-3}	Max Ind. m^{-3}	Contribution to total copepods %	SE	Min %	Max %
L4	1134	369	14	0	4791	17.1	0.4	0.0	67.9
LTER-MC	847	35	3	0	1624	3.7	0.2	0.0	55.7

Table II: Results of harmonic analysis of the main modes of variability F$_1$ and F$_2$ extracted with the EVF method from the fortnightly abundance of Oithona similis at L4 between 1988 and 2013 and at LTER-MC between 1984 and 2013

L4				LTER-MC			
F_1		F_2		F_1		F_2	
Significant harmonics (fortnights)	Associated variance (%)	Significant harmonics (fortnights)	Associated variance (%)	Significant harmonics (fortnights)	Associated variance (%)	Significant harmonics (fortnights)	Associated variance (%)
26	**24.9**	**26**	**34.9**	**26**	**66.9**	**26**	**76.7**
113	8.9	13	19.9	338	4.5		
338	8.2	14	4.9	169	4.3		
97	7.9	17	3.6	∞	3.9		
225	7.4	15	3.1				
52	6.2	22	2.7				
85	5.1						
75	3.6						
61	3.5						
34	3.2						
42	3.0						
∞	2.8						

Periodicities with the highest associated variance are shown in bold.

$8.9 \pm 0.17 − 16.3 \pm 0.15°C$; absolute range $6.8−19.2°C$) than at LTER-MC (mean range $14.2 \pm 0.11 − 26.1 \pm 0.36°C$; absolute range, $12.4−28.9°C$) (Fig. 2a and b). In contrast, the mean range in Chl *a* recorded at L4 (mean range, $0.6 \pm 0.1 − 2.68 \pm 0.3 \mu g\,L^{-1}$; absolute range, $0.1−11.7 \mu g\,L^{-1}$) was comparable with that measured at LTER-MC (mean range, $0.6 \pm 0.1 − 3.2 \pm 0.4 \mu g\,L^{-1}$; absolute range, $0.1−12.7 \mu g\,L^{-1}$) over the same period (Fig. 2c and d).

The mean annual cycle of *O. similis* at both L4 and LTER-MC was characterized by a main peak of abundance in spring (Fig. 2e and f). At L4, the spring peak of this species was followed by either a second large peak or by a series of smaller peaks throughout summer and autumn (Fig. 2e). In contrast, at LTER-MC, the spring peak of *O. similis* was followed by a rapid decrease in abundance to very low or zero values from May−June to December (Fig. 2f).

The abundance measured at L4 over the seasonal cycle was much higher than that measured at LTER-MC. Even during autumn and winter when it declined to a minimum at both sites, values at L4 remained >100 Ind. m^{-3}, whereas at LTER-MC the abundance dropped to <3 Ind. m^{-3} (Fig. 2e and f). The inter-annual variability of *O. similis* abundance was more pronounced in correspondence to the spring peak and low or negligible during the rest of the seasonal cycle at both sites (Fig. 2e and f). The spring peak took place at $\sim 12.5°C$ at L4 and at $\sim 16.5°C$ at LTER-MC, i.e. before the annual SST maximum at both sites. In contrast, abundance increased concomitantly to the spring increase in Chl *a* and peaked at $< 2 \mu g\,L^{-1}$ at both sites. However, whereas at L4 the spring peak of *O. similis* generally coincided with that of Chl *a*, at LTER-MC the peak of this species preceded the peak of Chl *a* (Fig. 2).

Relationship of *O. similis* abundance with SST and Chl *a*

The relationship between the abundance of *O. similis* with SST and Chl *a* differed between the Atlantic and the Mediterranean sites (Fig. 3 and Table III). At L4,
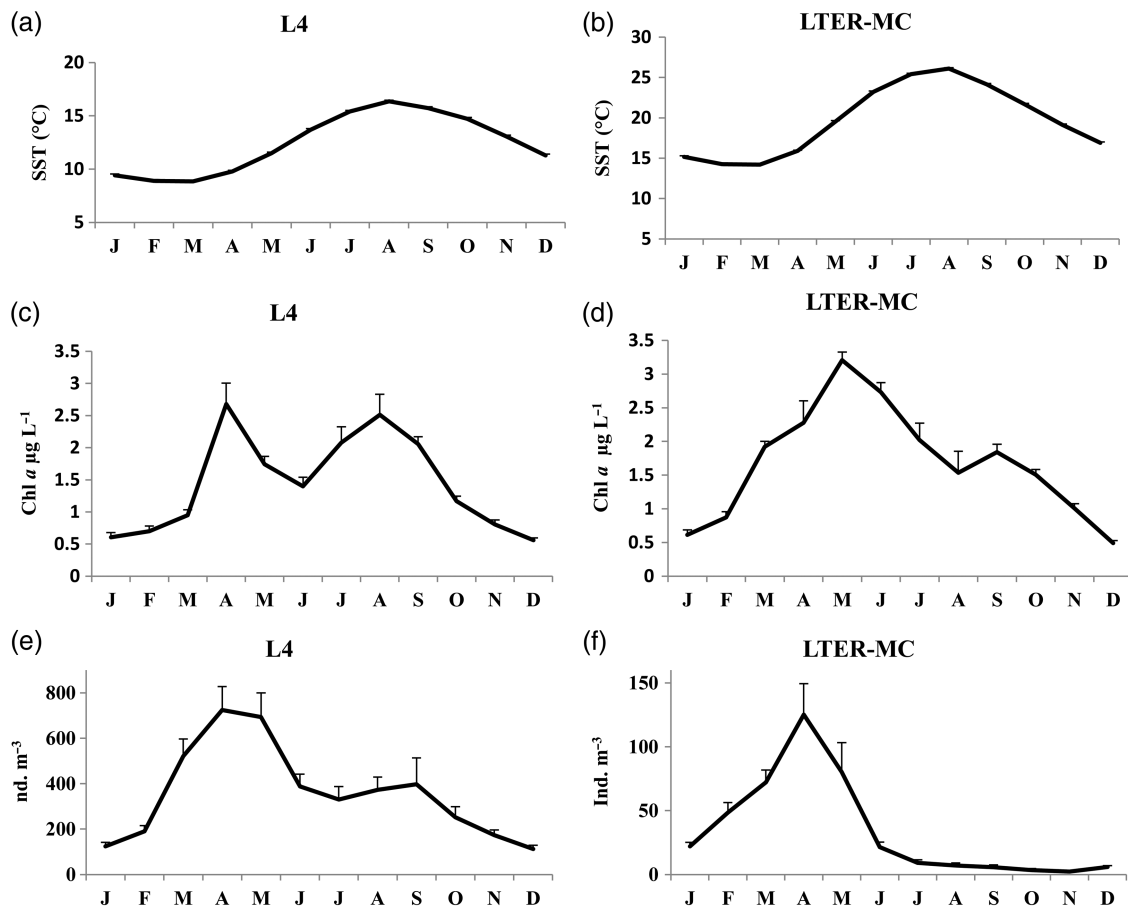
Fig. 2. Monthly mean ($\pm$ SE) temperature (SST, °C), chlorophyll a concentration (Chl a, μg L^{-1}) and *Oithona similis* abundance (Ind. m^{-3}) measured at L4 and LTER-MC between 1988 and 2013.

abundance remained relatively constant with SST, whereas at LTER-MC abundance declined with SST (Fig. 3a). The scatter of *O. similis* abundance with Chl a overlapped at both sites with no evident trend (Fig. 3b). The correlation analysis of the main modes of variability F_1 and F_2 of abundance and SST was significantly inversely correlated for LTER-MC but not for L4, indicating that higher temperature had a detrimental effect on the Mediterranean population (Table III). In addition, the F_2 of *O. similis* abundance was positively related with Chl a concentration in both the Gulf of Naples and the Western English Channel (Table III).

Environmental preferences

The results of the environmental preference analysis showed that at LTER-MC the largest significant differences between the cumulative curves of *O. similis* abundance and SST were recorded between 15 and 19°C with a maximum in the 16–17°C temperature range ($D = 0.2$; $P < 0.01$). However, no significant difference was measured at L4 indicating no temperature preference

at this site (Fig. 4a and b). No significant association was found between increasing abundance of *O. similis* and Chl a concentration at either site (Fig. 4c and d).

Phenology

Figure 5 shows the inter-annual variability of *O. similis* phenophases at L4 (Fig. 5a) and LTER-MC (Fig. 5b). The start, the middle and the end of the season took place on average (mean $\pm$ SE) on Day 104 ($\pm$ 4), 146 ($\pm$ 5), 223 ($\pm$ 7) at L4 and on Day 69 ($\pm$ 5), 99 ($\pm$ 6), 124 ($\pm$ 6) at LTER-MC, respectively. Hence, at LTER-MC these phases occurred on average 35, 47 and 99 days earlier than at L4.

The duration of the season of *O. similis* at L4 (mean $\pm$ SE, 119 $\pm$ 7 days) was approximately double than at LTER-MC (mean $\pm$ SE, 53 $\pm$ 4 days) (Fig. 6). Since *O. similis* has peak abundance at both L4 and LTER-MC during spring, the phenological changes were compared also over the first 6 months of the year. The results of this analysis showed that the timing of the spring peak in April has not changed over the years at either site occurring on average ~2 weeks earlier at LTER-MC (mean $\pm$ SE, Day
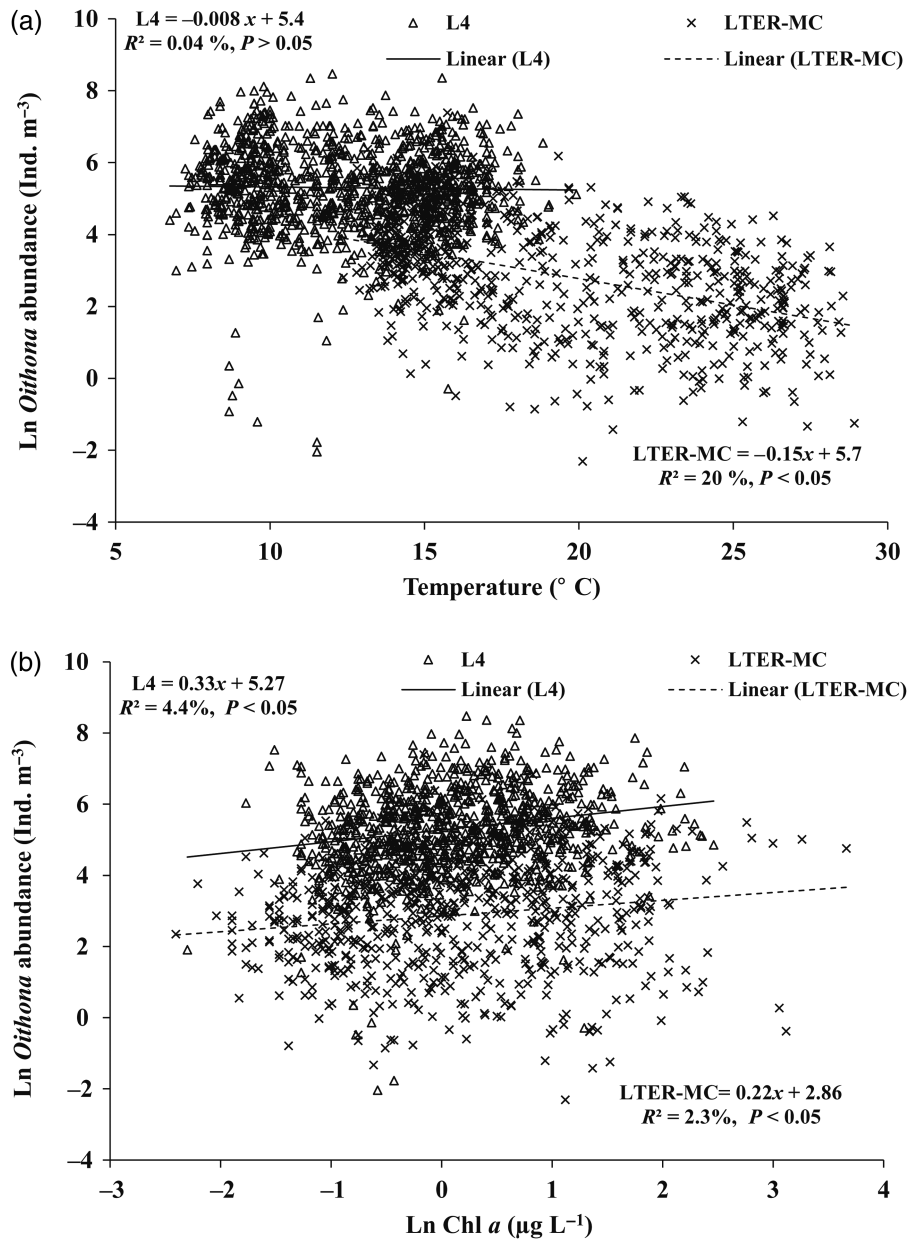
Fig 3. Scatterplots of the combined Ln abundance of *Oithona similis* (Ln, Ind. m^{-3}) versus temperature (SST, °C) and Ln chlorophyll *a* (Chl *a*, μg L^{-1}) at L4 (1988–2013) and LTER-MC (1988–2013). The continuous and broken lines are the fitted regression models.

101 ± 6) than at L4 (mean ± SE, Day 114 ± 5). However, the duration of the spring cycle at LTER-MC (mean ± SE, 47 ± 2.7 days) and L4 (45 ± 2.5 days) was similar.

At LTER-MC, the duration of the season was characterized by a significant negative trend between 1995 and 2013 ($n = 18$; $r = -0.51$; $P = 0.029$), suggesting that the seasonal cycle of this species has progressively shortened over the past 18 years (Fig. 6). At this site, the start ($N = 21$; $r = 0.46$; $P = 0.036$) and the middle ($N = 22$; $r = 0.46$; $P = 0.030$) of the season have been significantly delayed whereas the end of the season ($N = 22$; $r = 0.23$; $P = 0.34$) has not changed. This indicates that the duration of the seasonal cycle has shortened as a result of a progressive delay in the increase of the spring population. A negative significant correlation was also recorded between the anomalies of the duration of the season and the anomalies of SST at LTER-MC ($n = 22$; $r = -0.6$; $P < 0.05$), indicating that the cycle of *O. similis* at this site was shorter in warmer years (Fig. 7). Neither the duration of the season nor the day of the spring peak was correlated to Chl *a* concentration at either of the two sites (data not shown). In contrast, no significant

Table III: Results of correlation analysis between the main modes of variability F_1 *and* F_2 *of Oithona similis abundance (Ind. m^{-3}), temperature (SST, °C) and chlorophyll* a *(Chl* a*, mg m^{-3})*

	Oithona similis (F_1)				Oithona similis (F_2)			
	R	P	df*		R	P	df*	N
L4				L4				
SST (F_1)	0.00	n.s.	98	SST (F_2)	0.02	n.s.	143	676
Chl a (F_1)	0.22	n.s.	64	Chl a (F_2)	0.51	<0.001	121	546
LTER-MC				LTER-MC				
SST (F_1)	−0.56	<0.001	91	SST (F_2)	−0.54	<0.001	106	650
Chl a (F_1)	0.31	n.s.	38	Chl a (F_2)	0.32	<0.001	125	624

The Pearson correlation coefficient (*R*), the number of observations (*N*) and the number of degrees of freedom corrected for autocorrelation (*df**) are also shown.
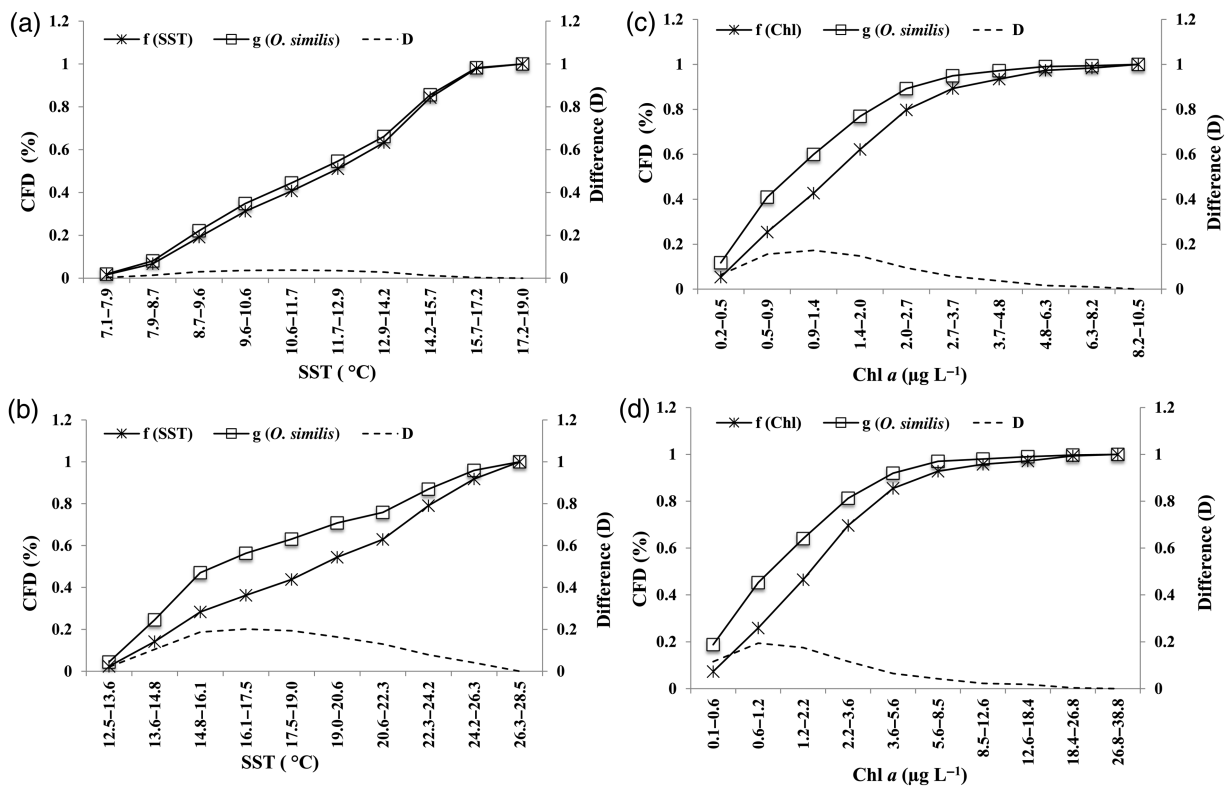

Fig. 4. Plot of *Oithona similis* abundance as cumulative frequency distribution (CFD, %) versus temperature (SST, °C) and chlorophyll *a* (Chl *a*, μg L^{-1}) intervals at L4 (**a**, **c**) and LTER-MC (**b**, **d**) between 1988 and 2013. The dashed line is the difference between the two curves.

phenological changes were detected for *O. similis* at L4 over the period of investigation.

DISCUSSION

### Temporal changes in *Oithona similis* abundance at L4 and LTER-MC

The main mode of temporal variability typifying the abundance of *O. similis* was represented by the seasonal cycle at both the Atlantic (L4) and the Mediterranean (LTER-MC) sites. Despite such similarity, the pattern of abundance differed substantially between the two locations. The consistent unimodal occurrence of *O. similis* we observed at LTER-MC in spring contrasted with the more variable occurrence and persistence at L4 between spring and autumn. The peak of abundance of *O. similis* spring at LTER-MC in the Tyrrhenian Sea is consistent with data for the rest of the Mediterranean (e.g. Siokou-Frangou *et al.*, 2010; Mazzocchi *et al.*, 2014), including the Gulf of Trieste in the Adriatic Sea (V. Tirelli, personal communication), whereas the mean bimodal
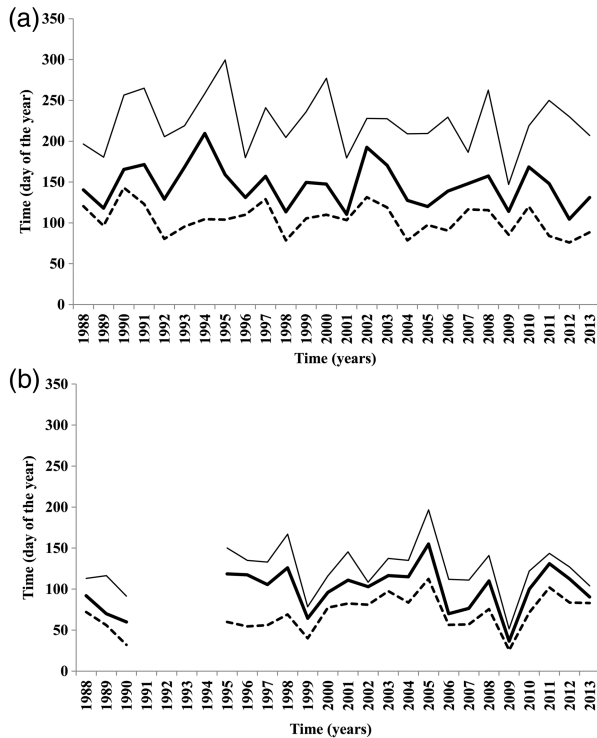
Fig 5. Phenology of *Oithona similis* at (**a**) L4 and (**b**) LTER-MC between 1988 and 2013. The curves represent the three phenophases: the start of the season (dashed line), the middle of the season (bold line) and end of the season (continuous line).
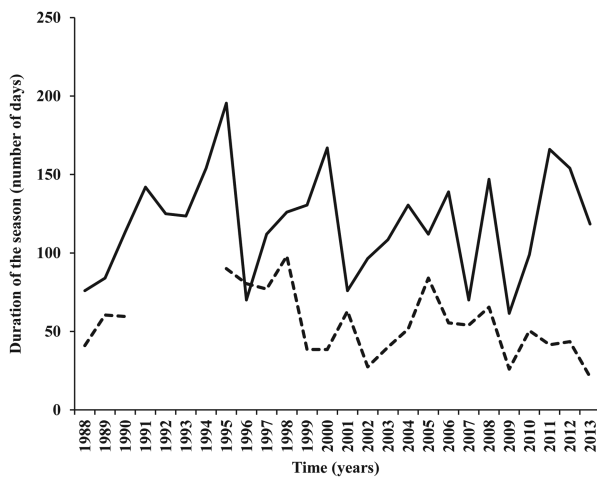
Fig. 6. Duration of *Oithona similis* seasonal cycle at L4 (continuous line) and at LTER-MC (dashed line) between 1988 and 2013.

distribution we found for this species at L4 is similar to that for total zooplankton measured at this site by Eloire *et al.* (Eloire *et al.*, 2010). The greater regularity in the annual abundance of *O. similis* we report for the Mediterranean site was substantiated by the higher variance associated with the 12-month periodicity at LTER-MC compared with that at L4. Overall, the
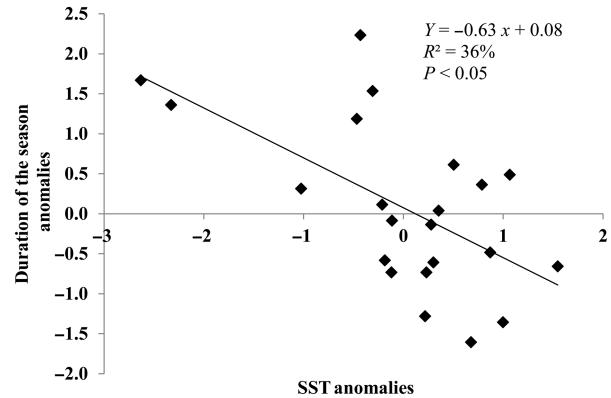
Fig. 7. Scatter plot of annual anomalies of the duration of the seasonal cycle of *Oithona similis* versus temperature (SST) anomalies at LTER-MC between 1988 and 2013. The fitted line represents the linear regression.

unimodal peak of abundance and the virtual disappearance of *O. similis* at LTER-MC during summer/autumn contrast strongly with the persistence and multimodal occurrence of this species at L4 pointing to fundamental differences in the drivers of change in the population within the two coastal systems.

O. similis **abundance and Chl** *a*

The positive significant relationship we found between the abundance of *O. similis* and Chl *a* suggests that the seasonal changes in occurrence at L4 and LTER-MC were partly due to prey availability. The spring increase did take place, at both sites, concomitantly with the increase in Chl *a*, but at a relatively constant temperature suggesting that population growth at this time was mainly promoted by increase in food resources. Moreover, at L4 the peak of abundance in spring and summer/autumn coincided with that of the Chl *a*, suggesting that at this site copepod growth was more closely coupled with prey concentration. The relationship we report between *O. similis* abundance and Chl *a* supports previous findings that, despite being numerically abundant in oligotrophic regions, this species reaches highest abundance in eutrophic conditions (Castellani *et al.*, 2007; Mazzocchi *et al.*, 2014).

Oithona similis peaked before the Chl *a* spring maximum at LTER-MC and reached highest abundance at relatively low Chl *a* concentration (i.e. $<2 \ \mu g \ L^{-1}$) at both sites suggesting that high population growth could be sustained by low prey availability. This finding is not surprising given the ability of *O. similis* to exploit a wide range of prey sizes and types and due to its relatively low metabolic rate, which allows it to prosper at food concentrations that would be limiting for other copepod species

(Gonzalez and Smetacek, 1994; Nakamura and Turner, 1997; Castellani *et al.*, 2005a, b). In this study, Chl *a* was used as a proxy for copepod prey availability as this variable has been consistently and regularly measured at both L4 and LTER-MC over the course of the time series, unlike microplankton community composition (Ribera d'Alcalà *et al.*, 2004; Widdicombe *et al.*, 2010). It could be argued that Chl *a* is not a good proxy for prey availability for *O. similis* as this species feeds preferentially on microzooplankton and other motile prey such as phyto-flagellates and dinoflagellates. Nevertheless, oithonids are also known to prey on non-motile phytoplankton, such as diatoms, when other food sources are scarce (Castellani *et al.*, 2005a; Pond and Ward, 2011). Moreover, some studies have found a good correlation between the fecundity of *O. similis* and Chl *a* (Ward and Hirst, 2007) suggesting that this parameter can represent a good proxy of food availability. Phyto-flagellates are very abundant at both L4 (Widdicombe *et al.*, 2010) and LTER-MC (Ribera d'Alcalà *et al.*, 2004) throughout the year and, therefore, these organisms can account for a considerable proportion of the Chl *a* concentration. Moreover, the pattern of phyto-flagellate abundance at both of these sites is similar to that of their main microzooplankton grazers, the ciliates (Ribera d'Alcalà *et al.*, 2004; Widdicombe *et al.*, 2010). *Oithona similis* has been maintained in the laboratory over multiple generations on a monoculture of the phyto-flagellate *Rhinomonas reticulata* (C. Castellani, unpublished data) and on a mixed flagellate diet (Sabatini and Kiørboe, 1994 and references therein) hence flagellates can sustain both growth and reproduction in this species. Moreover, studies investigating feeding preferences and energy requirements by *O. similis* have indicated that microzooplankton alone would not be sufficient to sustain reproduction in this species (Castellani *et al.*, 2005b). Since both flagellates and ciliates represent main food sources for *O. similis*, we conclude that Chl *a* in our study was a good proxy for prey availability.

O. similis abundance and mortality

Our results suggest that, although important for sustaining initial population increase, prey abundance was probably not the main factor limiting the occurrence of *O. similis* after spring, particularly at the Mediterranean site. At LTER-MC, the population declined sharply at the beginning of summer at Chl *a* concentrations >2 μg L^{-1}, which in contrast supported a relatively high *O. similis* abundance at L4. In temperate latitudes, predation mortality can play an important role in determining observed annual changes of zooplankton abundance particularly during summer when copepod predator number increases (Cushing, 1975; Ohman, 1986; Steele and Henderson, 1995; Daewel *et al.*, 2014). Given the limited resolution of the life stage composition of the population of *O. similis* in our analysis, we did not investigate in any detail the mortality rate and the impact of predation on this species. Although it has been argued that predation may represent a mortality source particularly for the younger life stages of *Oithona* spp. (Ussing, 1938; Castellani *et al.*, 2007), its impact on the abundance of this genus is generally considered low compared with other co-occurring copepod taxa (Logerwell and Ohman, 1999; Eiane and Ohman, 2004). For instance, Eiane and Ohman (Eiane and Ohman, 2004) showed that *O. similis* suffers lower mortality rates than *Calanus finmarchicus* and *Pseudocalanus elongatus*. Their smaller size, higher transparency, rapid escape response and reduced motion make *Oithona* spp. less conspicuous and elusive to both tactile and visual predators (Paffenhöfer, 1993; Paffenhöfer and Mazzocchi, 2002). Nevertheless, despite *O. similis*'s ability to minimize its predation mortality, we cannot exclude that their decline in abundance was partly due to predation.

O. similis abundance and SST

One of the main differences between the two sites was in the annual thermal range which was warmer and wider at LTER-MC (i.e. 12.4–28.9°C) and cooler and narrower at L4 (i.e. 6.8–19.2°C). Our study found that the abundance of *O. similis* was negatively correlated with SST only at LTER-MC, suggesting that the higher temperatures represented one of the main causes for the decrease and lower abundance of this species after spring at the Mediterranean site compared with the Atlantic site. The decline in *O. similis* abundance at SST >16.5°C in our study concurs with findings by Mazzocchi *et al.* (Mazzocchi *et al.*, 2014) who reported higher abundances of *O. similis* females between 0.3 and 17.3 Ind. m^{-3} in different areas of the Mediterranean basin in spring at mean temperatures below $\sim$17°C compared with 0.01–1.2 Ind. m^{-3} in autumn when the temperature was higher. Interestingly, the study by Hidalgo and Escribano (Hidalgo and Escribano, 2001) also showed that abundance of *O. similis* at a station off northern Chile declined sharply at SST >16.7°C as a result of an El Niño event which caused a warming of the water but no change in Chl *a* concentration. The abundance of *O. similis* at LTER-MC and L4 largely overlapped over the common temperature range and reached a minimum after $\sim$19°C. However, at LTER-MC, *O. similis* on average reached a maximum abundance at $\sim$16.5°C and had a temperature optimum between 15 and 19°C, whereas at L4 it peaked at $\sim$12.5°C showing no thermal optimum. It is noteworthy that the temperature at which *O. similis*

reached its maximum at LTER-MC corresponds to the mean annual maximum temperature (i.e. $16.3 \pm 0.15°C$) measured at L4. Thus, the lack of a temperature optimum for *O. similis* at L4 is probably due to the fact that, at this site, maximum water temperature seldom exceeded 19°C and, therefore, this species experienced optimal thermal conditions throughout the year. Therefore, we conclude that SST >19°C limited the persistence of the *O. similis* population at the LTER-MC site.

Our analysis also revealed a decreasing trend in abundance at LTER-MC and an increasing trend at L4 over the course of the time series. The negative correlation we found between *O. similis* abundance and SST at LTER-MC suggests that temperature increase might have been responsible for its long-term decline at this site. Although we detected no overall long-term change in SST at LTER-MC, analysis of the fortnightly data showed that, over the past 25 years, SST has increased between April and June at this site. In addition, the abundance of *O. similis* at LTER-MC has decreased significantly during June and this decline was correlated with the increase in SST from 14°C to up to 21.7°C during May. The L4 site has also undergone a temperature warming, which has resulted in an increase of ~0.88°C above the long-term average, consistent with rises reported across the UK shelf seas (Southward *et al.*, 2005; MCCIP, 2008; Smyth *et al.*, 2010). Similar to the LTER-MC site, the warming at L4 has taken place mainly during spring/summer (Mackas *et al.*, 2012). However, as already mentioned above, despite the warming trend, SST at L4 has remained within the thermal optimum of *O. similis*. Hence, it is likely that temperature increases in excess of 20°C resulted in a decline of *O. similis* at LTER-MC, whereas increases at L4 within the optimal range of this species promoted an increase in its abundance.

In their study, Eloire *et al.* (Eloire *et al.*, 2010) found no evidence of any long-term change in the abundance of *O. similis* at L4. However, the time series analyzed by Eloire *et al.* (Eloire *et al.*, 2010) was 6 years shorter than that analyzed in the present study. In addition, the EVF and harmonic analysis we used in this study represent very sensitive tools to investigate trends and periodicity in time series. Therefore, it is possible that the statistical approach we used resolved existing trends more accurately than the simple linear regression analysis employed by Eloire *et al.* (Eloire *et al.*, 2010).

Differences in *O. similis* phenology at L4 and LTER-MC

The timing of the spring peak occurred, on average, 2 weeks earlier at LTER-MC probably as a result of the warmer ambient conditions at this site. However, the timing of the peak of *O. similis* has not changed over the time series and was not correlated to changes in SST either at L4 or LTER-MC suggesting that the warming reported for these sites has had no effect on this phenological trait. Edwards and Richardson (Edwards and Richardson, 2004) found that, over the past 45 years, the spring peak of a number of zooplankton species in the central North Sea has shifted earlier in the year as a result of a long-term warming trend. Moreover, using the dataset of Edwards and Richardson (Edwards and Richardson, 2004), Mackas *et al.* (Mackas *et al.*, 2012) showed that the peak of abundance of *O. similis* occurred earlier in years with warmer spring months (i.e. March–May). In contrast, Mackas *et al.* (Mackas *et al.*, 2012) found that at L4 the association between the earlier peak timing with warmer temperature for most of the dominant zooplankton species including *O. similis* was weak (i.e. $r^2 = 0.08$). Hence, the lack of correlation between the timing of the spring peak of *O. similis* and SST we report at L4 concurs with findings of Mackas *et al.* (Mackas *et al.*, 2012) at this site. It is possible that the discrepancy in the timing of *O. similis* from the L4 site and the North Sea may be due to differences in the length and spatial coverage of these two time series, that is 45 years and basin scale in the North Sea and 25 years and single station based at L4 (Edwards and Richardson, 2004; Mackas *et al.*, 2012). Nevertheless, the reason for such difference is currently unclear and warrants further investigation.

The increase of *O. similis* abundance at L4 started later but adults and late juveniles persisted much longer than at LTER-MC. At L4, in fact, the duration of the season of *O. similis* was approximately twice as long as LTER-MC due to the persistence of this species in summer. However, when comparing the first 6 months of the year, the duration of the spring cycle was similar at the two sites. At LTER-MC, the duration of the season of *O. similis* has significantly shortened over the past 18 years (i.e. since 1995). The positive temporal trend we found for the start and the middle of the season indicates that the shortening of the cycle has partly occurred as a result of a progressive delay in the increase of the spring population. Given the cooling trend, we reported for LTER-MC between January and March, it is possible that a decrease in temperature at the beginning of the year resulted in slower increase in the abundance of *O. similis* at the beginning of its seasonal cycle. Furthermore, the negative correlation we found at LTER-MC between the duration of the season and SST suggests that temperature increase may have negatively affected the increase of *O. similis* during summer. Mackas *et al.* (Mackas *et al.*, 2012) argued that for spring-early summer copepod species such as *O. similis*, one important effect of the warming at the

LTER-MC and L4 site has been to truncate the duration of their annual population peak. Our study found no evidence of long-term changes for the end of the season of this species at LTER-MC. However, the fact that the abundance at the beginning of June was negatively correlated to temperature warming above 20°C in May suggests that this species has been declining at the end of its seasonal cycle at the Mediterranean site as a result of warming.

Effect of SST on *O. similis* abundance and spatial distribution

Our interest in the relationship between *O. similis* abundance with ambient temperature was motivated by contrasting reports in the literature regarding the cosmopolitan nature of this small copepod species. Despite widespread belief that *O. similis* can be found virtually everywhere in the pelagic realm, evidence suggests that it is generally more abundant at boreo-arctic and temperate latitudes (Nielsen and Sabatini, 1996; Castellani *et al.*, 2007; Dvoretsky and Dvoretsky, 2009; Weydmann *et al.*, 2014) compared with tropical latitudes where its presence is doubtful.

In our study, the abundance of *O. similis* at L4 was on average 10 times higher than that measured at LTER-MC site. The difference in abundance we report between these two sites was not due to sampling methodology since the same sampling method was used at both stations. The 200 μm mesh size net we used in this study would have sampled mainly adults and late copepodite stages and underestimated the total *O. similis* population (Calbet *et al.*, 2001). Nevertheless, mean annual abundances in the range between 35 Ind. m^{-3} at LTER-MC and 369 Ind. m^{-3} at L4 are comparable with abundances measured by other investigators using a similar net mesh size and sampling depth. Gislason and Astthorsson (Gislason and Astthorsson, 2004) reported abundances of between 60 and 211 Ind. m^{-3} (i.e. estimated from their 301–10 566 Ind. m^{-2} and a sampling depth of 50 m) sampling around Iceland during May with a 200 μm mesh size net vertically hauled to the surface. Dvoretsky and Dvoretsky (Dvoretsky and Dvoretsky, 2009) reported population abundances of *O. similis* (excluding nauplii) ranging from 110 to 560 Ind. m^{-3} (mean ± SD, 208 ± 19 Ind. m^{-3}) sampling with a 168 μm mesh size net at depth of 100 m in the Barents Sea between April and August at SST ranging from 1.5 to 8°C.

O. similis was not found in the Sargasso Sea (Deevey, 1971; Deevey and Brooks, 1977) and off Bermuda (Paffenhöfer and Mazzocchi, 2003). However, this species has been reported at tropical latitudes in the South China Sea (Hwang *et al.*, 2007), in coastal waters of Malaysia at temperatures between 28.8 and 29.8°C (Johan *et al.*, 2013), and in the Arabian Sea (Jose *et al.*, 2014). The main diagnostic characters (i.e. the number of spines on the exopodite of the swimming legs P1–P4, Nishida, 1985) reported by Jose *et al.* (Jose *et al.*, 2014) for the *O. similis* specimens in their samples differ from that published by authorities on the taxonomy of this species (Nishida, 1985). It is possible that the zooplankton studies in tropical areas misidentified *O. similis* with other species.

In our study, *O. similis* was found at LTER-MC at temperatures up to 28.9°C, but in very low number <1 Ind. m^{-3} (i.e. 0.29 Ind. m^{-3}). The low abundances we measured at LTER-MC at temperatures >19°C are similar to those reported in the literature for sub-tropical and tropical areas (Hwang *et al.*, 2007; Johan *et al.*, 2013) and much lower than abundances measured from arctic to cold temperate waters including L4 (Gislason and Astthorsson, 2004; Dvoretsky and Dvoretsky, 2009). These observations suggest that *O. similis* can and does probably occur in tropical waters. However, given the possibility of misidentification with congeneric species, its presence particularly in tropical Atlantic waters remains to be substantiated by further taxonomic verification. Following the above considerations, the widespread geographical distribution of *O. similis* also raises the question of whether copepods from different basins and latitudes really belong to the same species or form a species-complex characterized by the same/similar morphology but different genetic makeup (i.e. cryptic species) and different physiological adaptations. The similarity we found in the abundance of *O. similis*, particularly in the upper thermal range common to the two sites, would suggest that the population from LTER-MC and L4 responds in a similar way to temperature.

The decrease in abundance and low concentration at ambient temperatures >16.5°C at LTER-MC and at lower latitudes may be the result of the higher energy expenditure at these higher temperatures. The basal metabolic rate of *O. similis* and other poikilotherms generally increases with temperature up to a maximum after which the organism dies (Cossins and Bowler, 1987; Castellani *et al.*, 2005b). The successful performance of an organism and its population persistence depends on the balance between the energy allocated to growth and reproduction versus energy losses due to respiration. Increase in metabolic cost for basic organismal maintenance as a result of temperature increase means that less of the energy ingested or stored by the copepod can be allocated to reproduction and growth (e.g. Alcaraz *et al.*, 2014). Hence, it is possible that lower population abundance of *O. similis* at warmer latitudes is the result of a decrease in the reproduction rates of copepod exposed to temperature exceeding the optimum range for the species. The thermal optimum and upper thermal limit we report for *O. similis* in this study provide only information on the temperature that affects the adults and late copepodite stages but not

the earliest life stages whose sensitivity to temperature may differ.

CONCLUSIONS

Overall, our study provides insights into the upper thermal limits of *O. similis* and stresses the importance of studying the abundance and phenology of copepod species at different latitudes and over a long time scale for a better understanding of their ecological traits. Our results have important implications for the ecology and biogeography of *O. similis* particularly under a global-warming scenario. Further morphological and molecular taxonomic verification is required to clarify whether *O. similis* can be found in the tropical Atlantic and whether temperature increase resulting from global warming will affect the biogeography of this species.

DATA ARCHIVING

The L4 time series data used in the present study are archived with the British Oceanographic Data Center, BODC, http://www.bodc.ac.uk/. The LTER-MC time series data are archived at Stazione Zoologica Anton Dohrn, and in Pangaea from 1984 to 2006.

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