



Gulf of Trieste: A changing ecosystem

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Received 6 February 2008; revised 22 December 2008; accepted 12 January 2009; published 26 March 2009.

[1] Understanding the impact of climate change on zooplankton populations is of major importance, as they represent the basis for higher trophic levels in the marine food web. In this study we analyze the 36-year copepod abundance time series in the Gulf of Trieste, northern Adriatic, to investigate its interannual variability, with particular attention to species trends and phenology. Following the analysis of the local winter sea surface temperature, two periods are identified: 1970–1987 and 1988–2005. These periods are characterized by ecosystem-wide changes: an approximate doubling in total copepod abundance, the arrival of a new species (*Diaixis pygmoea*), the rise (*Paracalanus parvus*, *Oncaea* spp., *Oithona* spp., and *Euterpina acutifrons*) or decline (*Pseudocalanus elongatus*, *Clausocalanus* spp.) of several taxa, and changes in the phenology in several species, with predominantly forward shifts in the timing of the maximum peak. While *Acartia clausi* remains the dominant species, there is a general trend toward smaller species in the second period. Our results also indicate the large, possibly critical, reduction in the abundance of the species *Pseudocalanus elongatus*. We hypothesize that the changes in copepod abundances and community composition in the Gulf of Trieste are related to the general warming in the sea surface temperature and associated northerly displacement of the ecosystem and to the changes in the Mediterranean circulation that began at the end of the 1980s and affected the whole basin in the following years as part of the phenomenon called the Eastern Mediterranean Transient.

Citation: Conversi, A., T. Peluso, and S. Fonda-Umani (2009), Gulf of Trieste: A changing ecosystem, *J. Geophys. Res.*, 114, C03S90, doi:10.1029/2008JC004763.

1. Introduction

[2] Worldwide, the mesozooplankton community is dominated mainly by copepods. Copepods play a key role in the diet of juvenile stages of many fish species, and thus they are responsible for transferring phytoplankton carbon to higher trophic levels, such as fish, birds, and marine mammals [Bonnet *et al.*, 2005].

[3] This role is particularly important in the northern Adriatic, as this is one of the few regions of high permanent production in the Mediterranean Sea [Buljan, 1964; Franco, 1973; Fonda-Umani *et al.*, 1992, 2004]. It is indeed also one of the most productive areas in the Mediterranean, with mesozooplankton biomass ranging as dry weight from 2.5 to 177.2 mg m⁻³ [Benovic *et al.*, 1984], as opposed to the typical oligotrophic values of 3 mg m⁻³ usually found elsewhere [Gaudy and Champalbert, 1998; Deudero and Morales-Nin, 2001].

[4] The Gulf of Trieste (Figure 1) is the northernmost section of the Adriatic Sea, with a surface area of about 600 km² [Malej and Malačić, 1995], and a volume of 9.5 km³ [Olivotti *et al.*, 1986]. It is characterized by an overall

shallowness, with maximum depth around 23 m in the southern part, and 10% of the average bottom depth being less than 10 m; and by large and variable freshwater inputs [Fonda-Umani *et al.*, 1992; Russo and Artegiani, 1996]. The main freshwater input is through the Isonzo River from the northwest coast. Hydrodynamical conditions are forced by the wind regime, characterized by strong, abrupt wind events, by the interaction with the general circulation of the Adriatic Sea, and by the seasonal alternance of stratification and mixing [Cossarini *et al.*, 2002; Cossarini and Solidoro, 2007].

[5] The copepod community in the Gulf of Trieste is characterized by a few (approximately 30) coastal and estuarine species, which in turn can exhibit high dominance. Copepods dominate in all months except for June and July, when cladocerans (especially *Penilia avirostris*) take over [Cataletto *et al.*, 1995]. In particular, the copepod *Acartia clausi* dominates most of the year, composing at some points >80% of the total biomass, followed by *P. avirostris*, which can account for >37% in summer [Fonda-Umani, 1985]. Other species of copepods like *Oithona*, *Clausocalanus*, *Temora*, *Paracalanus*, and more recently *Oncaea*, can be considered relevant [Specchi *et al.*, 1981; Fonda-Umani and Cocchietto, 1988; Fonda-Umani and Ghirardelli, 1988; Fonda-Umani *et al.*, 2005; Kamburska and Fonda-Umani, 2006].

[6] Much of our knowledge on the Gulf of Trieste mesozooplankton is owed to the monthly time series col-

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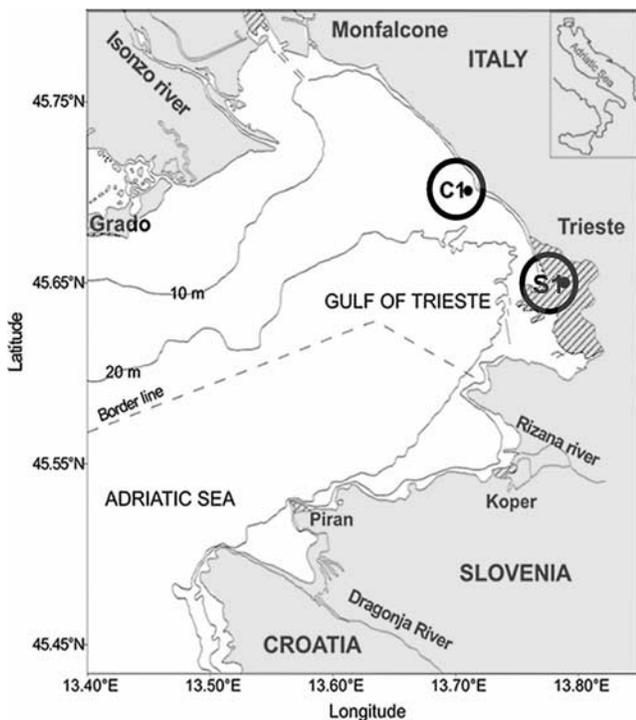


Figure 1. The Gulf of Trieste, northern Adriatic Sea showing location of the mesozooplankton sampling station (C1) and of the SST measuring site (S1).

lected at station C1 (Figure 1) since 1970. This is the longest-lasting zooplankton collection in Italy and one of the longest in the Mediterranean Sea, providing a picture, spanning more than three decades, of the mesozooplankton species composition, its diversity, and its temporal variability, at scales from intraannual to interannual.

[7] Previous studies on this time series have focused on group associations. *Cataletto et al.* [1995] found, during the first decade of monitoring (1970–1980), a regular late spring-summer appearance in a group characterized by *Acartia clausi* and *Temora longicornis*, and a regular autumn-winter appearance in a group characterized by *Temora stylifera* and *Oncaea* spp. Two main groups related to spring-summer and winter-autumn prevalence are also identified by *Kamburska and Fonda-Umani* [2006], who find several differences in patterns of abundance between 1970 and 1980 and 1986–1999 and attribute them to climate changes (North Atlantic Oscillation, El Niño/Southern Oscillation, Eastern Mediterranean Transient, sea surface temperature (SST) increase) in the northern hemisphere from 1987.

[8] Recent studies point out to the importance of linking the long-term variations of the individual species abundance to more specific endogenic factors. In particular, phenology, the study of periodic events in the life cycles of animals or plants, such as the timing of migrations and reproduction, has received definite attention as a possible indicator of climate change [*Parmesan and Yohe*, 2003; *Edwards and Richardson*, 2004; *Molinero et al.*, 2005; *Cleland et al.*, 2007].

[9] In this article, we review the interannual variations of the dominant copepod species in the Gulf of Trieste, with

particular attention to interannual changes, trends and shifts in the phenology.

[10] We begin by identifying changes in the physical system, as represented by winter SST, then test whether there are corresponding changes in the biological system, and finally in the Discussion we link these back to the interannual variations that happened at the end of the 1980s in the Ionian Sea and in the eastern Mediterranean circulation [*Roether et al.*, 1996; *Pinardi et al.*, 1997; *Malanotte-Rizzoli et al.*, 1999; *Korres et al.*, 2000; *Pinardi et al.*, 2005; *Roether et al.*, 2007].

[11] SST is used as an indicator of physical change in the ocean because organisms respond physiologically to temperature and it has been found to be important in many terrestrial phenological studies [*Hughes*, 2000]. In addition, long-term changes in SST have been found to be concurrent to widespread changes in the marine system, which range from benthos to plankton [*Kirby et al.*, 2007]. For the Gulf of Trieste, we have chosen winter SST as indicator because the Mediterranean circulation is mostly forced by the winter climate [*Korres et al.*, 2000].

2. Methods

2.1. Data

[12] Mesozooplankton were collected by vertical hauls from bottom (18 m) to surface, with a WP2 net, at a 200 m offshore station (C1) located at 45°42′03″N, 13°42′36″E (Figure 1). The use of a 200 μ m mesh probably determined a significant underestimation of small copepods (e.g., omeids, oithonids) [*Krsinic and Lucic*, 1994; *Paffenhöfer and Mazzocchi*, 2003; *Turner*, 2004; *Williams and Muxagata*, 2006], but the bias remained the same over time. The samples were fixed in 4% buffered formaldehyde. Taxonomic analyses were performed on subsamples composing 1/2 to 1/8 of the original sample, on at least 1000 individuals [*Kamburska and Fonda-Umani*, 2006].

[13] Thirty-six years (April 1970 to December 2005, with a 5-year gap from January 1981 to February 1986, inclusive) of monthly copepod abundances (number of individuals m^{-3}), comprising 20 copepod species and taxa, have been used for this work. In addition, total copepod abundance was computed as the sum of the abundance of all species per sample, and copepod diversity was computed as the number of taxa per sample, for a total of 22 biological variables and 8064 data points.

[14] Monthly sea surface temperature (SST) for the Gulf of Trieste region from January 1970 to December 2005 was derived from the long-term meteorological station of CNR-ISMAR-Trieste, located at 45°38′34″N, 13°45′14″E and sampled daily at noon at 2 m depth [*Caterini et al.*, 2007].

2.2. Statistical Analyses

[15] Seasonal SST averages were calculated over the following months: winter (January, February, and March), spring (April, May, and June), summer (July, August, and September) and autumn (October, November, and December).

[16] The cumulative sums technique was used to detect changes in the mean winter SST. The cumulative sums is a simple method, which allows a graphical detection of local changes in a time series and an assessment of the intensity and duration of these changes [*Ibañez et al.*, 1993;

Beaugrand et al., 2003]. Each value of the series is subtracted from a reference value (here the mean of time series), resulting in a new time series of residuals, which are used for the calculation of the cumulative sum (each element is summed to the previous). With this technique two periods (1970–1987 and 1988–2005) were identified.

[17] Copepod time series were subdivided in two subseries (1970–1987 and 1988–2005), and the Wilcoxon-Mann-Whitney (WMW) two-tail nonparametric test was used to evaluate the change in copepod abundances (non-normal distributions) between the two periods identified with the cum sum technique (the null H_0 being “no difference between the two periods”).

[18] Mean percentages (MP) of increase/decrease of each species between the two periods above were computed by using the geometric means of the series in order to remove the influence of a few large peaks in the data [*Olsen*, 2003], using the following formula:

$$MP = \frac{\Pi_2 - \Pi_1}{\Pi_1} \% \quad (1)$$

Where Π_1 is the geometric mean over period 1 (1970–1987) and Π_2 is the geometric mean over period 2.

[19] The timing of seasonal peak T was estimated for each taxon over the entire 36-year period, following the procedure outlined by *Edwards and Richardson* [2004]:

$$T = \frac{\sum_{m=1}^{12} mx_m}{\sum_{m=1}^{12} x_m} \quad (2)$$

Where x_m is the species abundance in the month m (m in January = 1, . . . , in December = 12).

[20] First, all taxa were classified as unimodal (one growing season, or a nondefined seasonal cycle) or bimodal (species presenting spring and autumn abundance peaks), following visual inspection of the average seasonal cycle of each taxon (average value of each month, calculated over the entire sampling period).

[21] For unimodal species the timing of seasonal peak T was then calculated throughout the entire year, whereas for bimodal species two indices T were calculated separately, one for the first six months (January to June) and one for the last six months (July to December) of the year [*Edwards and Richardson*, 2004].

[22] The variation of T of each taxon over 36 years was fitted with a linear trend, and the shift (Δt) in time of T was calculated as the difference between the trend values in 2005 and in 1970. All analyses were programmed in MATLAB language.

3. Results

[23] Overall, the copepod community in the Gulf of Trieste is dominated by the calanoid copepod *Acartia clausi*, which accounts, on average, for over 31% of the total abundance (approx. 1000 individuals m^{-3} per sample) for the entire period 1970–2005, followed by the cyclopoid *Oithona* spp. (18%), the poecilostomatoid *Oncaea* spp. (12%), and the calanoid *Paracalanus parvus* (9%) and *Clausocalanus* spp. (8%). Copepod diversity (number of

species per sample) over this period ranged from a minimum of 6 to a maximum of 20 species/taxa (out of 20) in any given month, with an average of 14 taxa per sample.

[24] The initial visual examinations of the long-term copepod records suggested that the whole community had undergone a substantial transformation over the 36-year period investigated, which, even taking into account the gap in the series, appeared to be mainly centered around the end of the 1980s to the beginning of the 1990s.

3.1. Physical System: Changes in SST

[25] To identify the period of change we have used the SST records in the Gulf of Trieste for the period 1970–2005. Overall, the Gulf of Trieste SST has increased by 0.5°C between 1970 and 2005 (SST records not shown), but this increase is not equally distributed between seasons: as a matter of fact, the winter SST shows no long-term change (Figure 2a), while the spring, summer, and fall temperatures increase by 0.6, 1.0, and 1.1°C, respectively (Figures 2c, 2d, and 2e).

[26] The cumulative sum technique [*Beaugrand et al.*, 2003], used to detect periods of change in the winter SST, indicates that the period of change in the water column starts in 1988 (Figure 2b).

[27] We therefore have chosen year 1987 as delimitator for the two-period analyses, with the first period being 1970–1987 and the second being 1988–2005.

[28] The changes that affect the Gulf of Trieste between these two periods include arrival of a new species, changes in overall copepod abundance, the rise or decline of several species, and changes in the phenology of individual species.

3.2. New Species Occurrence

[29] The southern Adriatic species *Diaixis pygmoea* in the Gulf of Trieste appears for the first time in February 1990, and since then has always been present (Figure 3), a fact which had already been documented by *Kamburska and Fonda-Umani* [2006].

[30] This neritic species is generally more notable in the middle Adriatic basin [*Fonda-Umani et al.*, 1994]. Although in the early 1970s *Hure and Krsinic* [1998] found the copepod to be abundant in the northern Adriatic area under the Po River influence, a cross comparison among five Adriatic bays, also in the 1970s, showed the absence of *D. pygmoea* in the gulfs of Piran and Trieste [*Fonda-Umani et al.*, 1984], which is consistent with the historical record results.

[31] The reason for the appearance and persistence of this species since 1990 is still unknown, but the general water warming trend was indicated as a possible cause of the northern expansion of this copepod [*Kamburska and Fonda-Umani*, 2006].

3.3. Long-Term Changes

[32] A noticeable feature in the long-term analysis is the overall change in copepod abundances in the Gulf of Trieste, seen in Figures 4 and 5. Even taking into consideration the gap in sampling in the early 1980s, most of the changes do not seem to happen gradually, but, conversely, within a short period at the end of the 1980s to the beginning of the 1990s.

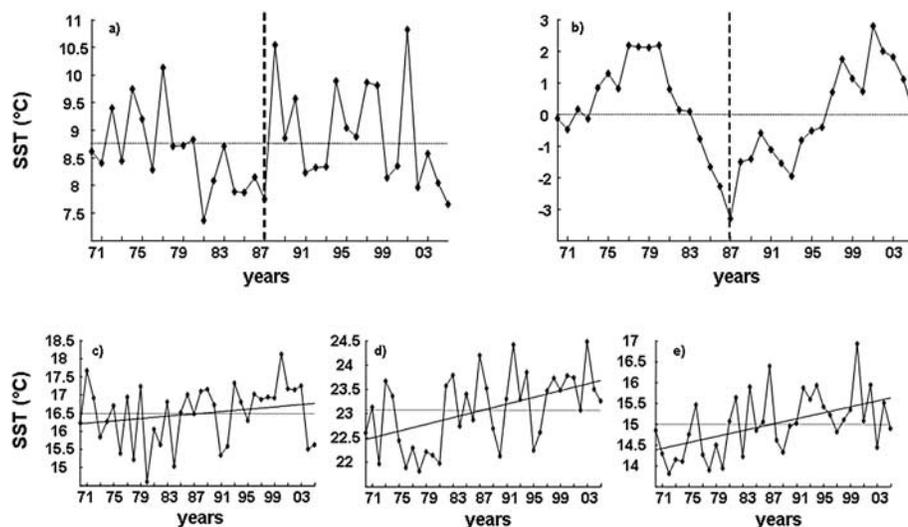


Figure 2. (a) Winter SST with long-term mean (dotted line) and (b) winter SST cumulative sums. For comparison, the (c) spring, (d) summer, and (e) fall SST values are reported with respective long-term mean (dotted line) and trend (solid lines). The vertical dashed line separates the two periods identified by the cumulative sums technique.

[33] We have therefore tested the hypothesis of no change between the two periods 1970–1987 and 1988–2005 with the nonparametric Wilcoxon-Mann-Whitney test. The test results confirm a significant ($p < 0.05$) change between these periods for total copepods, *Paracalanus parvus*, *Oncaea* spp., *Oithona* spp., and *Euterpina acutifrons* (all increasing), *Pseudocalanus elongatus*, *Clausocalanus* spp. and *Ctenocalanus vanus* (declining). More specifically, in the second period relative to the first one, while the total copepod abundance increases overall by 115% (Figure 4a and Table 1), there is a reduction in the abundance of the large copepods *P. elongatus*, which undergoes a 73% reduction (Figure 4c), and *Clausocalanus* spp., which halves (Figure 5a). On the other hand, *P. parvus* (Figure 4b), *Oithona* spp. (Figure 5c), and *Euterpina acutifrons* (not shown) increase approximately fourfold, and *Oncaea* sevenfold (Figure 5b).

[34] The net result of the aforesaid changes is a substantial difference in the composition of the copepod commu-

nity in the second period (Figure 6): during the years 1970–1987 *A. clausi* represented 40% of the total copepod population, followed by *Clausocalanus* spp. (19%; in the second period becomes 4.6%), *Oithona* spp. (11%), and *P. parvus* (5%). On the other hand, in the period 1988–2005 *A. clausi*, while still undoubtedly the most abundant species, represents just 28% of the total copepod population, and the second most abundant taxon becomes *Oithona* spp. (20%), followed by *Oncaea* spp. (14%; during the first period was 4%), and *P. parvus* (11%). The mean copepod diversity (number of species/sample), on the other hand, did not change significantly between the two periods, which suggests that this simple index is not suitable for this area.

3.4. Changes in the Phenology of the Species

[35] In this work we have hypothesized that the changes in abundance seen between the periods 1970–1987 and 1988–2005 entail changes in the timing of the peak of

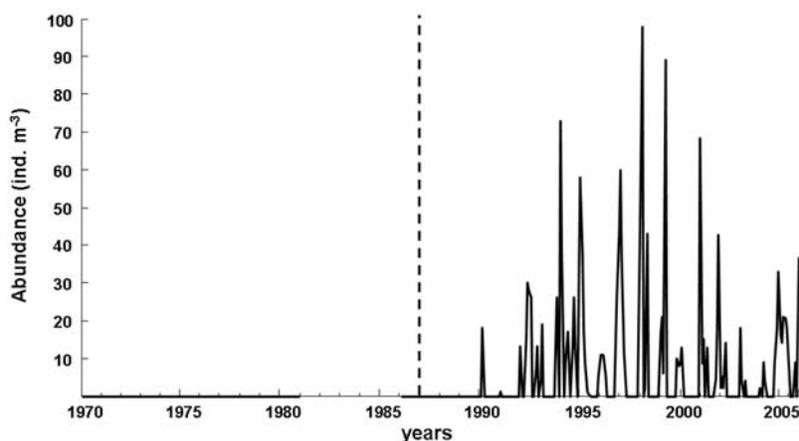


Figure 3. Long-term variations of *Diaixis pygmoea*. The vertical dashed line separates the two periods identified by the cumulative sums technique. Ind., individuals.

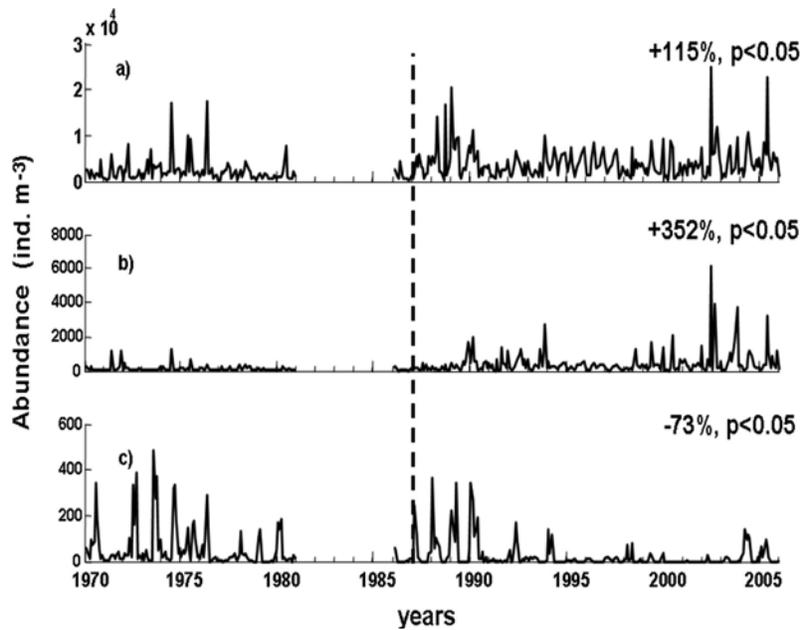


Figure 4. Long-term fluctuations of (a) total copepods, (b) *Paracalanus parvus*, and (c) *Pseudocalanus elongatus*. The vertical dashed line separates the two periods identified by the cumulative sums technique.

maximum abundance of the species. To test this hypothesis we have used the T index developed by *Edwards and Richardson* [2004] as an estimate of the variations in the timing of the seasonal peak.

[36] All copepod taxa (with the exception of the new species) were subdivided into “bimodal” and “unimodal” taxa (see Methods), and the T indices were calculated for each taxa over the 36 years.

[37] In Table 2 we show for each taxa the shift in time in the period of maximum abundance (Δt), calculated as the difference between the values in 2005 and in 1970 in the

trend line fitting the taxon’s T. Most of the taxa, including all of those which had shown, by the WMW test, a significant difference in abundance between the two periods, exhibit a shift in the timing of the maximum abundance greater than 4 weeks, although only six of the associated trends are significant at the 0.10 level: those of *Pseudocalanus elongatus*, *Calanus helgolandicus*, *Paracalanus parvus*, *Ctenocalanus vanus*, *Temora longicornis*, *Corycaeus* spp., and other copepods. It is noteworthy that for all cold species (*P. elongatus*, *C. vanus*, *C. helgolandicus*) the summer/autumn peak appears delayed by almost 2 months or more.

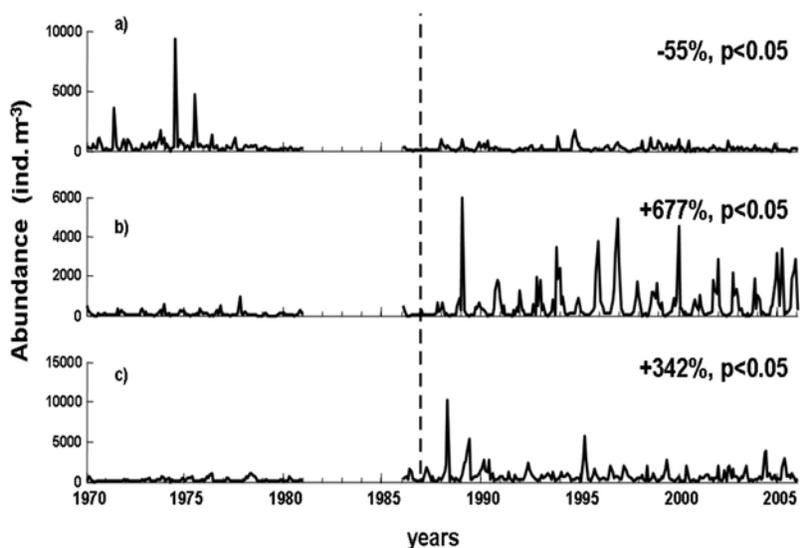


Figure 5. Long-term fluctuations of (a) *Clausocalanus* spp., (b) *Oncaea* spp., and (c) *Oithona* spp. The vertical dashed line separates the two periods identified by the cumulative sums technique.

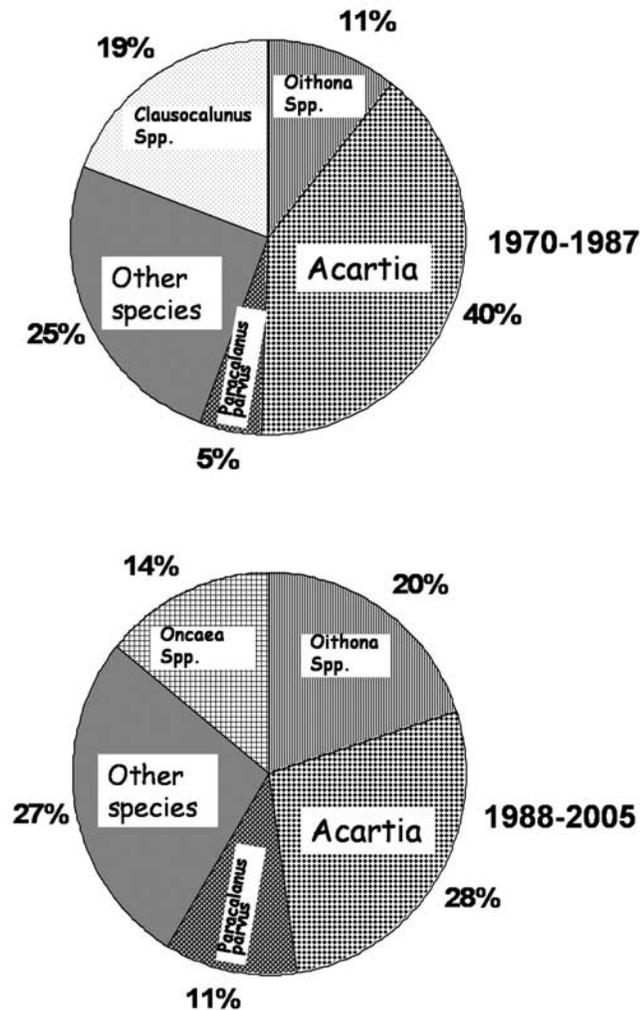


Figure 6. Percent composition of copepod species during the periods 1970–1987 and 1988–2005. Only species which represent $\geq 5\%$ are reported. Note that overall abundance is 115% greater in the second period.

[38] We have looked more in depth at the long-term variations of the T index for the relic boreal species *P. elongatus*, because its considerable (73%) reduction suggests that this species might be at risk of local extinction.

[39] The T index suggests a large (almost 3 months) delay in the summer/fall peak of *P. elongatus* (no change in the timing of the winter/spring peak; Figure 7a). However, when we compare the mean seasonal cycles calculated over 1970–1987 and 1988–2005 (Figure 7b), we see that the summer/fall peak has basically vanished, which is likely to be associated with the 73% decline of this species seen in Figure 4b. The abatement of the major summer/fall abundance peak during the second period of time is similarly seen also in *C. vanus* (another cold water species) and in *Clausocalanus* spp., which are both declining taxa (not shown).

[40] The comparison of these two analytical methods, T index calculation and mean seasonal cycle, reveals different insight in copepod dynamics: in fact, because the

T index is calculated over the entire growing season, it provides just the central tendency of the seasonal peak (shift in months), but provides no information about peak magnitude. Thus, although it identifies a gradual shift from July to October in *P. elongatus*, it cannot detect the concurrent abatement in abundance. In the case of species presenting large variations in their abundance, it is therefore important to use this index with caution, and to perform additional analyses.

4. Discussion

[41] The physical evidence for a change in the circulation around year 1987, based on both our SST analysis and a literature review (see below), is the basis for our choice of year 1987 as delimitator for the two-period analyses.

[42] Our results point to system-wide changes in the copepod community in the Gulf of Trieste between these two periods, whose potential influence on ecosystem functioning has still to be evaluated. Although total copepod abundance doubles between the two periods investigated, in general there seems to be a shift toward smaller species, as well as a northern displacement of several species within the system.

[43] The shift toward smaller species (already noticed by *Kamburska and Fonda-Umani* [2006]) is indicated by the increase of the genera *Oithona* and *Oncaea* (Figures 5b and 5c), and of the resident species *Euterpina acutifrons*. The relative increase in *Oithona* abundance is seen also elsewhere in the Mediterranean: *Christou* [1998] reports an increase in *Oithona* spp. (mainly *O. similis* and *O. plumifera*) in the Aegean Sea in the early 1990s (5-year record, 1989–1993), and finds an association with salinity. In the Adriatic Sea, *O. similis* is defined as ubiquitous by *Hure and Krsinic* [1998], but seems to be more abundant along the western coast and in the bottom layers [*Krsinic et al.*, 2007]. Both advection and water properties, such as salinity and temperature, could play a dominant role in the expanded northward distribution of this species.

[44] The northerly displacements are indicated by both the presence of species previously seen predominantly in the middle and southern Adriatic basins (e.g., *D. pygmoea*, *P. parvus*, Figures 3 and 4b) and by the decline of cold water species, such as *P. elongatus* (Figure 4c), and is supported by the general warming in the physical system (0.5°C increase in SST over 36 years). The increase in *P. parvus* seems not to be limited to this area, since it is also seen from 1990 in *Christou's* [1998] 5-year record in the Aegean.

[45] The 73% decline of *P. elongatus* deserves particular attention. *P. elongatus* is a cold water species, present, in the Mediterranean, only in the northern Adriatic Sea, eastern Mediterranean, and in the Alboran Sea, western Mediterranean [*Vives et al.*, 1981]; a few specimen, probably introduced from the Black Sea, where the species is also present, have however been sighted in the northeastern Aegean, restricted to an area of relatively low (<36) salinity [*Siokou-Frangou et al.*, 2004]. It is noteworthy that this species has not been found in the rest of the Aegean Sea, in the Levantine Sea, in the Ionian Sea, in the Tyrrhenian Sea, or in the Ligurian Sea. The northern Adriatic Sea population of *P. elongatus* is, according to *Vives et al.* [1981], a relic

Table 1. Basic Statistics of Copepod Abundances in the Gulf of Trieste Showing 1970–1987 Versus 1988–2005^a

	1970–1987					1988–2005					Percent Mean Increase
	Mean	95% Confidence Intervals	SD	Geographic Mean	95% Confidence Intervals	Mean	95% Confidence Intervals	SD	Geographic Mean	95% Confidence Intervals	
<i>Acartia clausi</i>	824	261	1599	302	232–390	1108	218	1678	361	287–454	20%
<i>Calanus helgolandicus</i>	6	4	25	3	2–3	14	6	48	3	2–3	10%
<i>Calanus</i> spp. ^b	7	4	22	2	2–3	30	10	81	5	4–6	106%
<i>Centropages kroyeri</i>	10	6	38	3	2–3	26	22	169	2	2–3	–23%
<i>Centropages</i> spp. ^c	27	11	68	5	4–7	71	24	183	10	8–13	93%
<i>Centropages typicus</i>	30	6	39	15	11–18	59	45	344	9	7–11	–39%
<i>Clausocalanus</i> spp. ^d	400	151	927	158	124–202	184	32	250	66	52–84	–58%
<i>Corycaeus</i> spp. ^e	17	7	42	5	4–7	53	23	180	9	7–11	65%
<i>Ctenocalanus vanus</i>	38	21	130	10	8–13	26	8	59	6	4–7	–44%
<i>Diaxius pygmaea</i>	0	0	0	1	0	7	2	15	3	2–3	
<i>Euterpina acutifrons</i>	29	7	44	9	7–12	123	21	160	42	33–53	356%
<i>Harpacticoida</i> ^f	16	7	42	3	3–4	9	6	44	3	2–3	–25%
<i>Oithona</i> spp. ^g	224	43	266	102	79–131	799	137	1052	449	385–524	342%
<i>Oncaea</i> spp. ^h	79	22	134	17	13–24	568	118	913	136	103–179	677%
Other copepods ⁱ	143	54	331	21	14–30	318	143	1105	22	15–32	7%
<i>Paracalanus parvus</i>	105	30	184	44	35–55	431	89	688	200	167–238	353%
<i>Pseudocalanus elongatus</i>	53	15	90	17	13–22	25	7	57	5	4–6	–73%
<i>Temora longicornis</i>	36	9	53	13	10–17	38	10	78	9	7–11	–31%
<i>Temora</i> spp. ^j	5	2	15	2	1–2	45	18	135	5	4–7	178%
<i>Temora stylifera</i>	21	10	64	5	4–7	77	54	413	8	6–10	58%
Total copepods	2079	400	2448	1368	1170–1601	4011	446	3436	2941	2636–3281	115%
Copepod diversity	14	1	3	14	14–15	13	0	3	13	13–14	

^aMean monthly abundances and associated 95% confidence intervals, standard deviations, geometric means and associated 95% confidence limits, for all copepod taxa. The last column represents the mean percent difference, based on geometric means, between period 2 and period 1 (positive = increase).

^b*Calanus* spp. includes *Calanus helgolandicus* and its copepodites.

^c*Centropages* spp. are copepodite stages of *C. kroyeri* and *C. typicus*.

^d*Clausocalanus* spp. includes *C. furcatus*, *C. pergens*, *C. jobei*, *C. paululus*, *C. arcuicornis*, and their copepodites.

^e*Corycaeus* was identified only at genus level.

^fThe order Harpacticoida includes *Clytemnestra scutellata*, *Microsetella rosea*, and *Canuella* spp.

^g*Oithona* spp. include *Oithona nana*, *O. similis*, *O. plumifera*, *O. setigera*, *O. helgolandica*, and their copepodites.

^h*Oncaea* spp. includes all species in the genus *Oncaea* and its copepodites.

ⁱThe group “other copepods” contains the rare taxa *Nannocalanus minor*, *Mecynocera clausi*, *Ischocalanus plumulosus*, *Candacia* spp., *Anomalocera* spp., *Sapphirina* spp., *Euchaeta* spp., *Calocalanus* spp., and their copepodite stages, as well as other Calanoida copepodites.

^j*Temora* spp. includes copepodites of *T. longicornis* and *T. stylifera*.

population of arctic origin, not associated with the western Mediterranean population. Earlier studies [Hure and Krsinic, 1998] indicate that in the mid 1970s this species had a wider distribution, encompassing in summer most of

the middle Adriatic. However, in a recent survey carried out in the whole northern Adriatic in 2001, Camatti et al. [2008] observed that *P. elongatus* was virtually absent in the area or present in very low numbers. Our results indicate

Table 2. Phenological Changes: Shifts in the Timing of the Peak of Maximum Abundance^a

Bimodal Species	ΔT Winter/Spring (m)	ΔT Summer/Fall (m)	Major Peak	Trend p-Value
<i>Calanus helgolandicus</i> ^b	0.7	1.7 ^b	Spring (May)	0.17
<i>Calanus</i> spp.	0.03	1.3	Irregular	0.76
<i>Clausocalanus</i> spp.	–0.4	1.1	Fall (Jul)	0.58
<i>Ctenocalanus vanus</i> ^b	–1.2 ^b	1.6 ^b	Fall (Jul)	0.09 ^b
<i>Paracalanus parvus</i> ^b	1.6 ^b	0.2	Jun–Aug	0.0005 ^b
<i>Pseudocalanus elongatus</i> ^b	0	2.8 ^b	Irregular	0.81
Unimodal Species	ΔT (m)	Month of Major Peak	Trend p-Value	
<i>Centropages typicus</i>	–1	Spring (Jun)	0.97	
<i>Corycaeus</i> spp. ^b	4.6 ^b	Fall (Oct)	0.0001 ^b	
<i>Euterpina acutifrons</i>	1.2	Winter (Nov–Dec)	0.37	
<i>Harpacticoida</i>	1.7	–	0.22	
<i>Oncaea</i> spp.	1.5	Winter (Oct–Dec)	0.40	
Other copepods ^b	2.2 ^b	–	0.10 ^b	
<i>Temora longicornis</i> ^b	–1.6 ^b	Spring (May)	0.01 ^b	

^aFor each taxon the shift Δt (in months) in the timing of the maximum peak is calculated as the difference between the values at points 2005 and 1970 of the linear trend fitting the T index line. Positive values indicate a shift forward in the peak (i.e., a delay in the season). The major peak (based on the visual inspection of the 36-year average seasonal cycle) is indicated, to distinguish spring-peaking from fall-peaking taxa. The last column shows the p-value of the linear trend fitting the T index line. For bimodal species the winter/spring T index is calculated on months 1–6, and the summer/fall T index is calculated on months 7–12.

^bHere p-values ≤ 0.10 .

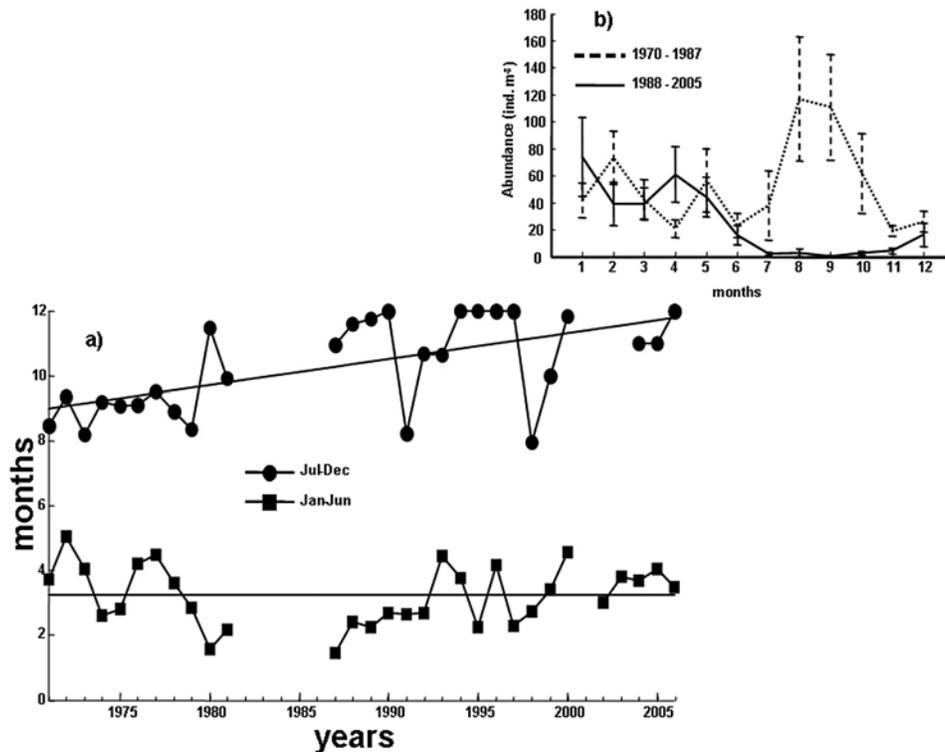


Figure 7. Changes in the seasonal peak of *Pseudocalanus elongatus*. Phenological changes: (a) changes in the timing of the seasonal peak (T index) over the entire 36-year period and (b) differences in the mean seasonal cycle: periods 1970–1987 versus 1988–2005. The vertical bars indicate the standard errors of the monthly means.

the large, possibly critical, reduction in the abundance of this species. We are unaware of whether the Alboran Sea population has also decreased at the end of the 1980s. However, in the Baltic Sea, where this species has an important role in the food web, its strong decline in the last two decades originates in this same late 1980s to the early 1990s period [Hinrichsen *et al.*, 2002]; this suggests that this species could be driven by factors that operate at a scale larger than regional. From our results it can be hypothesized that the 1°C increase seen in the summer and fall SST (Figure 2) can be associated with the disruption of the summer peak in this cold-water species (Figure 7b).

[46] The several changes that took place in the copepod community measured in the Gulf of Trieste at the end of the 1980s to the beginning of the 1990s (although we cannot exactly pin down the period because of the lack of sampling in the early 1980s) suggest an ecosystem wide response to some type of large-scale physical forcing. A literature review indicates, in fact, the existence of peculiar physical conditions at the end of the 1980s, which preconditioned a basin-wide alteration in the 1990s.

[47] Demirov and Pinardi's [2002] work on the interannual Mediterranean circulation (from 1979 to 1993) distinguishes two periods (1981–1987 and 1988–1993), which differ in precipitation and winter wind regimes. These two periods are very consistent with those identified in here.

[48] Utilizing data-validated simulations, Pinardi *et al.* [1997] and Korres *et al.* [2000], describe the dramatic changes that occur in the surface circulation in the summer of 1987. In particular, they show a reversal in the surface

current directions in the Ionian Sea, with the Atlantic/Ionian stream branching northward at 35.5°N , reversing both the southward flow along the Italian coast of the previous years, and the cyclonic Ionian gyre, which became anticyclonic. Pinardi *et al.* [1997] link the surface circulation changes to the previous winter anomalies in the winds and heat fluxes. The alteration lasted approximately 10 years, until 1997, when the gyre rereversed, as shown by altimetry data [Pujol and Larnicol, 2005; Pinardi *et al.*, 2005; Gertman *et al.*, 2006; Demirov and Pinardi, 2007].

[49] In effect, the exceptionally cold winter of 1987 and the Ionian gyre reversal are considered to have set up the initial conditions for the shift of the source of deep waters from its usual southern Adriatic source to a new Aegean source [Lascazatos *et al.*, 1999]. This phenomenon, called the Eastern Mediterranean Transient (EMT), peaked approximately between 1988 and 1995 [Roether *et al.*, 1996; Malanotte-Rizzoli *et al.*, 1999; Lascazatos *et al.*, 1999; Josey, 2003], and started relaxing at the end of the 1990s; however, in 2003 the water mass structure was still far different from pre-EMT conditions [Roether *et al.*, 2007].

[50] The link between the Ionian gyre reversal and the North Atlantic Water (NAW) northward flow of 1987 and the Adriatic Sea surface circulation is not completely articulated, as most of the subsequent studies have focused on the understanding of the switch of the formation of dense water from the Adriatic to the Aegean. However, the increase of NAW in the northern Ionian Sea from 1987 is shown by the data of Malanotte-Rizzoli *et al.* [1999] and Manca *et al.* [2003], and we can deduce that an alteration of

that magnitude affected the Adriatic surface circulation as well. This is supported by *Tsimplis and Rixen* [2002], who find the whole water column in the Adriatic to have become fresher in the period 1987–1992.

[51] It can therefore be hypothesized that the reversal in the surface current directions in the Ionian sea in 1987 (the Ionian gyre reversal) might have not only set up the conditions for the shift in deep water source from the southern Adriatic to the Aegean (the EMT), but also influenced the surface circulation in the Adriatic Sea, and, consequently, the copepod northerly extension and abundance in the Gulf of Trieste. Such hypothesis should be tested, but drifter studies indicate that the time for Lagrangian transport to the northern Adriatic for particles entering the southern Adriatic basin through the Strait of Otranto can be relatively short, in the order of 50–100 days [*Falco et al.*, 2000], i.e., that the physical mechanism of particle transport is possible and relatively fast.

[52] The work by *Mazzocchi et al.* [2003] provides some evidence of changes in the mesozooplankton community structure of the Ionian Sea in relation to the Eastern Mediterranean Transient. If the influence of the Ionian gyre reversal on Adriatic communities were confirmed, it could also explain other changes in the late 1990s to the early 2000s visible in the abundance of some species (see Figure 4; significance not tested), which could be associated to the rereversal of the Ionian Sea gyre in 1997 [*Pujol and Larnicol*, 2005].

[53] Finally, we note that changes at the end of the 1980s have been reported in the pelagic communities in other European seas [*Edwards et al.*, 2002; *Beaugrand and Reid*, 2003; *Alheit et al.*, 2005]. A compared investigation to evaluate whether the reported changes in the copepod communities in different European seas are connected, as part of a larger-scale phenomenon, seems therefore advisable.

5. Conclusions

[54] Our results indicate that entire copepod community in the Gulf of Trieste started to change, presumably at the end of the 1980s, early 1990s. The statistical comparisons of the two periods, 1970–1987 and 1988–2005, identified through the Trieste winter SST cumulative sums, point out several differences between the second and the first period, including the arrival of a new species and the significant rise or decline of several key species.

[55] While total copepod abundance more than doubles during the 36 years sampled, the community as a whole appears to have shifted toward smaller species (e.g., the striking increase of *Oncaea* spp.) and toward species that previously had a more southern distribution (i.e., *Diaixis pygmoea*, *Paracalanus parvus*), at the expenses of cold-water species (i.e., *Ctenocalanus vanus*, *Pseudocalanus elongatus*). This latter species deserves particular attention because seems to be at risk of extinction, having undergone a 73% reduction, and being confined to this area.

[56] We hypothesize that these changes in the copepod community are driven by the basin-wide changes that altered the Mediterranean surface and deep circulation beginning in 1987. A modified input of water of N. Atlantic origin to the Adriatic, starting after 1987 could explain both the abrupt appearance and affirmation of species with a

southern distribution, and the changes in the abundance of key copepod species that began after that period.

[57] On the other hand, the reduction in abundance in cold water species, accompanied by the delay of the summer/fall and the anticipation of the spring maximum peaks, seen in the phenological index, suggests that temperature may have a direct role (as opposed to being solely an indicator of circulation changes), and that the general warming of the system may also be driving these changes.

[58] These two hypotheses, circulation changes versus system warming, are not mutually exclusive, and the relative importance of each one, and specifically of endogenous (such as changes in the species phenology) versus exogenous (such as advection) factors should be verified via specific target studies.

[59] **Acknowledgments.** We are indebted to Fulvio Crisciani and Renato Colucci for providing us with the SST data and for sharing their knowledge on the physical system. We are thankful to Alessandra de Olazabal and to several of Fonda-Umani's students for taxonomical analyses. We are grateful to Maurizio Ribera d'Alcalà for valuable insight; to Mariangela Ravaioli for overall support; and to Annalisa Griffla, Susanna Corti, Nadia Pinardi, and Gian Pietro Gasparini for precious suggestions. Two anonymous reviewers provided helpful criticism. This work has been supported by the Italian Project VECTOR (Vulnerability of the Italian coastal area and marine Ecosystems to Climatic changes and Their role in the Mediterranean carbon cycles (<http://vector-conisma.geo.unimib.it/>) funded by the Italian Ministry of University and Research.

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