

Temporal patterns of the calanoid copepod community in Veliko Jezero, an isolated marine lake (South Adriatic Sea): links to a larger-scale climate changes

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(Received 29 September 2014; accepted 23 January 2015; first published online 29 June 2015)

We compiled and analysed a long-term calanoid community data set (1952–2009) with respect to environmental variations in nearly closed seawater lake Veliko Jezero (South Adriatic Sea). Changes in hydrographic properties were influenced by deepening and broadening the channel between Veliko Jezero and the sea in the early 1960s, which was in particular reflected by increasing salinity. Calanoid abundance displayed high intra- and inter-annual fluctuations but lacked any regular and recurrent pattern. Calanoids in the lake comprised 22 coastal and estuarine species, with five of them present over the entire study period (*Calanus helgolandicus* (Claus, 1863), *Paracalanus parvus* (Claus, 1863), *Centropages kroyeri* Giesbrecht, 1893, *Isias clavipes* Boeck, *Acartia (Acartiura) clausi* Giesbrecht, 1889). Four sample groups were identified by cluster analysis, with the highest degree of dissimilarity between samples from the 1950s and those from the 1990s and onwards. Observed changes – low densities in early 1980s; a shift in the dominant species; reduction and, finally, disappearance of *Pseudocalanus elongatus* (Boeck); increases in *Paracalanus parvus* and *Diaixis pygmaea* (Scott T., 1894) – can be associated with synchronous changes across trophic levels that have occurred in other European seas. The results presented here underline the importance of long-term studies of semi-closed marine lakes and lagoons, as these are particularly sensitive to global climatic changes.

Keywords: calanoid copepods; Mediterranean Sea; long-term dynamics; Adriatic Sea; seawater lake

Introduction

Copepods constitute the most important component of the mesozooplankton in Mediterranean coastal waters, where they often account for over 80–90% of total zooplankton biomass. This is mainly due to their ability to adapt to fluctuating environments and maintain a stable standing stock, even in the presence of variable food sources (Mazzocchi and Ribera D'Alcalà 1995). They also play a key role in the diet of many juvenile fish and thus are responsible for transferring phytoplankton carbon to higher trophic levels occupied by fish, birds, and marine mammals (Bonnet et al. 2005).

Zooplankton, especially copepods, are sensitive indicators of the state of pelagic ecosystems (Landry et al. 2001). Retrospective analyses of historically collected zooplankton data sets have provided useful information on the response of ecosystems to climatic and environmental changes over various spatio-temporal scales

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(e.g. Perry et al. 2004). Long-term trends in zooplankton abundance have been documented in a variety of systems and are closely related to long-term changes in environmental parameters, with climatological changes often being the driving force. Similar long-term changes in biological components have been reported for all Mediterranean seas (e.g. the Adriatic, Aegean and Black Sea). These include blooms of phytoplankton and jellyfish in the 1980s; extremely low net-zooplankton abundance in the same period; a dramatic decline in anchovy biomass; a break-point in biological interactions in 1990–1992; and an inverted pattern of phytoplankton and net-zooplankton composition in 1996–1997 (Baranović et al. 1993; Siokou-Frangou et al. 1998; Oguz 2006). Taken together, this suggests the influence of common controlling factors and thus a connection to global oceanic events (Fromentin and Planque 1996; Beaugrand et al. 2000; Hänninen et al. 2000).

Veliko Jezero (VJ), a nearly closed seawater lake on the southern Adriatic island of Mljet, offers ideal conditions for investigating zooplankton dynamics. By confining a representative plankton community, it offers the opportunity of studying ecological processes at a much larger, but still manageable, scale than otherwise would be practical in either the laboratory or in the open sea. Owing to its unique setting, VJ has long been recognized as an interesting ecological setting for investigating the structure and function of marine systems. The first systematic studies of zooplankton in this area were conducted in the early 1950s and focused on the qualitative and quantitative composition of the zooplankton community, its vertical distribution, and the biology of *Calanus helgolandicus* (Claus 1863; Vučetić 1957, 1961, 1964). After a lapse, research on the lake's plankton resumed in 1985 and has continued into the present (e.g. Kršinić and Lučić 1994; Benović et al. 2000; Malej et al. 2007; Turk et al. 2008; Miloslavić et al. 2014).

This article compiles published and unpublished records of the lake zooplankton from 1952 to 2009, with particular attention to inter-annual changes in the abundance and diversity of calanoids. The aim is to clarify the regional response of calanoid community structure to changing environmental conditions of the lake ecosystem.

Material and methods

Study site

The marine lakes of this study are on the north-western side of Mljet Island in the southern Adriatic Sea (42.77145°N, 17.36992°E). The surface area of VJ is 1.45 km² with a maximum depth of 46 m. VJ is connected to a smaller marine lake, Malo Jezero by a narrow strait (depth 0.8 m, width 2.0 m). These lakes are naturally formed karstic depressions that filled with seawater 5000–7000 years ago during the Holocene ingression (Schmidt 1993). Exchange of oligotrophic southern Adriatic water, which is influenced by incoming Ionian Sea water (Zore-Armada et al. 1991), is through the channel (depth 2.5 m, width 10 m) and is driven by tides. Up to the early 1960s the channel was shallower and narrower, which resulted in lower salinities in the lake (Buljan and Špan 1976). With the help of more or less continuous monitoring of the lake pelagial, we were able to track changes that have taken place following an increase in communication with the open sea.

The environmental and biological characteristics of VJ are defined mainly by bathymetry and its restricted communication with the open sea (Benović et al. 2000).

Recent studies show that the lake is as much as 2–3°C colder than the open sea during the winter and as much as 4°C warmer during the summer (Vilibić et al. 2010). Strong thermal stratification during summer and occasional hypoxia in bottom layers during autumn influence species distributions and interactions. Water below the thermocline (~20 m depth) is characterized by low temperature (<13°C) and high salinity (38.3 psu–38.6 psu) throughout the year. Species composition and abundance of phytoplankton is comparable to the oligotrophic open South Adriatic (Jasprica et al. 1995). Zooplankton populations in VJ show higher biomass and lower species richness than the neighbouring Adriatic. In addition to copepods, cladocerans, the chaetognath *Parasagitta setosa* Müller, 1847, pteropod *Limacina* spp., and mero-plankton larvae (Miloslavić 2012) are also numerically important. The scyphomedusa *Aurelia*, one of the most important zooplankton predators, is present in the lake all year round (Benović et al. 2000; Colombo et al. 2009).

Data collection

This study assembled all available data, both published and unpublished, on copepod composition and abundance in the lake. In total, 66 samples were taken at the deepest part of the lake (Table 1, Figure 1) by vertical hauls during daylight. These were fixed immediately with buffered formalin (3–4% final concentration). To reduce errors associated with different collection gear (mesh sizes from 333 to 125 µm), biological data included only calanoid species. Additionally, when the samples were taken in two depth layers, the average value for the entire water column was calculated.

Table 1. List of the samples used in this study. All samples were taken at the deepest part of lake.

Author	Year	Month	Sampling depth	Zooplankton net (mesh size)
Vučetić 1964	1952	II, IV, V, VI, VII, VIII, IX, XI, XII	46–0 m	Hensen (333 µm)
	1953	I, III, V, VI, VIII, IX, IX	46–0 m	
Lučić and Bender-Pojatina 1995	1985	V, VII, VIII, IX, X, XI	46–0 m	Nansen (250 µm)
	1986	I, III, IV, V	46–0 m	
Lučić unpublished	1997	IX, X, XI	46–0 m	Nansen (125 µm)
Benović et al. 2000	1998	II, III, V, VI, VII, VIII, IX, X, XI, XII	46–0 m	
	1999	I	46–0 m	
Lučić unpublished	2000	XII	46–20 m; 20–0 m	Nansen (125 µm)
	2001	I, II, III, IV, V, VI, VII, VIII, IX, X, XI, XII	46–20 m; 20–0 m	
Miloslavić 2012	2008	II, III, IV, V, VI, VII, VIII, IX, X, XI, XII	46–20 m; 20–0 m	Nansen (125 µm)
	2009	I, II	46–20 m; 20–0 m	

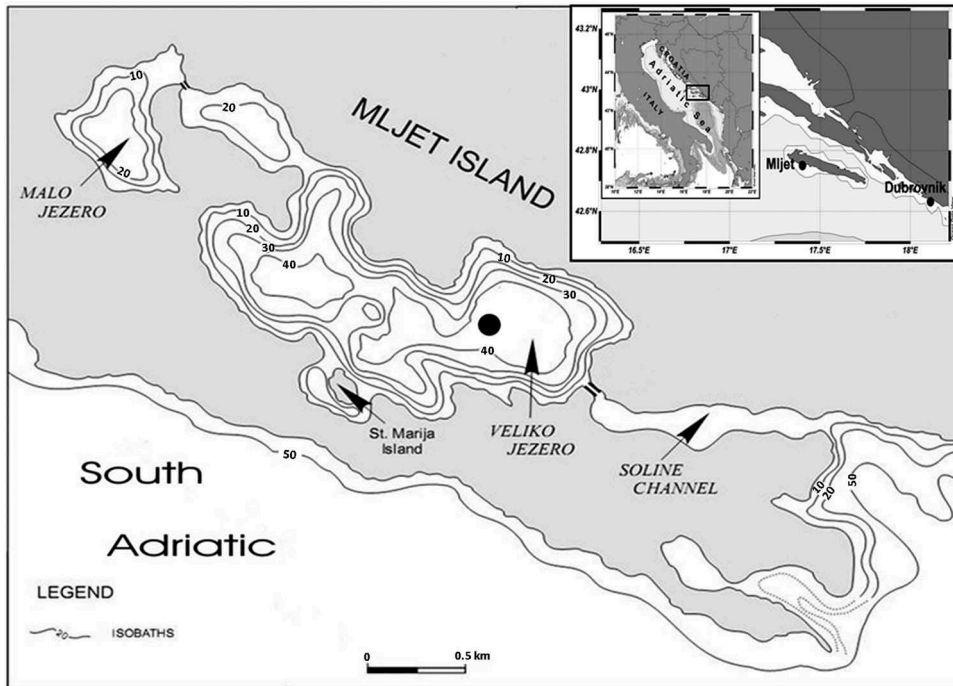


Figure 1. Study area with the sampling station.

Zooplankton abundance was expressed as number of individuals per m^3 . Temperature and salinity were recorded for each sample.

The circulation of the Mediterranean Sea is mostly forced by the winter climate (Korres et al. 2000). Thus, without complete annual data of water column temperature, only winter (January–March) sea surface temperatures (SST) were used. A long-term temperature and salinity data set was used to identify a possible correlation with copepod dynamics. All hydrographic and biological data were averaged for each month and grouped in five temporal groups: 1950s, 1980s, 1990s, early 2000s, and late 2000s.

Data analysis

An analysis of variance (ANOVA) followed by Tukey's HSD post-hoc test was used to examine whether hydrographic variables (temperature and salinity) significantly differed between decades. The difference was significant if $p < 0.05$. For univariate biodiversity measures, Margalef's species richness (d), and Shannon–Wiener diversity index (H') were calculated for each sample. The former (Margalef 1968) compares the number of taxa in a sample to the total number of organisms comprising those taxa and is given by $d = (S - 1)/\ln(N)$, where S is the number of taxa in a sample and N is the total number of individuals. The latter (Shannon and Wiener 1963) evaluates how individuals are distributed among taxa and is calculated as $H' = -\sum_i P_i \ln P_i$, where P_i is the proportion of the i -th species of the total number of individuals in the sample.

Calanoid communities were identified through cluster analysis, which groups samples based on similarities in taxon presence and abundance. Similarities between 66 samples with abundances for 22 taxa were measured by relative Euclidean distance measure using Ward's linkage method (McCune and Grace 2002). The resulting matrix was used to generate a dendrogram scaled to both percentage of information remaining and Wishart's (1969) objective function. Groups were identified by pruning to 45% retained information.

The contribution of each species to the average Bray–Curtis similarity within defined groupings was analysed using the similarity percentage procedure (SIMPER). Results were used to help interpret the faunal change responsible for the patterns of the dendrogram.

Spearman rank correlation (Zar 1996) was used to examine relationships between environmental parameters and individual metrics of zooplankton community composition or the proportional abundance of individual taxa. Copepod abundances were $\log(x + 1)$ transformed.

Univariate biodiversity measures and SIMPER analysis were done with PRIMER-5 (Clarke and Gorley 2001). Cluster analysis was performed with PC-ORD v. 5.32 (McCune and Mefford 2006) and finally the Spearman rank correlation test and ANOVA with STATISTICA v. 7.0 (StatSoft, Inc. 1997).

Results

Hydrographical state

Water column temperature ranged from 9.1°C to 19.9°C and salinity from 35.5 psu to 39.2 psu. Monthly averages of salinity and winter SST over the five study periods are shown in Figure 2. Average winter SST was lowest in the 1950s ($9.7^{\circ}\text{C} \pm 0.93$) and highest in the early 2000s (average $12.7^{\circ}\text{C} \pm 0.61$). Changes in hydrographic properties were influenced by deepening and broadening the channel between VJ and the sea in the early 1960s: from 0.6 m deep and 4.5 wide to 2.5 m deep and 10 m wide. This was reflected in average salinity: from 36.2 ± 0.58 psu in 1950s to the highest values in the 1990s and early 2000s ($38.3 \text{ psu} \pm 0.58$ and $38.3 \text{ psu} \pm 0.36$, respectively).

According to the analysis of variance ANOVA with Tukey's test, statistically significant differences were recorded between temperature and salinity values ($F = 11.428$, $p < 0.0001$; $F = 44$, $p < 0.0001$, respectively) over the study period. Results of Tukey's HSD postcomparison test, $p > 0.05$, are shown in Table 2.

Abundance, taxonomic composition, and community structure

Calanoids contributed, on average, 42% (min 4%, max 97%) of lake mesozooplankton abundance throughout the investigated period. Higher values generally were found in late winter and in spring (Figure 3). Calanoid abundance displayed high intra- and inter-annual fluctuations. Highest abundances were in the 1950s (average, 935 ± 1332 individuals per m^3), while the lowest were in the 1980s (average, 182 ± 90 individuals per m^3). Low densities of total mesozooplankton were found throughout the 1980s. Calanoids were the most abundant, contributing an average 64% of total numbers. In the early 2000s, however, calanoids were only 24% of the zooplankton in VJ, with the minimum (4%) in July.

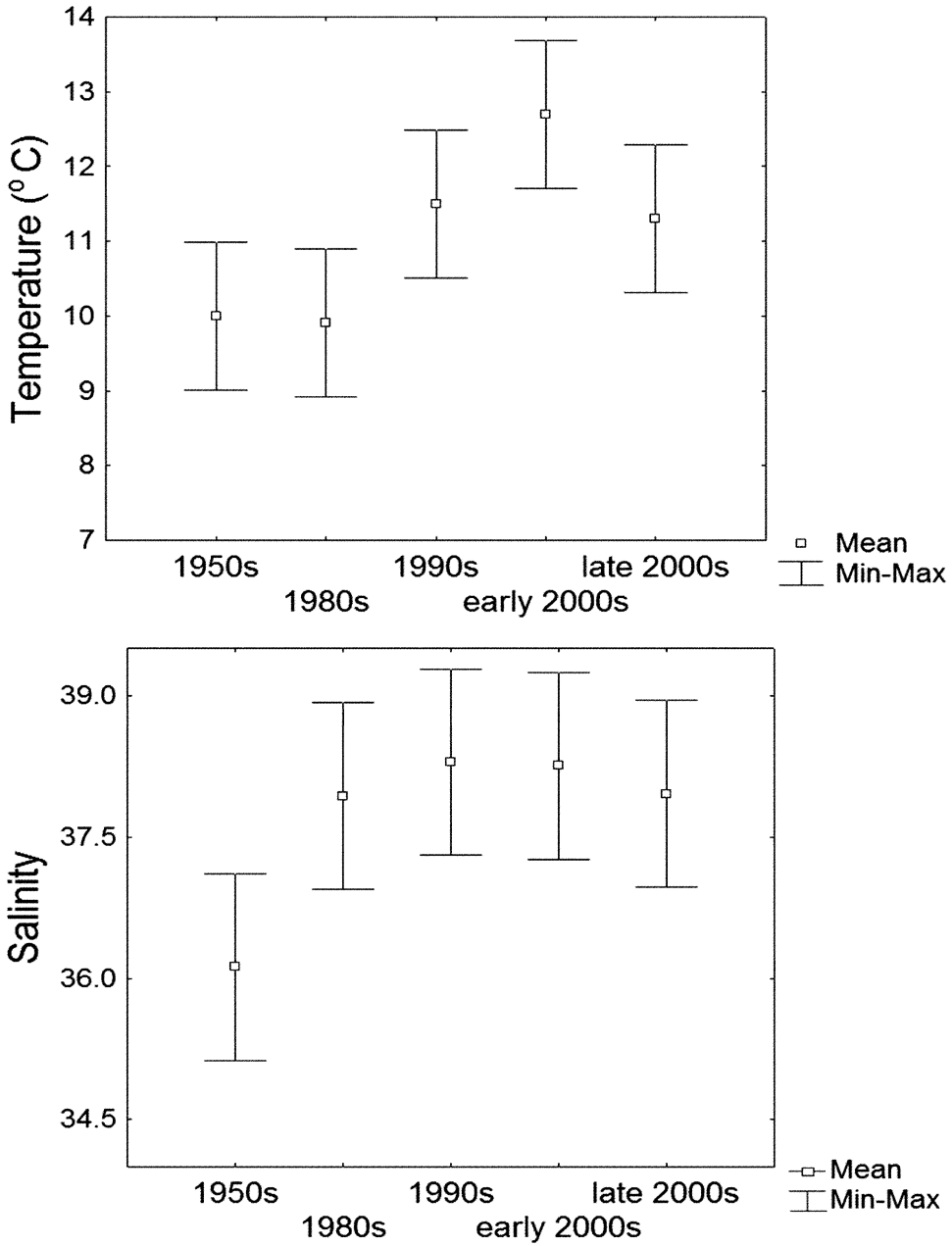


Figure 2. Seasonal and inter-annual patterns of hydrographic parameters (temperature and salinity) over the study period.

Calanoids in VJ comprised 22 coastal and estuarine species belonging to 15 genera and 10 families (Table 3). In the 1950s, only six species were found, while in the 1990s there were 19. Only five species were present over entire study period:

Table 2. Post hoc Tukey test results for differences in temperature ($n = 72$, $df = 65$) and salinity ($n = 53$, $df = 47$) between the study periods.

Temperature	1950s	1980s	1990s	Early 2000s
1950s				
1980s	0.99			
1990s	0.05	0.18		
Early 2000s	0.00**	0.00**	0.37	
Late 2000s	0.00**	0.04*	0.99	0.00**
Salinity				
1950s				
1980s	0.00**			
1990s	0.00**	0.99		
Early 2000s	0.00**	0.01*		
Late 2000s	0.00**	0.35	0.39	0.39

* $p < 0.05$; ** $p < 0.01$.

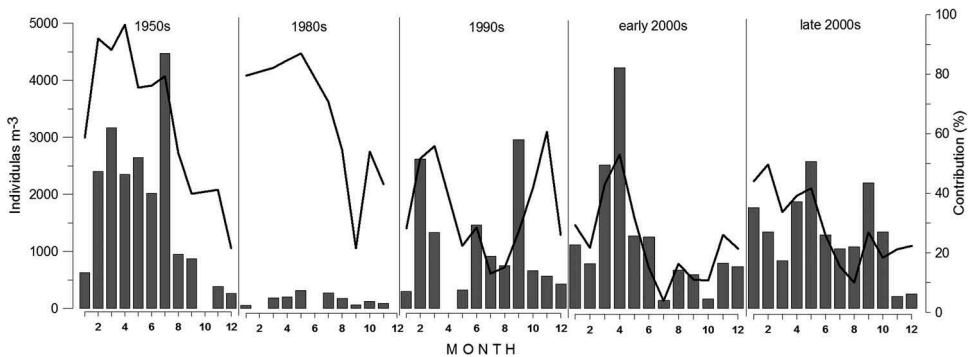


Figure 3. Seasonal and inter-annual patterns of total calanoid abundance (individuals per m^3) (left scale and bars) and their contribution (%) to total mesozooplankton abundance (right scale and line) over the study period.

Calanus helgolandicus, *Paracalanus parvus* (Claus, 1863), *Centropages kroyeri* Giesbrecht, 1893, *Isias clavipes* Boeck, 1864 and *Acartia (Acartiura) clausi* Giesbrecht, 1889. Both the Margalef's index and Shannon–Wiener diversity index were highest during the 1980s (Figure 4).

Cluster analysis identified four groups (Figure 5). Group 1 consists of samples collected in the 1950s; Group 2, the 1980s; Group 3, mostly from the 1990s and late 2000s; and Group 4, mostly from the early 2000s. The contribution of species to the groupings obtained with CLUSTER and average dissimilarity of the zooplankton communities was determined with SIMPER (Table 4). The highest degree of dissimilarity was between samples from the 1950s and those from the 1990s and onwards. In the 1950s, *Pseudocalanus elongatus* (Boeck, 1864) was the distinguishing species in the lake. In all others, *Paracalanus parvus* and *Calanus helgolandicus* were dominant. In terms of hydrography, Group 4 is characterized by higher salinity (average,

Table 3. Calanoid species found in each sampling period and their average abundance (ind. m⁻³).

	1950s	1980s	1990s	Early 2000s	Late 2000s
<i>Calanus helgolandicus</i> (Claus, 1863)	74	27	37	56	80
<i>Mesocalanus tenuicornis</i> (Dana, 1849)			18	1	
<i>Calocalanus pavo</i> (Dana, 1852)			<1		<1
<i>Calocalanus contractus</i> Farran, 1926		<1	<1	3	4
<i>Paracalanus parvus</i> (Claus, 1863)	265	98	430	377	533
<i>Paracalanus nanus</i> Sars G.O., 1925			1		<1
<i>Paracalanus denudatus</i> Sewell, 1929			2	<1	
<i>Mecinocera clausi</i> Thompson I.C., 1888			<1	<1	<1
<i>Clausocalanus arcuicornis</i> (Dana, 1849)		<1	<1		<1
<i>Clausocalanus jobei</i> Frost & Fleminger, 1968		1	3	<1	<1
<i>Clausocalanus furcatus</i> (Brady, 1883)		<1	<1	<1	<1
<i>Clausocalanus pergens</i> Farran, 1926			<1		<1
<i>Ctenocalanus vanus</i> Giesbrecht, 1888		<1	1	<1	7
<i>Pseudocalanus elongatus</i> (Boeck, 1864)	562	25			
<i>Diaixis pygmaea</i> (Scott T., 1894)		1	8	35	14
<i>Mesaiokeras hurei</i> Kršinić, 2003				37	4
<i>Centropages typicus</i> Krøyer, 1849		1	<1	<1	9
<i>Centropages kroyeri</i> Giesbrecht, 1893	13	6	11	3	9
<i>Isias clavipes</i> Boeck, 1864	2	6	18	26	10
<i>Temora stylifera</i> (Dana, 1849)		2	2	<1	1
<i>Candacia giesbrechti</i> Grice & Lawson, 1977				<1	
<i>Acartia (Acartiura) clausi</i> Giesbrecht, 1889	20	14	102	32	46

38.1 ± 0.34; min 37.4, max 38.6) and lower temperature (14.3 ± 3.19; min 7.9, max 18.4), while salinity and temperature in Group 3 were, respectively, 37.9 ± 0.37 (37.2–38.9) and 14.9 ± 2.92 (10.6–19.9). *Mesaiokeras hurei* Kršinić, 2003 contributed greatly to the observed similarity of the Group 4, while *Acartia (Acartiura) clausi* was the important species of Group 3. Table 5 collects Spearman rank correlation results for calanoids and hydrographical data.

Discussion

Different mesh sizes, sampling nets and lack of temporal continuity may affect the number of taxa and abundance of copepods taken into account in this study. Differences in abundance using 125 µm and 200 µm mesh nets showed, however, no significant difference in adult calanoid densities in 2008/2009 (Miloslavić et al. 2014). On the other hand, the smaller-mesh nets used from the 1990s onward were responsible for higher numbers of *Oithona*, which was the dominant taxon in the late 2000s (Miloslavić 2012). This might be one of the reasons for the significantly lower proportion of calanoids in total zooplankton numbers over the recent period of this study.

Despite different sampling protocols, the 1980s were characterized by extremely low abundances, both calanoid and total zooplankton. Similar changes were reported in the Gulf of Trieste: after 1986, copepod abundance doubled and average

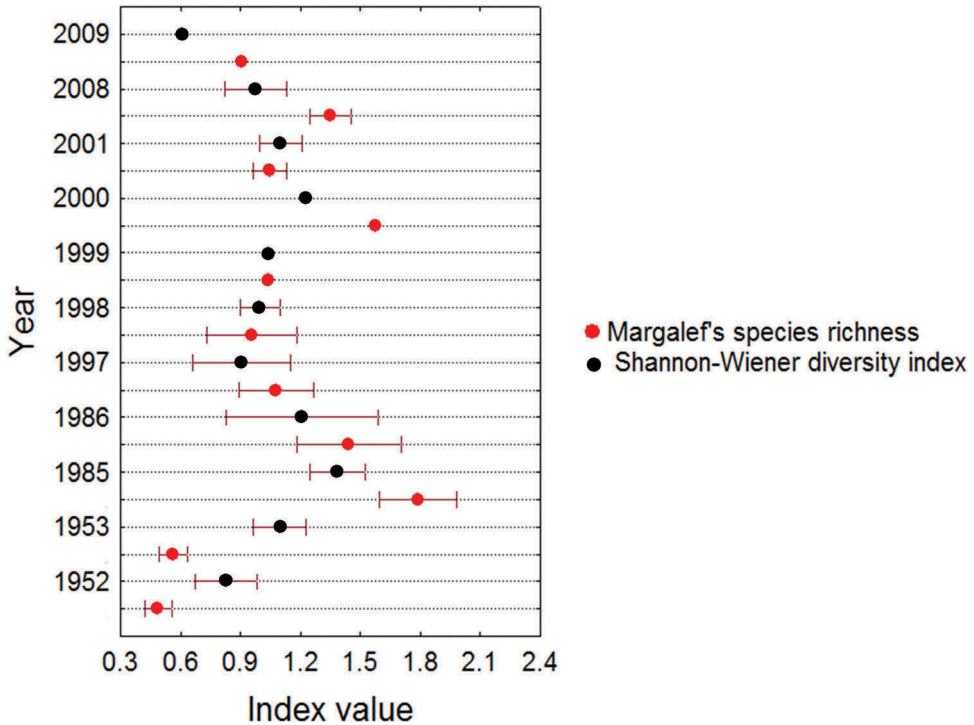


Figure 4. Mean Margalef's species richness and Shannon–Wiener diversity index values per year; 90% confidence intervals are shown.

abundance over 1987–2005 was approximately twice that of typical values from 1970 to 1980 (Conversi et al. 2009). This is related to a major change in Mediterranean surface circulation and deep-water convection (i.e. the eastern Mediterranean Transient). Changes at the end of the 1980s also have been reported for the pelagic communities of other European seas (e.g. Edwards et al. 2002; Alheit et al. 2005; Conversi et al. 2010) with resulting shifts in species phenology, reductions and increases in abundances of distinct species, shifts in dominant species, and shifts in the community structure, which suggest that local hydrography is linked to a larger-scale northern hemisphere climate processes. Although similar changes were observed in VJ, owing to the lack of the continuous data a more detailed analysis of abundance was not attempted. This limits the ability to distinguish local and global influences with any confidence.

The plankton species present in any particular coastal system reflect the exchange between local and offshore water. The VJ ecosystem has experienced a dramatic change in hydrographic conditions since the early 1960s because of increased communication resulting from stronger inflow of more saline open-sea water. These changes, in turn, have driven reorganization of the lake's zooplankton, mainly reflected by the introduction of new copepod species and higher diversity. Hence, the high species richness of the 1980s – during which period the highest Shannon–Wiener diversity index was recorded – probably resulted from the generally low abundances.

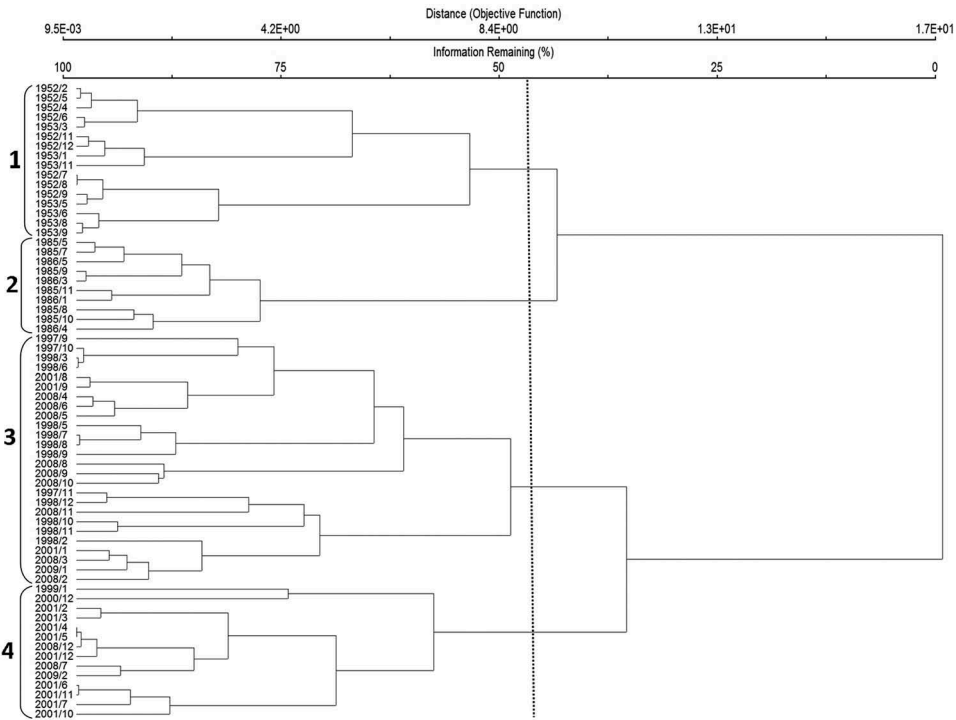


Figure 5. Dendrogram of sample units identified by cluster analysis.

Five calanoids were present in the lake over entire study period: *Calanus helgolandicus*, *Paracalanus parvus*, *Centropages kroyeri*, *Isias clavipes* and *Acartia (Acartiura) clausi*. With the exception of *C. kroyeri*, which is markedly thermophilic, these are common coastal-neritic species in the south Adriatic (Hure and Kršinić 1998) and are well adapted to fluctuating environments. Interestingly, calanoids that inhabited the lake from the 1980s onwards (e.g. *Calocalanus* spp., *Clausocalanus* spp., *Ctenocalanus vanus* Giesbrecht, 1888, and *Temora stylifera* (Dana, 1849)), remained at low densities in VJ over entire study period, even when comprising an important fraction of the copepods of the coastal Adriatic (Hure and Kršinić 1998; Vidjak et al. 2012) and Mediterranean (Siokou-Frangou 1996; Christou 1998; Ribera D'Alcalà et al. 2004) waters. In contrast, the resident population of *C. helgolandicus* maintained a consistently high share of the total calanoid community.

There was a clear shift in dominant species. In the 1950s, *Pseudocalanus elongatus* dominated the lake mesozooplankton (up to 75.6% of total numbers) with the vertical distribution mostly in bottom layers (Vučetić 1957). This species was found in the lake until the mid-1990s. Its decline after the late 1980s was recorded at larger spatial scales, from the northern Adriatic (Camatti et al. 2008; Conversi et al. 2009) to the Baltic (Hinrichsen et al. 2002). Since this is a cold water species, its reduction in abundance in the Gulf of Trieste was linked with rising SST. According to the present study, higher salinity appears to have been a dominant factor in the decrease of

Table 4. SIMPER analysis (cut-off 90%) for copepod densities per group and average percentage dissimilarity of zooplankton communities determined with the cluster dendrogram.

Group and characteristic species	Average abundance	Contribution (%)	
Group I			
<i>Pseudocalanus elongatus</i>	562	34.56	
<i>Paracalanus parvus</i>	265	29.78	
<i>Calanus helgolandicus</i>	74	26.34	
Group II			
<i>Paracalanus parvus</i>	98	22.21	
<i>Calanus helgolandicus</i>	27	17.18	
<i>Pseudocalanus elongatus</i>	25	13.93	
<i>Isias clavipes</i>	6	10.71	
<i>Centropages kroyeri</i>	6	10.46	
<i>Acartia (Acartiura) clausi</i>	14	10.45	
<i>Diaixis pygmaea</i>	1	5.15	
Group III			
<i>Paracalanus parvus</i>	484	33.12	
<i>Calanus helgolandicus</i>	54	18.82	
<i>Acartia (Acartiura) clausi</i>	85	18.16	
<i>Diaixis pygmaea</i>	12	8.85	
<i>Isias clavipes</i>	13	6.89	
<i>Centropages kroyeri</i>	11	5.85	
Group IV			
<i>Paracalanus parvus</i>	375	30.48	
<i>Calanus helgolandicus</i>	63	19.42	
<i>Mesaiokeras hurei</i>	36	14.85	
<i>Diaixis pygmaea</i>	31	13.20	
<i>Acartia (Acartiura) clausi</i>	16	9.94	
<i>Isias clavipes</i>	26	7.82	
Average dissimilarity (%)	Group II	Group III	Group IV
Group I	39.46	53.03	55.35
Group II	–	40.86	43.02
Group III	–	–	37.47
Group IV	–	–	–

P. elongatus, although global drivers (e.g. rising temperatures) cannot be excluded. It was replaced in VJ starting in the 1980s by the morphologically similar *Paracalanus parvus*. This is another suspension feeder and is capable of ingesting particles such as small single cells or diatom chains. Its rise in the 1990s also was reported in the Aegean Sea (Christou 1998) and the Gulf of Trieste (Conversi et al. 2009).

Fluctuations in coastal marine environments, due to variability and interplay of natural and anthropogenic factors, may induce diverse responses to external forcing in pelagic species and communities. The results of cluster and SIMPER analyses show strong separation of samples from the 1950s and the 1980s from recent ones. The majority of the samples collected in the early 2000s form a separate group, Group 4.

Table 5. Spearman rank correlation coefficients for associations between copepod density and depth-averaged temperature and salinity.

	Temperature	Salinity
<i>Calanus helgolandicus</i>	-0.077	-0.194
<i>Mesocalanus tenuicornis</i>	-0.105	0.251
<i>Calocalanus pavo</i>	-0.009	0.241
<i>Calocalanus contractus</i>	-0.120	0.540**
<i>Paracalanus parvus</i>	-0.219	0.224
<i>Paracalanus nanus</i>	-0.069	0.175
<i>Paracalanus denudatus</i>	-0.296*	0.043
<i>Mecinocera clausi</i>	-0.329*	0.052
<i>Clausocalanus arcuicornis</i>	-0.094	0.035
<i>Clausocalanus jobei</i>	-0.163	0.083
<i>Clausocalanus furcatus</i>	-0.222	-0.011
<i>Clausocalanus pergens</i>	-0.079	0.154
<i>Ctenocalanus vanus</i>	-0.093	0.261*
<i>Pseudocalanus elongatus</i>	-0.072	-0.709**
<i>Diaixis pygmaea</i>	0.040	0.613**
<i>Mesaiokeras hurei</i>	-0.061	0.626**
<i>Centropages typicus</i>	0.059	0.198
<i>Centropages kroyeri</i>	0.482**	-0.084
<i>Isias clavipes</i>	-0.304*	0.392**
<i>Temora stylifera</i>	0.259*	0.310*
<i>Candacia giesbrechti</i>	-0.177	-0.071
<i>Acartia (Acartiura) clausi</i>	-0.128	0.098

* $p < 0.05$; ** $p < 0.01$.

This group has a lower density of *Acartia (Acartiura) clausi* and higher densities of small calanoid species (*Diaixis pygmaea*, *Mesaiokeras hurei*) than Group 3. This may be due to slightly higher average salinity in Group 4, as both calanoids were positively correlated with salinity. In contrast, *A. (Acartiura) clausi* is an estuarine species with extremely high tolerance of low salinities (e.g. Alcaraz 1983; Pastorinho et al. 2003). Even well-defined environmental forcings, however, sometimes fail to account for observed distributions (e.g. Pinel-Alloul et al. 1990). In such cases, a weak relationship between species occurrence and abiotic environmental factors suggests that biotic factors play a fundamental role in structuring planktonic communities in terms of species composition. Although the environmental factors that determine the taxa in Groups 3 and 4 are not easily identified, it seems probable that some biological and behavioural interactions play a major role in defining these two groups.

VJ is characterized by considerable inter-annual variability and absence of a regular and recurrent pattern in the calanoid community. Nevertheless, observed changes – low densities in early 1980s; a shift in the dominant species; reduction and, finally, disappearance of *Pseudocalanus elongatus*, increases of *Paracalanus parvus* and *Diaixis pygmaea* (Scott T., 1894) – can be associated with synchronous changes across trophic levels that have occurred in other European seas. The results presented here underline the importance of long-term studies of semi-closed marine

lakes and lagoons, as these are particularly sensitive to global climatic changes. Increased tidal mixing resulting from rising sea level – itself associated with climate change – may drive greater shifts in the distribution of zooplankton populations all over the world. VJ can provide a framework for studying such changes, especially those most likely to have an impact on Mediterranean marine ecosystems.

Acknowledgements

The authors would like to thank Zoran Jurić and Marko Žarić for their help during the fieldwork. We are grateful to the Mljet National park authorities for their hospitality during fieldwork. And finally, we would like to thank the anonymous reviewers for their constructive suggestions that significantly improved this manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This study was supported by the Croatian Science Foundation [project number 6433].

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