

# Long-term copepod dynamics in the Gulf of Trieste (Northern Adriatic Sea): recent changes and trends

Lyudmila Kamburska<sup>1,\*</sup>, Serena Fonda-Umani<sup>2</sup>

<sup>1</sup>European Commission-DG Joint Research Centre, Institute for Environment and Sustainability, via Enrico Fermi 1, TP 272, Ispra 21020, Italy

<sup>2</sup>Dipartimento di Biologia, Università di Trieste, via Valerio 28/A, Trieste 34143, Italy

**ABSTRACT:** Cluster and time series analyses were applied to a 1970–1999 data set of zooplankton collected from the Gulf of Trieste (Northern Adriatic Sea). Two time periods were compared: 1970–1980 and 1986–1999. Associations of copepod species were identified and an attempt was made to reveal their long-term dynamics and significant patterns over the study period. Two main groups with 2 and 3 subgroups each were identified. We observed a seasonal alternation of the 2 main groups, albeit with remarkably different patterns during the 2 periods. Time-series analyses suggested recent changes in the periodicity of the associations. The long-term annual mean copepod abundance showed an increase in the late 1990s in comparison to the 1970s; however, this increase was not constant. Small-sized copepods increased in the second period, indicative of changes in the phytoplankton size spectrum. Shifts in the 1990s appeared to be related to climate change in the Northern Hemisphere that appeared abruptly after 1987. Climate change is thus recognized as the most important factor (more so than anthropogenic change) affecting inter-annual and inter-decadal variability of plankton dynamics. The strong signal recorded in the zooplankton community seems to reflect this, identifying the Gulf of Trieste as one of the most sensitive areas in the Mediterranean.

**KEY WORDS:** Copepod associations · Long-term dynamics · Northern Adriatic

*Resale or republication not permitted without written consent of the publisher*

## 1. INTRODUCTION

In recent decades, scientific knowledge on marine ecosystem responses to global scale climatic changes has significantly increased (Hänninen et al. 2000, Conversi et al. 2001, Piontkovski & Williams 2001). Climatic features (e.g. air temperature, precipitation, wind speed and direction etc.) determine changes in long-term plankton dynamics, reproductive cycles, growth and survival. The North Atlantic Oscillation (NAO) and El Niño Southern Oscillation (ENSO) strongly affected the Northern Hemisphere in the second half of the 1980s, and had long-lasting effects on oceanic processes (Barber & Chàvez 1986, Jacobs et al. 1994, Hurrell 1995, Karl et al. 1995, Petchey et al. 1999). Plankton dynamics were associated with NAO and ENSO events in 1982–1983, 1991–1992 and 1997–1998 (Fromentin & Planque 1996, Reid et al.

1998, Beaugrand et al. 2000, Dippner et al. 2000, Hänninen et al. 2000, Conversi et al. 2001).

The Northern Adriatic basin is one of few regions of permanently high biological production in the Mediterranean Sea (Fonda-Umani et al. 1992). The biological characteristics of the ecosystem are controlled by bathymetry, meteorology and hydrodynamics and by river run-off (about 20% of the total Mediterranean river runoff) (Fonda-Umani et al. 1992, Russo & Artegiani 1996). The waters from the Po River, the frequency of N and NE winds (e.g. the Bora wind), and water exchange with the Southern Adriatic have a strong influence on the composition and activity of pelagic communities in the Northern Adriatic (Gilmartin & Revelante 1981). The Adriatic ecosystem is especially sensitive to seasonal and long-term variations in anthropogenic nutrient load, whose impact can be significantly modified by changes in oceanographic con-

\*Email: lyudmila.kamburska@jrc.it

ditions due to climatic fluctuations (Degobbis et al. 2000). These changes impact the whole Mediterranean and modify the water exchange regime between the Adriatic and the Eastern Mediterranean.

The Gulf of Trieste was one of the coastal areas in the Northern Adriatic exposed to monospecific 'red tides' caused by dinoflagellate blooms in the 1980s (Sellner & Fonda-Umani 1999). During the last 15 yr it has been affected by several mucilage events (Degobbis et al. 1999). Both red tides and mucilage lead to an increase in oxygen demand in the bottom layer, the results of which affect both tourism and fisheries (Fonda-Umani 1996).

Temporal dynamics of zooplankton in the Gulf of Trieste reflect the fluctuations of a few dominant species such as *Acartia clausi*, *Penilia avirostris* and genera *Temora* and *Oithona* (Specchi et al. 1981, Cataletto et al. 1995, Fonda-Umani 1996). The semi-enclosed shallow system, subjected to pulses of freshwater input and large episodic water mass advectations from the middle Adriatic (modified Levantine intermediate waters [MLIW]), is characterized by strong inter-annual variability (Mozetic et al. 1998) without clear and recurrent species succession in the zooplankton community (Feoli et al. 1983). Some species such as *Noctiluca scintillans* may disappear for years (Fonda-Umani et al. 2004), while others appear each year, albeit in different months. Cataletto et al. (1995) identified some ecological associations sensu Estrada et al. (1985) with a recurrent successional pattern on the basis of an 11 yr time-series analysis. By adapting the same approach in this paper, we investigated whether long-term copepod ecological associations revealed stable patterns in the Gulf of Trieste over the period 1970–1999, in spite of climatic changes that occurred in the area.

## 2. MATERIALS AND METHODS

### 2.1. Study area and parameters

Zooplankton samples were collected on a monthly basis between April 1970 and December 1999 at one site (Stn C1) in the Gulf of Trieste (Fig. 1) by vertical haul (WP-2, 200  $\mu\text{m}$  mesh size) from the bottom (depth 18 m) to the surface, and fixed in 4% buffered formaldehyde. Taxonomic and quantitative analyses were performed on sub-samples (comprising one-half to one-eighth, of the original samples). Historical data published for the period 1970–1980 (Cataletto et al. 1995) and unpublished data (Marine Biology Laboratory, Trieste 1986–1999) were used for constructing the long-term data set. Data was not available for the period 1981–1985. Data on the most frequent 22 taxa

observed over 299 mo were organized into a single matrix. Results of Period 1 (1970–1980) were compared with those of Period 2 (1986–1999). Single missing monthly data were restored by interpolation of adjacent points. A long-term data set for average monthly water temperature ( $T^{\circ}\text{C}$ ) at the same site was used to identify any possible correlation with copepod dynamics (Stravisi 2000).

### 2.2. Statistical methods

Cluster analysis was applied in order to obtain merged groups of species, using the Matedit program. The correlation analysis was applied on the matrix of species abundance [ $\text{ind. m}^{-3}$ ] monthly data, so that associations could be found irrespective of their amounts.

To highlight the frequency of cycle oscillations, single spectral Fourier analysis was performed separately for both investigation periods with the original data sets (number of observations: 131 for 1970–1980; 168 for 1986–1999). Data series were de-trended linearly, mean values were subtracted before spectral decomposition, and series lengths were padded with zeros (e.g. the number of observations equal to a power of 2) for fast Fourier transform algorithm (FFT). Seasonal patterns were examined via autocorrelation functions (ACF) and auto-correlograms (lag = 1, white-noise

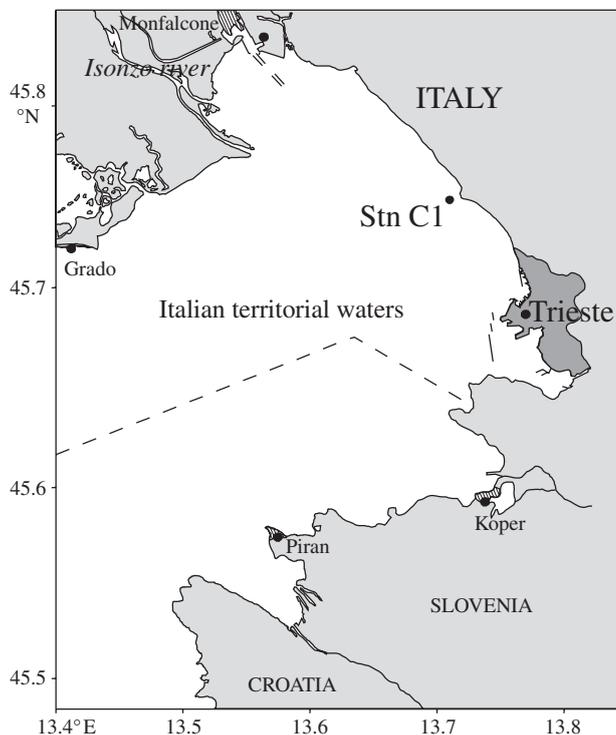


Fig. 1. Sampling area in the Gulf of Trieste

SEs, and  $\alpha = 0.05$ ) (Bloomfield 2000) (FFT results and graphs are available from the authors on request).

### 3. RESULTS

#### 3.1. Cluster analysis: temporal dynamics of copepod ecological associations

Cluster analysis distinguished 2 main groups, Group 1 and Group 2, which were subdivided into 2 and 3 subgroups, respectively (Table 1, Fig. 2).

Group 1 showed a maximum abundance during spring-summer in Period 1 (1970–1980); in Period 2 (1986–1999) the highest abundance was recorded in winter-spring. During Period 2, the annual and inter-annual fluctuations of the group were wider, concomitant with a higher mean abundance (Fig. 3).

Species *Diaixis pygmoea*, *Calanus tenuicornis* and *Oithona similis* constituted Subgroup 1.1. A high inter-annual variability was evident and a remarkable increase was detected in Period 2 owing to the appearing of *D. pygmoea* (Fig. 4) and to an enhanced abundance of *O. similis*.

Subgroup 1.2 was characterised by dominant *Acartia clausi*, and by co-dominant genera *Oithona* (*O. nana*, *O. plumifera*, *O. setigera*), *Temora* (*T. longicornis* and its copepodite stages), *Centropages* (*C. typicus* and its copepodites) and *Pseudocalanus elongatus*. This subgroup had 2 annual maxima in Period 1: the highest

Table 1. Ecological copepod groups obtained by cluster analysis (numbers correspond to those in Fig. 2)

Group 1	Group 2
<b>Subgroup 1.1</b>	<b>Subgroup 2.1</b>
1 <i>Diaixis pygmoea</i>	12 <i>Calanus helgolandicus</i>
2 <i>Calanus tenuicornis</i>	13 <i>Temora stylifera</i>
3 <i>Oithona similis</i>	14 <i>Paracalanus parvus</i>
	15 <i>Euterpina acutifrons</i>
	16 <i>Oncaea</i> spp.
<b>Subgroup 1.2</b>	<b>Subgroup 2.2</b>
4 <i>Pseudocalanus elongatus</i>	17 <i>Centropages krøyeri</i>
5 <i>Temora longicornis</i>	18 <i>Coryceus</i> spp.
6 <i>Temora</i> spp. (copepodite stages)	19 Harpacticoida ( <i>Clytemnestra scutellata</i> , <i>Microsetella rosea</i> , <i>Sapphirina</i> spp.)
7 <i>Oithona nana</i>	
8 <i>Oithona</i> spp. ( <i>O. plumifera</i> , <i>O. setigera</i> )	
9 <i>Centropages typicus</i>	
10 <i>Centropages</i> spp. (copepodite stages)	
11 <i>Acartia clausi</i>	<b>Subgroup 2.3</b>
	20 <i>Ctenocalanus vanus</i>
	21 <i>Clausocalanus</i> spp. ( <i>C. furcatus</i> , <i>C. pergens</i> , <i>C. arcticornis</i> )
	22 other copepods ( <i>Calocalanus</i> spp., <i>Candacia</i> spp., <i>Nannocalanus minor</i> , <i>Mecynocera clausi</i> , <i>Calanoida</i> spp., and their copepodite stages)

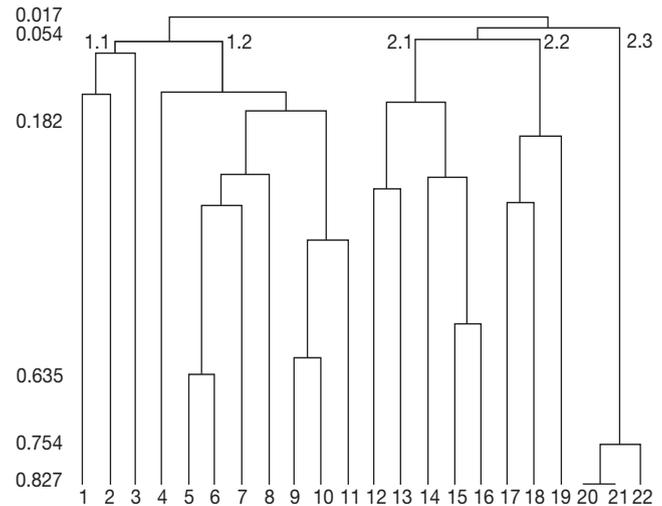


Fig. 2. Cluster classification of the most significant copepods, 1970–1999. Numbers at left: correlation coefficients; numbers at bottom: species (see Table 1)

maxima in April–May and the second, weaker maxima in November. In Period 2, the second yearly maximum was delayed until December–January (Fig. 3). The average abundance of Subgroup 1.2 during Period 2 was slightly higher (2000 ind. m<sup>-3</sup>) than for Period 1 (1200 ind. m<sup>-3</sup>).

A general characteristic of Group 2 was a high diversity due to the assemblage of numerous genera, which were subdivided into 3 subgroups (Table 1, Fig. 5). Subgroup 2.1 contained common species such as *Calanus helgolandicus*, *Paracalanus parvus*, *Temora stylifera*, *Euterpina acutifrons* and *Oncaea* spp. In contrast to Period 1, when average abundance of that association was 230 ind. m<sup>-3</sup>, mean abundance in Period 2 was 4 times higher due to a greater contribution of small-sized species such as *E. acutifrons* and *Oncaea* spp. (Fig. 6).

Subgroup 2.2 included less abundant species: *Centropages krøyeri*, *Coryceus* sp. and Harpacticoida. This subgroup was regularly presented during Period 1, while in Period 2 its abundance was halved or species were almost absent.

Subgroup 2.3 comprised the common and coastal area genus *Clausocalanus* (*C. furcatus*, *C. pergens*, *C. arcticornis*), *Ctenocalanus vanus* and the category 'other copepods', which constituted rare species (Table 1). Long-term dynamics of this subgroup manifested a large degree of variability between years. In Period 1, Subgroup 2.3 had maxima in December–February and June–July, whereas in Period 2 these maxima shifted to September–January and May.

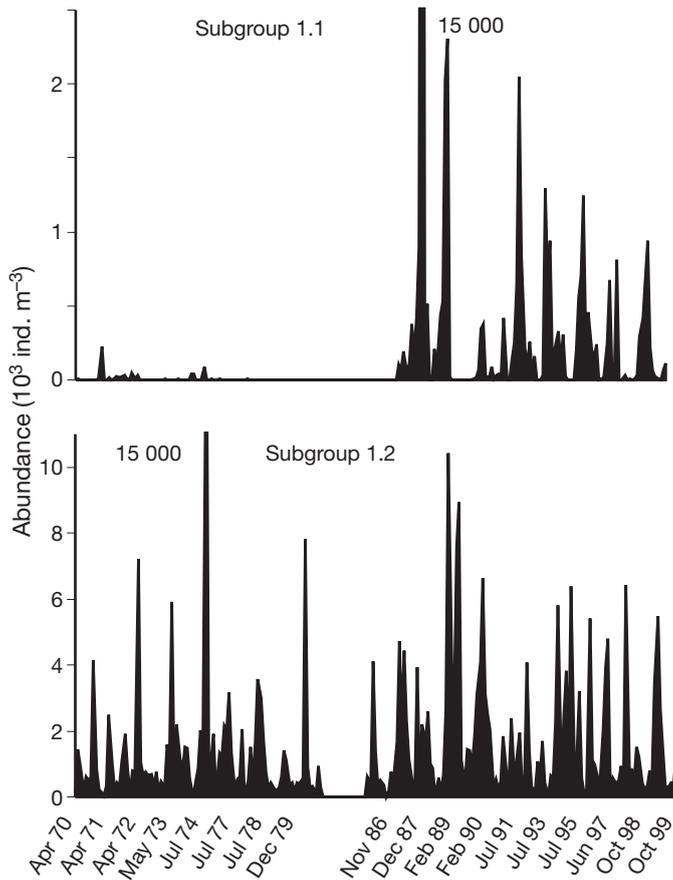


Fig. 3. Monthly abundance of Group 1 (Subgroups 1.1 and 1.2) 1970–1980 and 1986–1999. Nos. in figure: values that exceeded the scale

**3.2. Temperature-copepod dynamic relationship**

Long-term monthly mean water temperature in the Gulf of Trieste shows an increase of  $0.5 \pm 0.26^\circ\text{C}$  over the last 15 yr with the exception of February (Fig. 7).

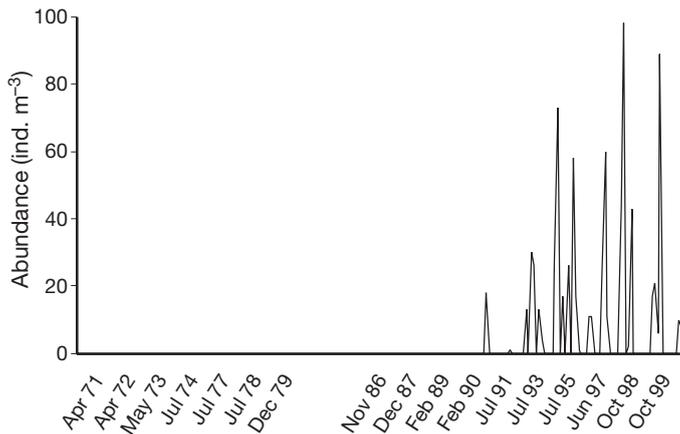


Fig. 4. *Diaixis pygmoea*. Monthly abundance, 1970–1980 and 1986–1999

Group 1 showed a significant increase in Period 2 from December to May but maintained the same abundance during the summer-fall (Fig. 8a). During Period 1, Group 2 was recorded throughout the year with summer and autumn maxima. Conversely, in Period 2, the maxima extended from autumn to winter. This group exhibited a slight decrease during late spring–early summer, and a significant increase from September to February over the last 15 yr (Fig. 8b).

Total copepod abundance was plotted against temperature (Fig. 9). An increasing abundance during 1986–1999 was evident, even though from 1989 to 1991 abundance tended to decline. The same period was characterized by a sharp temperature decrease. Copepod abundance then increased until 1995, following increases in temperature. During the last 5 yr the 2 patterns diverged.

Marginally significant positive correlation coefficients were found between Group 2 and Subgroups 2.1 and 1.1 on the one hand, and temperature on the other, over the whole investigated period ( $R = 0.43$  and  $R = 0.54$ , respectively,  $p < 0.05$ , Table 2).

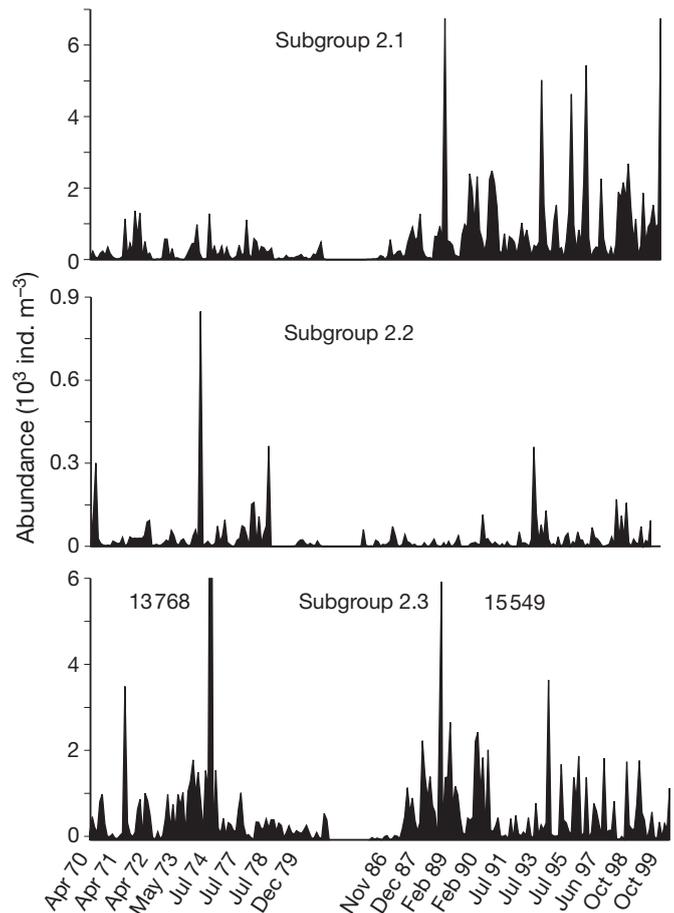


Fig. 5. Monthly abundance of Group 2 (Subgroups 2.1, 2.2 and 2.3) 1970–1999. Nos. in figure: values that exceeded the scale

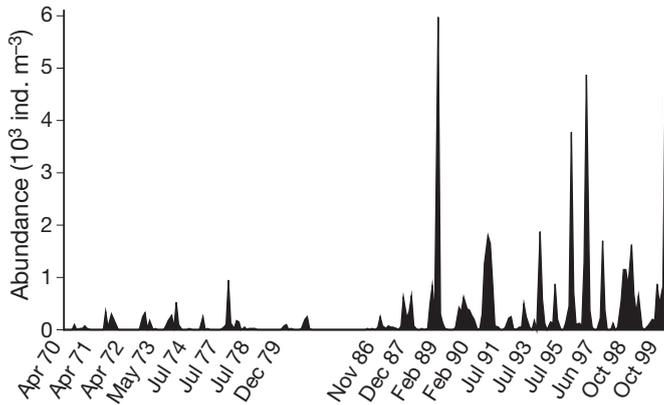


Fig. 6. *Oncaea* spp. Monthly abundance, 1970–1980 and 1986–1999

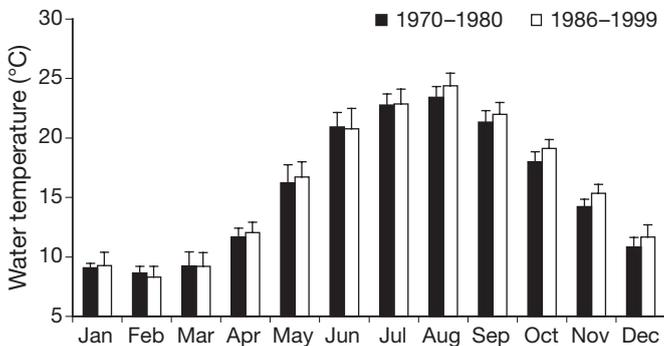


Fig. 7. Monthly mean water temperature at Stn C1, Gulf of Trieste, 1970–1980 and 1986–1999. Error bars: SD

### 3.3. Time series analyses: spectral density and cyclic oscillations

When applied to total copepod abundance, FFT revealed a strong 6 mo and 1 yr cycle in Period 1, the latter confirmed by ACF. During Period 2, the 6 mo cycle was absent, instead substituted by a 10–12 mo and a 5 yr cycle. ACF did not show clear cyclic oscillations (Table 3).

FFT analysis highlighted strong cycles of 6 and 12 mo in Period 1, confirmed by ACF, for Group 1. These cycles were totally absent in Period 2, when cyclical oscillations with 5.3 yr were visible but not yet sufficiently clear. The ACF indicate a cycle of 1 yr.

Subgroups 1.1 and 1.2 had clear cycles of 6 and 12 mo in Period 1, confirmed by ACF. These cycles were again absent during Period 2, when oscillations of 4.2 and 5.3 yr were evident for Subgroup 1.1 and 1.2 respectively. The ACF revealed a cyclic oscillation of 11.6 mo for Subgroup 1.2.

FFT and ACF did not reveal any clear seasonal or annual periodicity of Group 2 in Period 1. In Period 2, FFT indicated an unclear cycle of 5 yr, while a 10 mo

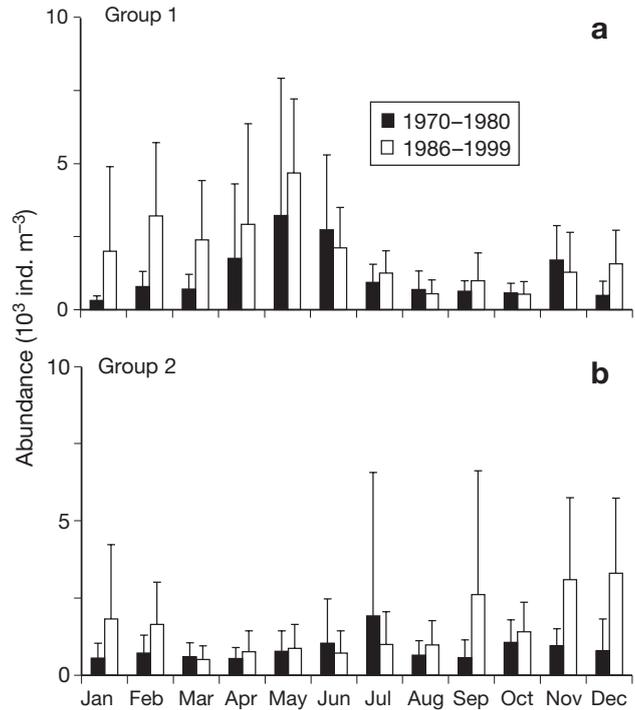


Fig. 8. Monthly mean abundance of (a) Group 1, (b) Group 2, 1970–1980 and 1986–1999. Error bars: SD

cyclic oscillation was demonstrated by ACF. For Subgroup 2.1, FFT did not register any cyclic oscillations in Period 1; however, ACF revealed a 1 yr cyclic oscillation. In Period 2, an unclear frequency of 11.2 mo was observed. Subgroups 2.2 and 2.3 did not demonstrate any oscillations in Period 1. During Period 2, both manifested a significant 5.3 yr cyclic oscillation.

## 4. DISCUSSION

Cluster analysis clearly identified 2 main ecological associations (i.e. Groups), subdivided in 2 and 3 subgroups respectively, whose dominance alternates

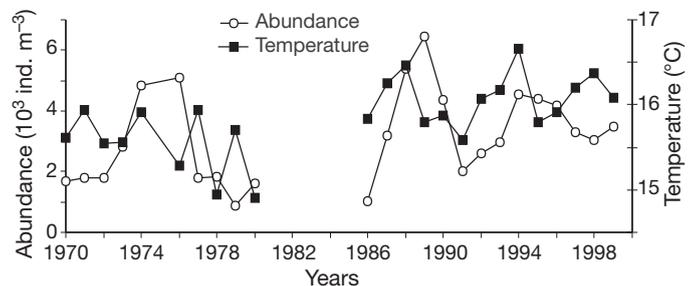


Fig. 9. Annual mean sea surface temperature and total copepod abundance at Stn C1, Gulf of Trieste

Table 2. Correlation matrix of parameter for 1970–1999 (no. of observations = 299; \*significant at  $p < 0.05$ )

Parameter	Group 1	Group 1.1	Group 1.2	Group 2	Group 2.1	Group 2.2	Group 2.3	Total copepod abundance
$T^{\circ}\text{C}$	0.12	0.54*	-0.05	0.43*	0.43*	0.06	0.25	0.35

Table 3. Summary results of time series analyses

	1970–1980		1986–1999	
	FFT analysis periodicity	ACF	FFT analysis periodicity	ACF
Total copepods	6 mo, 1 yr	1 yr	5.3, 1 yr	–
Group 1	6 mo, 1 yr	1 yr	5.3, 1 yr	1 yr
Group 1.1	6 mo, 1 yr	1 yr	4.2, 1 yr	–
Group 1.2	6 mo, 1 yr	1 yr	5.3, 1 yr	11.6 mo
Group 2	–	–	5.3, 1 yr	10 mo
Group 2.1	–	1 yr	11.2 mo	11.2 mo
Group 2.2	–	–	5.3 yr	–
Group 2.3	–	–	5.3 yr	–

during the year. Group 1 can be considered a spring–summer association, whereas Group 2 is prevalent in autumn.

Significant differences were observed for both ecological associations between Period 1 (1970–1980) and Period 2 (1986–1999). For Group 1, the absolute maximum in Period 1 always occurred in spring–summer while a second maximum occurred in November, confirming a strong seasonality. During Period 2, maxima were recorded in February and May, with a very pronounced maximum apparent in December. A substantial increase in winter–spring abundance during the last 15 yr was evident. In the latter period, the long-term annual and monthly dynamics of this group became much less regular and its fluctuations wider, seemingly due to the enhanced significance of Subgroup 1.1, including species typical of late winter–spring and small-sized organisms (*Diaixis pygmoea*, genera *Oithona*). *O. similis* was rare during Period 1, whereas in Period 2 it became a constant component. *D. pygmoea* is typically found in the Middle and Southern Adriatic basins (Fonda-Umani et al. 1994) and was totally absent in Period 1 (Fig. 4). It was recorded for the first time in the Gulf of Trieste in January 1990, after which time its presence became regular. The enhancement of this group might be due to the higher frequency of MLIW injections and the increase in their resilience time in the Gulf of Trieste. The appearance of this species could be used as an indicator for MLIW advections in the area. The year 1990 was indeed characterized by reduced inputs of fresh water in the Gulf (Mozetic et al. 1998). The maximum extension of salty waters (salinity  $>38.4$ ) was during winter and early spring (Russo & Artegiani

1996), which corresponded to the seasons of highest copepod abundance and variability. The observed increase in abundance of autumn–winter copepods, especially in the late 1990s, can be attributed to more frequent MLIW intrusions and their longer resilience in the Gulf. This in turn can be related to the recently observed salinity decrease of the inflowing current from the Aegean Sea, which allowed intrusions to reach the Northern Adriatic due to smaller density differences (Demirov & Pinardi 2002).

The investigated area was dominated by Subgroup 1.2 (for the most part by *Acartia clausi*). Subgroup 1.2 was already identified by Cataletto et al. (1995) for 1970–1980 as a typical summer association of diluted and eutrophic environments. This subgroup now includes some new elements such as *Centropages typicus* and *Pseudocalanus elongatus*. Two annual maxima in Period 1 were present: the strongest in April–May, and a second in November. In Period 2 the second annual maximum was delayed until December–January. Species such as *A. clausi* and *Temora longicornis* have been shown to be sensitive to the climate variability in the Baltic Sea (Dippner et al. 2000). In our study area, the significant increase in autumn temperatures can account for the change in the period of maximum abundance for this group.

The average monthly abundance of Group 2 during Period 2 did not show great changes in spring compared to Period 1, whereas a slight increase occurred during autumn–winter. The average abundance of Group 2 exhibited a rising trend in more recent years. During Period 2, the average abundance of Subgroup 2.1 was 4 times higher as a result of the increased contribution of small-sized species such as *Euterpina acutifrons* and *Oncaea* spp.

As discussed above, abundance of the genus *Oithona* expanded during the latter years of the study, whereas large-sized species such as *Centropages krøyeri* and Harpacticoida decreased in abundance. Evidence suggests a shift in the copepod community towards the prevalence of small-sized species. Possible reasons are: (1) reduction in food supply in the area (Hirst & Sheader 1997), related to a general decrease of the trophic state in the Gulf of Trieste (Malej & Fonda-Umani 1998), (2) modifications of the phytoplankton size spectrum (Calbet et al. 2001), which has indeed been observed since 1989 (Fonda-Umani et al. 1996).

Average copepod abundance decreased in the late 1970s, sharply increased between 1986 and 1989, then sharply decrease again until 1991. This was followed by a rising trend until 1994 and, finally, a slight diminution over the last 5 yr. The decrease in copepod abundance in the late 1970s was correlated with blooms of the jellyfish *Pelagia noctiluca* in the Adriatic Sea during 1977–1985 and *Noctiluca scintillans* (Vucetic 1985, Fonda-Umani 1991, Cataletto et al. 1995). Reduced anchovy biomass since 1978 and collapse of the anchovy stock in 1986–1990 (Regner 1996) may have led to enhanced copepod abundance during that period.

The time period after 1987 was characterized by wider annual fluctuations and an enhanced monthly variability compared to the first period of observations. This could be attributed to climatic changes in the second half of the 1980s, which had long-lasting effects in the Northern Hemisphere (Roether et al. 1996, Demirov & Pinardi 2002). The changes to the copepod community which occurred in 1989 might be related to the short period of cooling in 1989–1991 (Jones et al. 1997) and to the ENSO event of 1991–1992. The warming after 1992 could have triggered a recent shift in copepod population dynamics. This is particularly true for Groups 2.1 and 1.1 (characterized by a high percentage of small-size herbivorous copepods), which illustrate a positive correlation with temperature for the whole period. Rising sea surface temperature provokes phytoplankton alterations, which propagates along the food web from copepod herbivores to zooplankton carnivores because of tight trophic coupling (Richardson & Schoeman 2004). The effect of the NAO index could be a reason for copepod alterations after 1987. A high NAO index caused a decrease in *Calanus finmarchicus* in the NE Atlantic, around the British Isles (Fromentin & Planque 1996) and in the North Sea (Colebrook 1985), but was positively related to abundance of *C. finmarchicus* along the north-eastern US shelf with a 2 yr lag (Conversi et al. 2001). The increasing abundance of copepods in the Gulf of Trieste during that period mirrors the same positive relationship apparent in the Northern Adriatic. A completely different mode of interaction appeared after 1996 in the Adriatic Sea, similar to that of the early 1970s. As suggested by Planque & Reid (1998), the correlation between NAO and *C. finmarchicus* seemed to break down in 1996–1997.

Another important observation from our analyses was the disappearance of the annual and semi-annual periodicity in some groups and the detection of longer cycles for others in Period 2. FFT analysis and ACF revealed cycles of 6 and 12 mo periods for Group 1 in Period 1, which were completely absent in Period 2. Cyclical oscillations with a period of 5.3 yr were visible but not sufficiently clear. ACF still revealed the typical

cycle of 1 yr. Group 1 still dominated the Gulf of Trieste, but recently it seems that some factors induced changes in its cyclic oscillations and frequently led to less regular fluctuations. Subgroup 1.1 and 1.2 manifested strong cycles of 6 and 12 mo during Period 1, whereas in Period 2 neither cycle was present and only oscillations of 4.2 and 5.3 yr, respectively, were observed.

Group 2 showed a regular oscillation of 1 yr as well as an unclear period of 5 yr during the last 15 yr. In particular, Subgroup 2.1 had a periodicity with a frequency of 11.2 mo, whereas Subgroups 2.2 and 2.3 only showed a cyclic oscillation of 5.3 yr.

Patterns of cyclic oscillations in zooplankton and bacterial abundance with 5.5 and 7.3 yr periodicity were reported by Baranovich et al. (1993) in the middle Adriatic Sea: the first was correlated with salinity and southerly weather, the second with temperature and was close to the 8 yr period of solar activity.

According to Svendsen et al. (1995), the correlation between biological and physical variability related to drastic climatic change occurs on a time scale of 5 to 10 yr.

Observed changes in copepod dynamics appeared to be coupled to the altered regime in 1988–1993, which started with an abrupt change in 1987, viz. modified surface forcing in the Northern Hemisphere. During 1987–1995 a shift of sources of Eastern Mediterranean deep waters from the Adriatic to deep waters of the Aegean Sea was recorded (Roether et al. 1996). That period was marked by 3 extremely cold winters (1987, 1992, 1993), changes in winter wind fields over the Mediterranean and stronger northerly winds (Demirov & Pinardi 2002). The NAO index, particularly important in winter (the season with the strongest interdecadal variability) also appeared to be linked to the observed climatic changes (Demirov & Pinardi 2002).

The Adriatic Sea shows considerable intra- and inter-annual fluctuations in oceanographic properties. According to Pucher-Petkovich & Zore-Armada (1973), primary and secondary production increases in years of intensive advections of MLIW. More recently, several events of mucilage took place in the Northern Adriatic (in 1988, 1989, 1991, 1997, 2000, 2002 and 2004). These can directly influence temporal and spatial copepod variability by affecting the naupliar stages (Malej & Harris 1993), or indirectly by altering food-web structure and functioning (Cataletto et al. 1996).

The Gulf of Trieste, the northernmost and shallowest part of the Northern Adriatic, is an area of high sensitivity. It is under the influence of local meteorological variability, and is affected by riverine inflows, sewage discharges and episodic intrusions of MLIW with different resilience times. This area responds more intensely than the rest of the basin to climatic change.

The hydrodynamic variations induced by climatic forcing directly affect plankton community structure and dynamics. The observed changes in copepods (associations, seasonal, annual abundance dynamics and periodicity) could result from climate forcing in the area. Their pattern breakdowns often overlapped (or had a short lag time) with the periods of most significant climatic change. Zooplankton depends upon prey availability, which in turn is affected by climatic changes and anthropogenic impacts.

One of the most evident environmental changes in the Northern Adriatic Sea over the last 15 yr was the reduction in inorganic phosphorus, brought about by an Italian law banning phosphorus from detergents. Even so, it is hard to define whether climatic changes or anthropogenic impacts played the major role in shaping zooplankton structure and its temporal evolution during this time.

In all regional Mediterranean seas (Aegean, Adriatic, Black Sea etc.) long-term changes in biological components have been reported, e.g. extremely low net-zooplankton abundance in the 1980s, blooms of phytoplankton and jellyfish in the same period, strong decline of anchovy biomass, a break-point in biological interactions in 1990–1992, inverse ecological pattern of phytoplankton and net-zooplankton composition in 1996–1997 (Baranovich et al. 1993, Siokou-Frangou et al. 1998, Oguz 2005). Altogether, they support the theory of common controlling factors and potential teleconnections in the global oceans (Fromentin & Planque 1996, Beaugrand et al. 2000, Dippner et al. 2000, Hänninen et al. 2000).

## 5. CONCLUSIONS

(1) Regular seasonal alternations of 2 main associations, albeit with different patterns, during the periods 1970–1980 and 1986–1999.

(2) An evident increase in abundance of small-sized copepods could reflect limited food supply, or a shift towards smaller sized phytoplankton from 1989 onwards, which possibly continued thereafter.

(3) The 1990s were characterized by irregular intra-annual and inter-annual fluctuations, and frequently interrupted copepod abundance modes, which overlapped (or had a short time lag) with periods of significant climate change. The effect of the abrupt change in oceanographic properties of the whole Adriatic Sea after 1987 is particularly evident.

(4) Altered seasonality, species composition and cyclic periodicity of copepod associations during Period 2 can be seen as a response to modified environmental conditions caused by the drastic change in climate regime in the 1990s.

(5) The strong signal recorded in the plankton community can be interpreted as evidence of the high sensitivity of the Gulf of Trieste, which is under the influence of local meteorological variability and the extreme dynamics of the whole Adriatic Sea.

Zooplankton, and especially copepods, emerge as a highly sensitive component of the pelagic ecosystem. Analysis of their dynamics can test and evaluate how climate forces affect the ecology of the ocean.

*Acknowledgements.* This study was funded by the SINAPSI project. L.K., who spent 1 yr at the Marine Biology Laboratory, Trieste (Italy), received a Postdoctoral fellowship (2000–2001) by Consorzio per lo Sviluppo Internazionale, dell'Università degli Studi di Trieste. We thank B. Boglich, who performed some initial statistical analyses. We are also grateful to several students who analyzed plankton samples, in particular A. De Olazabal who not only processed many of the samples but also passed on much knowledge on taxonomical analyses to the young researchers. We thank H. Dumont for his thoughtful comments and help in preparing the text, and 2 anonymous reviewers for their useful suggestions.

## LITERATURE CITED

- Baranovich A, Solic M, Vucetic T, Krstulovic N (1993) Temporal fluctuations of zooplankton and bacteria in the middle Adriatic Sea. *Mar Ecol Prog Ser* 92:65–75
- Barber RT, Chàvez FP (1986) Ocean variability in relation to living resources during the 1982–1983 El Niño. *Nature* 319:279–285
- Beaugrand G, Ilbarez F, Reid CP (2000) Spatial, seasonal and long-term fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. *Mar Ecol Prog Ser* 200:93–102
- Bloomfield P (2000) Fourier analysis of time series. An introduction. J Wiley & Sons, New York
- Calbet A, Garrido S, Saiz E, M Alcaraz, Duarte CM (2001) Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. *J Plankton Res* 23:319–331
- Cataletto B, Feoli E, Fonda-Umani S, Cheng-Yong S (1995) Eleven years of time-series analysis on the net-zooplankton community in the Gulf of Trieste. *ICES J Mar Sci* 52: 669–678
- Cataletto B, Feoli E, Fonda-Umani S, Monti M, Pecchiar I (1996) Analyses of relationships between mucous aggregates and phytoplankton communities in the Gulf of Trieste (North Adriatic Sea) by multivariate techniques. *PSZN I: Mar Ecol* 17:291–308
- Colebrook JM (1985) Sea surface temperature and zooplankton, North Sea, 1948 to 1983. *J Cons Int Explor Mer* 42: 179–185
- Conversi A, Piontkovski SA, Hameed S (2001) Seasonal and interannual dynamics of *Calanus finmarchicus* in the Gulf of Maine (Northeastern US Shelf) with reference to the North Atlantic Oscillation. *Deep-Sea Res II* 48:519–530
- Degobbi D, Malej A, Fonda-Umani S (1999) The mucilage phenomenon in the Northern Adriatic—a critical review of the present scientific hypotheses. *Ann Ist Super Sanità* 35:373–381
- Degobbi D, Precali R, Ivancic I, Smodlaka N, Fuks D, Kveder S (2000) Long-term changes in the Northern Adriatic

- ecosystem related to anthropogenic eutrophication. *Int J Environ Poll* 13:1–6
- Demirov E, Pinardi N (2002) Simulation of the Mediterranean Sea circulation from 1979 to 1993: Part I. The interannual variability. *J Mar Syst* 33–34:23–50
- Dippner JW, Kornilovs G, Sidrevics L (2000) Long-term variability of mesozooplankton in the Central Baltic Sea. *J Mar Syst* 25:23–31
- Estrada M, Vives F, Alcaraz M (1985) Life and productivity of the open sea. In: Margalef R (ed) *Western Mediterranean*. Pergamon Press, Oxford, p 148–197
- Feoli E, Fonda-Umani S, Lagonegro M (1983) Periodicity of zooplankton community of Gulf of Trieste in contingency table analysis. *Rapp Comm Int Mer Mediterr* 28:201–203
- Fonda-Umani S (1991) General features of the planktonic system in the Gulf of Trieste and their variations in the last decade. *UNEP MAP Tech Rep Ser* 47:82–101
- Fonda-Umani S (1996) Pelagic production and biomass in the Adriatic Sea. *Sci Mar* 60:65–77
- Fonda-Umani S, Franco P, Ghirardelli E, Malej A (1992) Outline of oceanography and the plankton of the Adriatic Sea. In: Colombo G, Ferrari I, Ceccherelli VU, Rossi R (eds) *Marine eutrophication and population dynamics*. Olsen & Olsen, Fredensborg, p 347–365
- Fonda-Umani S, Specchi M, Cataletto B, De Olazabal A (1994) Distribuzione stagionale del mesozooplankton nell'Adriatico settentrionale e centrale. *Boll Soc Adriat Sci* 1:145–176
- Fonda-Umani S, Cheng Yong S, Feoli E, Cataletto B, Cabrini M, Milani L (1996) Is it possible to identify any plankton succession in the Gulf of Trieste (North Adriatic Sea)? In: Eleftheriou A, Ansell AD, Smith CJ (eds) *Biology and ecology of shallow coastal waters*. Elsevier Science Publishers, New York, p 59–65
- Fonda-Umani S, Beran A, Parlato S, Zollet T, De Olazabal A, Virgilio D, Lazzarini B, Cabrini M (2004) *Noctiluca scintillans* MacCartney in the Northern Adriatic Sea: long term dynamic, relationships with temperature and eutrophication, and role in plankton food webs. *J Plankton Res* 26:545–561
- Fromentin JM, Planque B (1996) *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. *Mar Ecol Prog Ser* 134:111–118
- Gilmartin M, Revelante N (1981) Regional variations in phytoplankton standing crops in the Northern Adriatic Sea. *Rapp Comm Int Mer Mediterr* 27:85–87
- Hänninen J, Vuorinen I, Hjelt P (2000) Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnol Oceanogr* 45:703–710
- Hirst AG, Shearer M (1997) Are *in situ* weight-specific growth rates body-size independent in marine planktonic copepods? A reanalysis of the global syntheses and a new empirical model. *Mar Ecol Prog Ser* 154:155–165
- Hurrell JW (1995) Decadal trends in North Atlantic oscillations: regional temperatures and precipitations. *Science* 269:676–679
- Jacobs GA, Hurlburt HE, Kindle JC, Metzger EY, Mitchell JL, Teague WY, Wallcraft AY (1994) Decade-scale trans-Pacific propagation and warming effects of an El Niño anomaly. *Nature* 370:360–363
- Jones PD, Jonsson T, Wheeler D (1997) Extension of the North Atlantic Oscillation using early instrumental pressure observations from Gibraltar and South-West Iceland. *Int J Clim* 17:1433–1450
- Karl DM, Letelier R, Hebel D, Tupas L, Dore J, Christian J, Winn C (1995) Ecosystem changes in the North Pacific subtropical gyre attributed to the 1991–92 El Niño. *Nature* 373:230–234
- Malej A, Fonda-Umani S (1998) Evoluzione delle interazioni trofiche nell'ecosistema del Golfo di Trieste. In: Regione Emilia Romagna Provincia Ravenna Autorità di bacino del fiume Po, Proc 'Evoluzione dello stato trofico in Adriatico: analisi degli interventi attuati e future linee di intervento', 28–29 September 1995, Marina di Ravenna, p 61–70
- Malej A, Harris RP (1993) Inhibition of copepod grazing by diatom exudates: a factor in the development of mucus aggregates? *Mar Ecol Prog Ser* 96:33–42
- Mozetic P, Fonda-Umani S, Cataletto B, Malej A (1998) Seasonal and inter-annual plankton variability in the Gulf of Trieste (Northern Adriatic). *ICES J Mar Sci* 55:711–722
- Oguz T (2005) Black Sea ecosystem response to climatic teleconnections. *Oceanography* 18:122–133
- Petchey LO, McPhearson PT, Casey TM, Morin PJ (1999) Environmental warming alters food-web structure and ecosystem function. *Nature* 402:69–72
- Piontkovski SA, Williams R (2001) Zooplankton abundance, species diversity and climate change in the tropical Atlantic Ocean in comparison to northern latitudes. *Oceanography* 14:43
- Planque B, Reid PC (1998) Predicting *Calanus finmarchicus* abundance from a climate signal. *J Mar Biol Assoc UK* 78:1015–1018
- Pucher-Petkovich T, Zore-Armada M (1973) Essai d'évaluation et pronostic de la production en fonction des facteurs du milieu dans l'adriatique. *Acta Adriat* 15:1–37
- Regner S (1996) Effects of environmental changes on early stages and reproduction of Anchovy in the Adriatic Sea. *Sci Mar* 60:167–177
- Reid PC, Planque B, Edwards M (1998) Is variability in the long-term results of the continuous plankton recorder survey a response to climate change? *Fish Oceanogr* 7:282–288
- Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305:1609–1612
- Roether W, Manca B, Klein B, Bregant D, Georgopoulos D, Beitzel V, Kovacevic V, Luchetta A (1996) Recent changes in Eastern Mediterranean deep waters. *Science* 271:333–335
- Russo A, Artegiani A (1996) Adriatic Sea hydrography. *Sci Mar* 60:33–43
- Sellner GK, Fonda-Umani S (1999) Dinoflagellate blooms and mucilage production. In: Malone TC, Malej A, Harding LW Jr, Smolaka N, Turner RE (eds) *Ecosystems at the land-sea margin: drainage basin to coastal sea*. *Coast Estuar Stud* 55:173–206
- Siokou-Frangou I, Papatthanassiou E, Lepretre A, Frontier S (1998) Zooplankton assemblages and influence of environmental parameters on them in a Mediterranean coastal area. *J Plankton Res* 20:847–870
- Specchi M, Fonda-Umani S, Radini G (1981) Les fluctuations du zooplankton dans une station fixe du Golfe de Trieste (Haute Adriatique). *Rapp Comm Int Mer Mediterr* 27:97–100
- Stravisi F (2000) La temperatura del mare a Trieste 1964–1999. *Hydrores Inf* 20:6–7
- Svendsen E, Aglen A, Iversen SA, Skagen DW, Smestad O (1995) Influence of climate on recruitment and migration of fish stocks in the North Sea. In: Beamish RJ (ed) *Climate change and northern fish populations*. *Can Spec Publ Fish Aquat Sci* 121:641–653
- Vucetic T (1985) Relationship between the jellyfish *Pelagia noctiluca* occurrence and catch of tunny fish in the Mediterranean (Adriatic). *Rapp Comm Int Mer Mediterr* 29:331–332