

Annual cycle of the gelatinous invertebrate zooplankton of the eastern South Adriatic coast (NE Mediterranean)

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*Frequent sampling at a fixed South Adriatic station over 1996 was designed to capture the annual cycle of life-history stages of the dominant gelatinous invertebrate zooplankton, which are very seldom encountered in the world literature. Two groups of dominant species were distinguished by their periods of most intense reproduction, one in late summer–autumn and the other in late summer–autumn and winter. Of 66 species identified, there were 19 hydromedusae, 14 calyco-phores, 3 ctenophores, 2 heteropods, 12 pteropods, 8 polychaetes and 8 chaetognaths. Compared with historical data, the numerically dominant species of calyco-phores, pteropods and polychaetes have changed dramatically. The calyco-phore *Muggiaea atlantica*, newly observed in the Adriatic, has replaced its formerly dominant congener *M. kochi*; the pteropod *Creseis virgula* has supplanted *C. acicula*, and the previously very rare *Pelagobia longicirrata* now is the dominant pelagic poly-chaete. Faunal changes coincide with—and perhaps partly are owed to—newly documented circu-lation changes in the Eastern Mediterranean, the proximate source of southern Adriatic water. Thus, using an extended description of Adriatic zooplankton, data presented herein provide baseline information that is essential in the evaluation of biological changes in the Adriatic, which have appeared possible as a consequence of larger-scale oceanographic processes on zooplankton commu-nity structure.*

INTRODUCTION

The southern Adriatic basin is a semi-circular pit (max. depth ~1230 m) delimited to the north by the Palagruža Sill (~150 m) and to the south by the Strait of Otranto (sill depth ~800 m). Interaction with the main body of the Mediterranean Sea includes inflow of Levantine Intermediate Water and Ionian Surface Water along the Adriatic's eastern border. The strength of this flow varies from year to year depending on the climatic oscillations that occur from the Atlantic to the southeast Mediterranean (Grbec *et al.*, 2002). This is part of the broader North Atlantic Oscillation (NAO), a climatic process that influences hemispheric patterns

(Ribera *et al.*, 2000). Its impact on inter-annual changes in the zooplankton population is evident over a wide latitudinal range (Molinero *et al.*, 2005; Piontkovski *et al.*, 2006). The NAO appears to be a contributor of changes in the thermohaline circulation referred to as the Eastern Mediterranean Transient (EMT), a phenom-enon evident from the early 1990s (Zervakis *et al.*, 2004). The South Adriatic is particularly interesting because recent changes in its plankton composition appear to be related to these large-scale climatic changes.

Studies on gelatinous zooplankton in the Mediterranean and Adriatic Sea (e.g. Benović, 1973;

Rampal, 1975; Gamulin and Kršinić, 1993; Buecher *et al.*, 1997; Goy, 1997; Daly Yahia, *et al.*, 2003), which are often a very important component of biomass (Pagés, 1997; Batistić, 2003), have focussed mostly on only a particular group and species, rather than on the larger trophic assemblage of which they are a part. In addition, available studies on the annual variability of gelatinous zooplankton in the Mediterranean usually implemented monthly sampling programs (e.g. Gili *et al.*, 1987; Gamulin and Kršinić, 1993; Sardou *et al.*, 1996), and so can be expected to have missed short-term changes in population and environment (Boucher *et al.*, 1987; Underwood, 1989). More frequent sampling is especially important to capture the patterns of fast-growing populations such as those of many gelatinous zooplankton. Most published data also have paid little or no attention to life-history stages (c.f. Batistić *et al.*, 2004), though this level of detail is important in understanding annual patterns of abundance (Bougis, 1974).

Only the most recent data from the open South Adriatic (1993–94) document the composition and seasonal variation of gelatinous invertebrate zooplankton, including their life-history stages (Batistić *et al.*, 2004). The present study extends this work to the coastal South Adriatic, with particular attention to the life-history stages of the most frequently encountered species and the role played by environmental factors on their annual cycles.

METHOD

The study area

The sampling station is located in the southeastern Adriatic Sea, about one-half NM southwest of Lokrum Island, near Dubrovnik (Fig. 1). This area is strongly influenced by northwest inflow of an oligotrophic current originating in the eastern Mediterranean (Zore-Armanda, 1969; Orlić *et al.*, 1992). On the basis of phytoplankton standing stock, this station is characterized as oligotrophic (Viličić, 1989).

Sampling and laboratory procedures

A total of 31 samples were collected at intervals of 1–3 weeks during 1996 using a Nansen net with a 200 μm mesh (57 cm in diameter and 255 cm in length). Vertical hauls were made from 75 m to the surface, always between 09:00 and 11:00. The volume of filtered seawater was calculated on the basis of a test with a low-speed flowmeter (General Oceanics, Inc.). Samples were preserved in a buffered 2.5% formaldehyde–seawater solution.

Water samples for oceanographic measurements and chlorophyll *a* (Chl *a*) were taken with 5 L Niskin bottles at standard depth of 0, 5, 10, 20, 50 and 75 m (IOC, 2004). Seawater temperature was measured using a reversing thermometer. Salinity was determined by

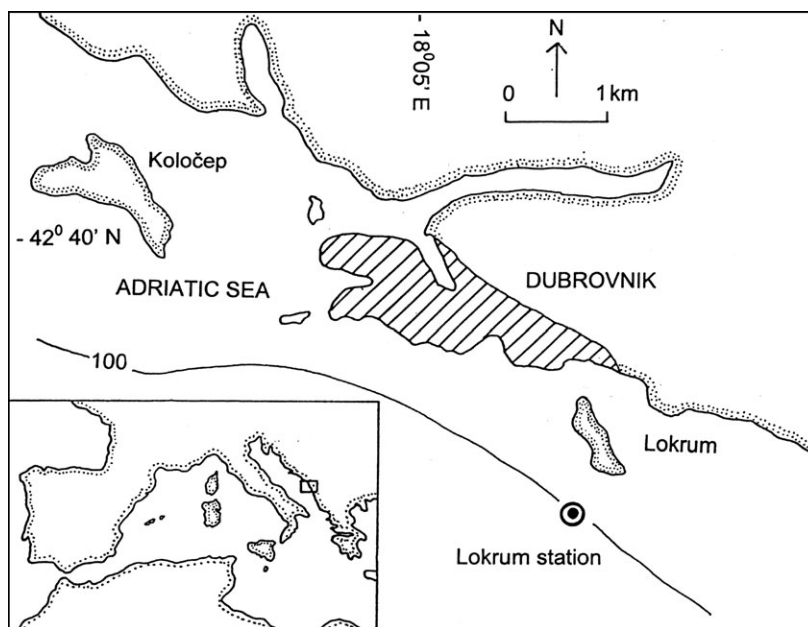


Fig. 1. Location of sampling station.

argentometric titration, using IAPSO Standard Seawater (salinity: 34.997 and 38.274) for standardization of the silver nitrate solution. Dissolved oxygen was determined by the Winkler method and oxygen saturation (O_2/O_2') was calculated from solubility of oxygen in seawater as a function of temperature and salinity (Weiss, 1970; UNESCO, 1973).

Phytoplankton biomass as Chl *a* was determined from 0.5 dm⁻³ sub-samples filtered through Whatman GF/F glass-fiber filters and stored at -20°C. Chl *a* was measured fluorometrically with a Turner TD-700 Laboratory Fluorometer (Sigma) calibrated with pure Chl *a*. Filtered samples were homogenized and extracted in 90% acetone for 24 h at room temperature (Strickland and Parsons, 1972).

Taxonomic identification and counting of individuals were performed with a Zeiss stereomicroscope at ×25 and ×40. All samples were completely analyzed. Abundance of all groups except calyphorans is presented as number of specimens per 10 m³ (ind./10 m³). Calyphorae abundance was expressed according to the number of nectophores (polygastric) of each species (nectophores/10 m³). The total number of gonophores (eudoxid) also is given (gonophores/10 m³).

Chaetognath life-history stages were classified according to Thomson's (Thomson, 1947) criteria, which are based on ovary development. Developmental stages for males of *Sagitta decipiens* were determined as follows: no visible testes, juvenile; testes visible, Stage I; seminal vesicles present, Stage II; seminal vesicles full, Stage III.

Juveniles of the most numerous hydromedusae were distinguished according to standard criteria (Bouillon, 1993), based primarily on the presence or absence of gonads. Standard criteria were used to distinguish non-transparent juvenile pteropods (Rampal, 1975; Bandel and Hemleben, 1995) and polychaetes (Fauvel, 1923; Zei, 1956).

The relationship between groups, dominant species and environmental parameters was tested using the Spearman's rank correlation coefficient. The dominant species of a particular group are determined according to their contribution in total number (percentage number, PN >10%) and frequency of occurrence ($F > 0.5$). Multidimensional scaling ordination (MDS) was used to identify different faunal patterns according to abundance and temporal distribution of species. The Bray-Curtis similarity coefficient was used as a measure of distance (Legendre and Legendre, 1983). Analysis of similarities (ANOSIM) was used to test whether faunal patterns differed statistically. Margalef's

species richness index D was used to analyze diversity changes during the year:

$$D = \frac{S - 1}{\log N}$$

where S is the number of species and N is the total number of individuals.

Statistical analyses were performed using the PRIMER 5 software package.

RESULTS

Environmental conditions

Temperature varied between 10.9°C (February) and 25.2°C (August) (Fig. 2). A period of isothermy occurred in March–April, and from the end of November to the beginning of December. During May, the sea surface temperature increased considerably, from 15.1 to 20.7°C. Between June and September there was a marked thermal stratification, with thermocline positioned between 10 and 20 m depth. An unusual and considerable temperature decrease (ca. 5°C) in the upper 10 m layer was found on June 18 and July 24. The thermal gradient between sea surface and the bottom was maximal in August (10.4°C). The average sea temperature of the water column in October was still high (18.2°C). Inverse stratification occurred from December to the end of February in the upper 5 m (Fig. 2). The vertical salinity distribution indicated that major fluctuations occurred in the upper 10 m, with lowest values in May (25.28; 0 m), (Fig. 2). Minimal fluctuations were in February and during the autumn isothermal period. A halocline was formed from the end March to September and occurred most frequently at a depth between 0 and 5 m, with maximal salinity gradient of 1.95 m⁻¹ on July 4. Below 20 m, salinity was in most cases greater than 38.00 (Fig. 2). Oxygen saturation were between 50 (at 20 m in July) and 127% (at 20 m in January), with average of 98 ± 12%. Most frequently, saturation was around 100%, indicating a good aeration in the water column.

The annual cycle of Chl *a*, (mg m⁻³) is shown in Fig. 3. The range was between 0.013 and 0.312 mg m⁻³ (avg. 0.087 ± 0.07). Two peaks of Chl *a* were observed throughout the year. The highest values occurred in March–April and in July. The present findings are consistent with those of other studies of phytoplankton biomass distribution in Eastern Adriatic coastal waters (Jasprica and Carić, 2001).

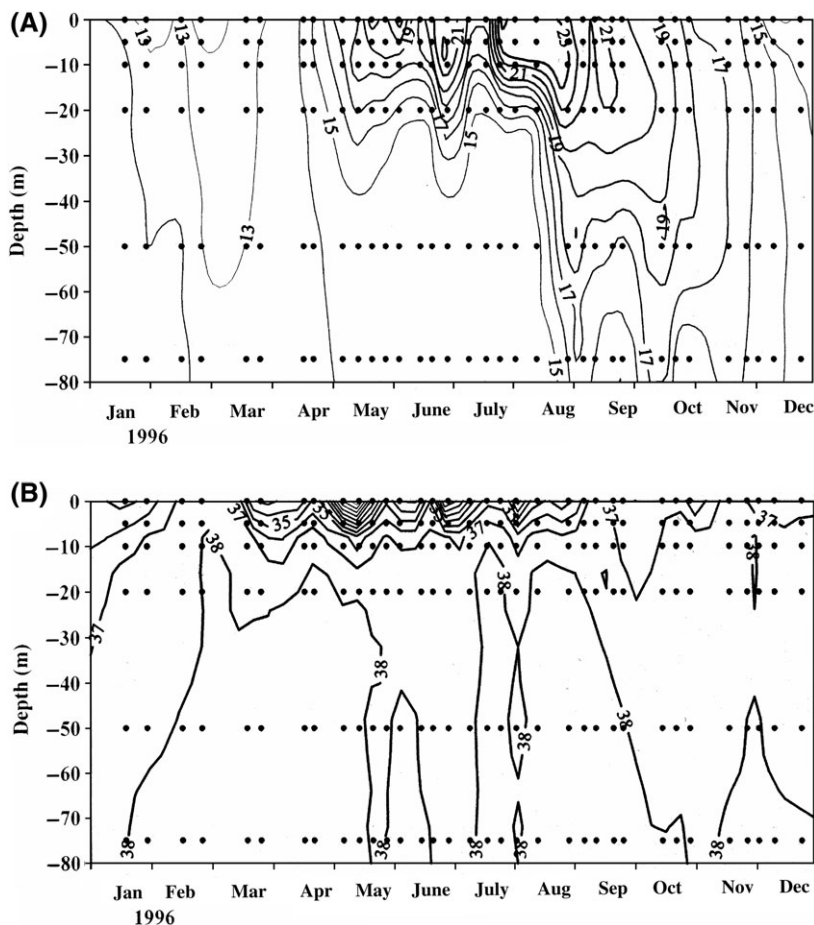


Fig. 2. Distribution of temperature (A) and salinity (B) in the water column from 0 to 75 m at Lokrum station in 1996.

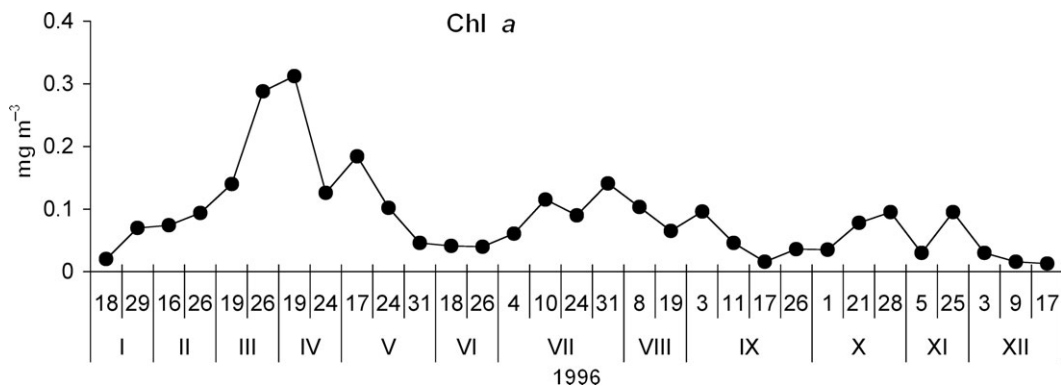


Fig. 3. Chl a concentrations (values are expressed as water column mean, from 0 to 75 m) at Lokrum station in 1996.

Annual cycle of gelatinous invertebrate zooplankton groups

The most abundant groups with highest contribution in total abundance were (Fig. 4): chaetognatha (average: 219, maximum: 692 ind./10 m³), pteropoda

(average: 90, maximum: 1178 ind./10 m³), hydromedusae (average: 81, maximum: 953 ind./10 m³) and calycophorae (average: 22, maximum: 89 nectophores/10 m³). Other groups which include planktonic polychaeta (average: 4, maximum: 10 ind./10 m³),

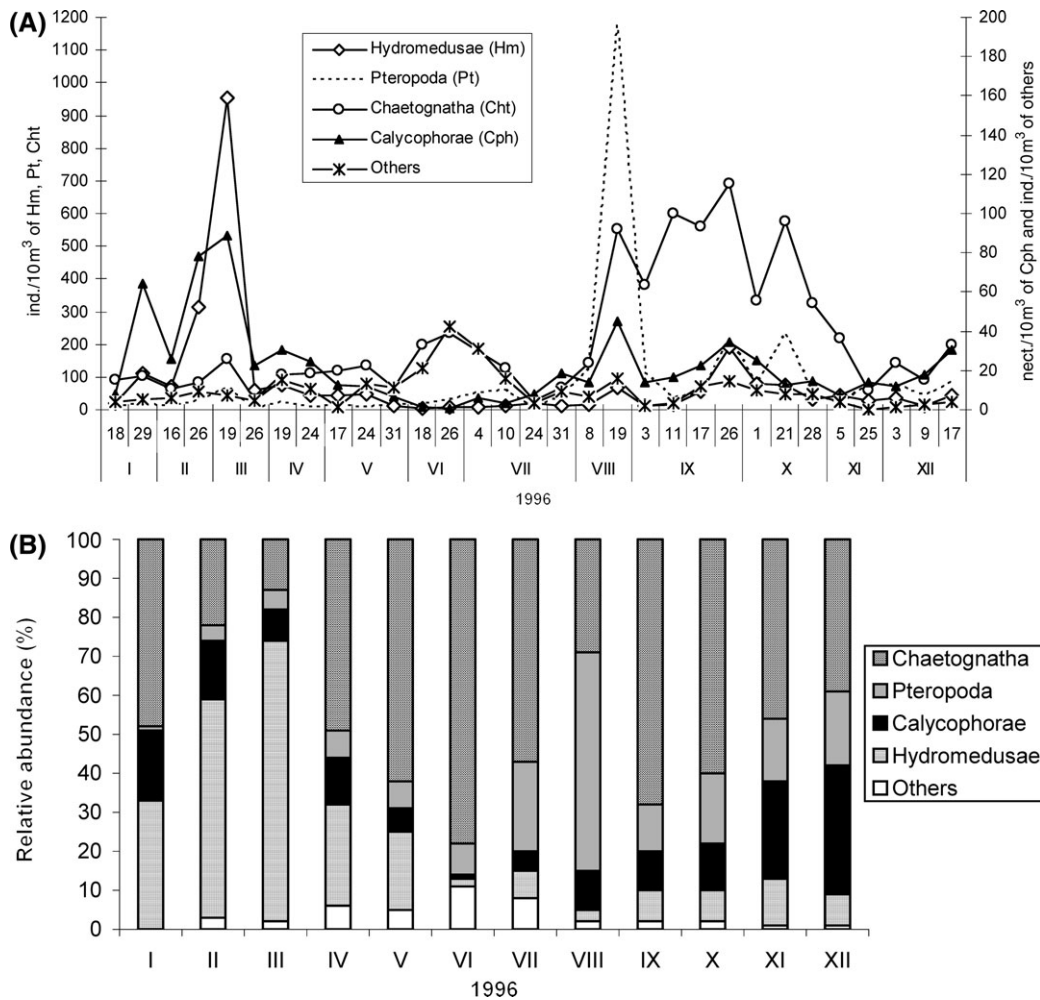


Fig. 4. Distribution of gelatinous zooplankton groups and percentage contribution of each to total abundance at Lokrum station in 1996.

heteropoda (average: 5, maximum: 42 ind./10 m³) and ctenophora (average: 1, maximum: 9 ind./10 m³) made less than 10% in total abundance (Fig. 2). Chaetognatha and pteropoda showed a late summer–autumn increases in abundance (Fig. 4), a period during which the thermocline became less pronounced but temperature was still high throughout the water column (Fig. 2). Hydromedusae and calycophorae showed higher abundance in winter (Fig. 4), favoring periods with cooler temperatures and greater mixing (Fig. 2). Lower values of all investigated groups were found from April to July, the period when the thermo- and haloclines formed and stabilized. In particular, there was a considerable decrease in abundance of all groups on July 24 when an unusual and considerable temperature decrease, ca. 5°C, was recorded in the upper 10 m (Figs 2 and 4). This time of year generally features the highest fluctuations of hydrographic

parameters, hence the greatest exposure to short-term stress.

There was a significant correlation between the abundance of chaetognatha, pteropoda, ctenophora and heteropoda with temperature (Table I). Only calycophorae abundance correlated with salinity. All cnidarians are correlated with oxygen saturation (Table I).

Species composition

Sixty-six species were identified: 19 hydromedusae, 14 calycophores, 3 ctenophores, 2 heteropods, 12 pteropods, 8 polychaetes and 8 chaetognaths (Table II). The maximum (43) and the minimum (22) number of species were found in September and June, respectively. Margalef's species richness index varied between 3.38 and 6.09 throughout the year (Table III).

Table I: Spearman rank correlation coefficient between different taxa and environmental variables (n = 31)

| Taxa | Temperature | Salinity | Oxygen saturation | Chl a |
|-------------------------------|-------------|----------|-------------------|---------|
| Groups | | | | |
| Hydromedusae | -0.295 | 0.135 | 0.488* | 0.148 |
| Calycophorae | 0.181 | 0.380* | 0.386* | -0.212 |
| Ctenophora | -0.429** | 0.168 | 0.429** | 0.402 |
| Heteropoda | 0.538*** | -0.198 | -0.284 | -0.149 |
| Pteropoda | 0.584*** | 0.134 | 0.151 | -0.106 |
| Polychaeta | 0.151 | 0.210 | 0.216 | 0.238 |
| Chaetognatha | 0.689*** | 0.259 | 0.224 | -0.343 |
| Species | | | | |
| <i>Aglaura hemistoma</i> | -0.344 | 0.047 | 0.463** | 0.063 |
| <i>Rhopalonema velatum</i> | 0.020 | 0.223 | 0.109 | -0.058 |
| <i>Liriope tetrphylla</i> | -0.167 | -0.007 | 0.333 | 0.049 |
| <i>Lensia subtilis</i> | -0.543*** | 0.151 | 0.316 | 0.390* |
| <i>Muggiaea kochi</i> | 0.267 | 0.146 | 0.342 | 0.019 |
| <i>M. atlantica</i> | -0.267 | 0.304 | 0.505** | 0.139 |
| <i>Limacina inflata</i> | 0.437** | 0.297 | 0.136 | -0.043 |
| <i>Creseis virgula</i> | 0.590*** | 0.162 | 0.170 | -0.222 |
| <i>Pelagobia longicirrata</i> | -0.064 | -0.290 | 0.038 | 0.484** |
| <i>Sagitta enflata</i> | 0.650*** | 0.308 | 0.170 | -0.340 |
| <i>S. minima</i> | 0.654*** | -0.090 | 0.092 | -0.121 |
| <i>S. setosa</i> | -0.081 | -0.232 | 0.165 | 0.102 |

*P < 0.05.
 **P < 0.01.
 ***P < 0.001.

Table II: Mean (ind./10 m³) standard deviation (SD), frequency of occurrence (F) and percentage number (PN, %) of the different taxa in the whole collection

| Taxa | Mean | SD | F | PN |
|----------------------------------|-------|--------|------|-------|
| Hydromedusea | | | | |
| <i>Sarsia gemmifera</i> | 0.48 | 1.50 | 0.10 | 0.56 |
| <i>Euphysa aurata</i> | 0.05 | 0.21 | 0.06 | 0.06 |
| <i>Corymorpha nutans</i> | 0.04 | 0.13 | 0.06 | 0.04 |
| <i>Zanclaea costata</i> | 0.02 | 0.10 | 0.03 | 0.02 |
| <i>Hydractinia minima</i> | 0.52 | 2.82 | 0.03 | 0.61 |
| <i>H. areolata</i> | 0.02 | 0.10 | 0.03 | 0.02 |
| <i>Hydractinia</i> spp. | 1.05 | 5.15 | 0.10 | 1.23 |
| <i>Rhatkea octopunctata</i> | 0.02 | 0.21 | 0.03 | 0.02 |
| <i>Bougainvillia ramosa</i> | 0.09 | 0.28 | 0.10 | 0.10 |
| <i>Laodicea undulata</i> | 0.02 | 0.10 | 0.03 | 0.02 |
| <i>Obelia</i> spp. | 0.46 | 0.84 | 0.40 | 0.52 |
| <i>Clytia hemisphaerica</i> | 0.57 | 1.00 | 0.40 | 0.67 |
| <i>Liriope tetrphylla</i> | 15.57 | 20.37 | 1.00 | 18.52 |
| <i>Aglaura hemistoma</i> | 51.66 | 161.65 | 1.00 | 60.75 |
| <i>Persa incolorata</i> | 2.43 | 8.26 | 0.40 | 2.86 |
| <i>Rhopalonema velatum</i> | 8.31 | 5.89 | 1.00 | 10.00 |
| <i>Solmundella bitentaculata</i> | 1.18 | 1.82 | 0.60 | 1.38 |
| <i>Solmaris leucostyla</i> | 0.45 | 1.30 | 0.10 | 0.53 |

(continued)

Table II: Continued

| Taxa | Mean | SD | F | PN |
|--------------------------------|--------|--------|------|-------|
| <i>Solmaris solmaris</i> | 1.23 | 2.24 | 0.10 | 0.79 |
| Calycophorae | | | | |
| <i>Sulculeolaria chuni</i> | 0.05 | 0.21 | 0.06 | 0.24 |
| <i>S. quadrivalvis</i> | 0.05 | 0.21 | 0.03 | 0.24 |
| <i>Lensia campanella</i> | 0.04 | 0.20 | 0.03 | 0.16 |
| <i>L. meteoris</i> | 0.05 | 0.16 | 0.10 | 0.23 |
| <i>L. subtilis</i> | 8.76 | 12.67 | 0.90 | 36.19 |
| <i>L. fowleri</i> | 0.02 | 0.10 | 0.03 | 0.08 |
| Muggiaea atlantica | | | | |
| <i>M. kochi</i> | 6.12 | 7.22 | 0.90 | 27.08 |
| <i>M. kochi</i> | 4.52 | 4.88 | 0.90 | 19.35 |
| Chelophyes | | | | |
| <i>appendiculata</i> | 0.21 | 0.52 | 0.30 | 0.94 |
| Eudoxoides spiralis | | | | |
| <i>Eudoxoides spiralis</i> | 0.94 | 1.39 | 0.50 | 4.02 |
| Sphaeronectes gracilis | | | | |
| <i>Sphaeronectes gracilis</i> | 1.35 | 1.49 | 0.70 | 5.98 |
| S. irregularis | | | | |
| <i>S. irregularis</i> | 0.85 | 1.87 | 0.40 | 3.77 |
| S. gamulini | | | | |
| <i>S. gamulini</i> | 0.16 | 0.35 | 0.20 | 0.71 |
| Abylopsis tetragona | | | | |
| <i>Abylopsis tetragona</i> | 0.21 | 0.33 | 0.30 | 0.94 |
| Ctenophora | | | | |
| <i>Beroa ovata</i> | 0.04 | 0.13 | 0.06 | 18.09 |
| <i>Mertensia ovum</i> | 0.05 | 0.29 | 0.03 | 27.30 |
| <i>Hormiphora plumosa</i> | 0.11 | 0.49 | 0.06 | 54.61 |
| Heteropoda | | | | |
| <i>Atlanta peroni</i> | 1.03 | 2.00 | 0.40 | 96.69 |
| <i>Firoloida desmaresti</i> | 0.04 | 0.13 | 0.06 | 3.31 |
| Pteropoda | | | | |
| <i>Limacina inflata</i> | 54.63 | 183.69 | 1.00 | 62.83 |
| <i>L. trochiformis</i> | 4.04 | 4.97 | 0.80 | 4.64 |
| <i>L. bulimoides</i> | 0.18 | 0.97 | 0.03 | 0.20 |
| <i>Styliola subula</i> | 0.20 | 0.63 | 0.13 | 0.23 |
| <i>Creseis virgula</i> | 21.05 | 33.81 | 1.00 | 24.21 |
| <i>C. acicula</i> | 4.82 | 12.77 | 0.40 | 5.54 |
| <i>Hyalocylix striata</i> | 0.07 | 0.18 | 0.03 | 0.08 |
| <i>Clio pyramidata</i> | 0.09 | 0.39 | 0.06 | 0.10 |
| <i>Cavolinia inflexa</i> | 0.89 | 2.12 | 0.40 | 1.02 |
| <i>Peracilis reticulata</i> | 0.89 | 1.65 | 0.40 | 1.02 |
| <i>Cymbulia peroni</i> | 0.09 | 0.32 | 0.10 | 0.10 |
| <i>Desmopterus papilio</i> | 0.02 | 0.10 | 0.02 | 0.02 |
| Polychaeta | | | | |
| <i>Tomopteris helgolandica</i> | 0.63 | 0.70 | 0.40 | 16.02 |
| <i>T. elegans</i> | 0.02 | 0.10 | 0.03 | 0.48 |
| <i>Vanadis crystallina</i> | 0.04 | 0.13 | 0.06 | 0.97 |
| <i>Callizonella lepidota</i> | 0.11 | 0.22 | 0.20 | 2.90 |
| <i>Pelagobia longicirrata</i> | 2.08 | 2.34 | 0.70 | 56.83 |
| <i>Sagitella kowalevskii</i> | 0.12 | 0.23 | 0.20 | 3.38 |
| <i>Travislopsis lanceolata</i> | 0.72 | 1.21 | 0.40 | 18.94 |
| <i>Typhloscolex muelleri</i> | 0.02 | 0.10 | 0.03 | 0.48 |
| Chaetognatha | | | | |
| <i>Sagitta enflata</i> | 105.26 | 148.82 | 1.00 | 47.54 |
| <i>S. minima</i> | 100.73 | 81.82 | 1.00 | 45.50 |
| <i>S. setosa</i> | 5.72 | 5.88 | 1.00 | 2.58 |
| <i>S. serratodentata</i> | 6.97 | 10.30 | 0.70 | 3.15 |
| <i>S. bipunctata</i> | 0.62 | 1.19 | 0.40 | 0.28 |
| <i>S. decipiens</i> | 0.41 | 1.40 | 0.20 | 0.18 |
| <i>S. lyra</i> | 1.55 | 2.34 | 0.50 | 0.70 |
| <i>Krohnitta subtilis</i> | 0.14 | 0.78 | 0.03 | 0.06 |

Dominant species are in bold.

Annual cycle of the main species

The annual cycle of the most frequent and abundant species and their life stages are presented in Figs 5–9. Ctenophores appeared sporadically and were not

Table III: Variability in Margalef's species richness index

| Months | Index |
|-----------|-------|
| January | 3.83 |
| February | 4.89 |
| March | 4.54 |
| April | 5.87 |
| May | 6.09 |
| June | 3.38 |
| July | 5.36 |
| August | 5.20 |
| September | 5.23 |
| October | 5.43 |
| November | 5.03 |
| December | 4.77 |

abundant enough to allow detailed description of their annual distribution. These, however, may have been underestimated owing to their rather fragile

constitution: The relatively “rough” treatment of standard plankton collection techniques used in this study may have rendered many unidentifiable.

The most frequent and abundant hydromedusae—*Aglaura hemistoma*, *Liriope tetraphylla* and *Rhopalonera velatum* (Table II), generally had higher densities in autumn and winter (Fig. 5). There was a marked increase in the abundance of *A. hemistoma* at the end of February (Fig. 5), with a maximum of 864 ind./10 m³ (91.5% adults) on March 19; this was followed only 7 days later by a rapid decrease (<40 ind./10 m³). Juveniles were present throughout the year but their highest contribution was in January, February (20–49%) and mid-September (34–57%). *Liriope tetraphylla* showed two annual increases, one in autumn and another in winter-spring (Fig. 5) having its maximum on September 26 (87 ind./10 m³). Juveniles had an average contribution of 65% in the population of this species. The lowest

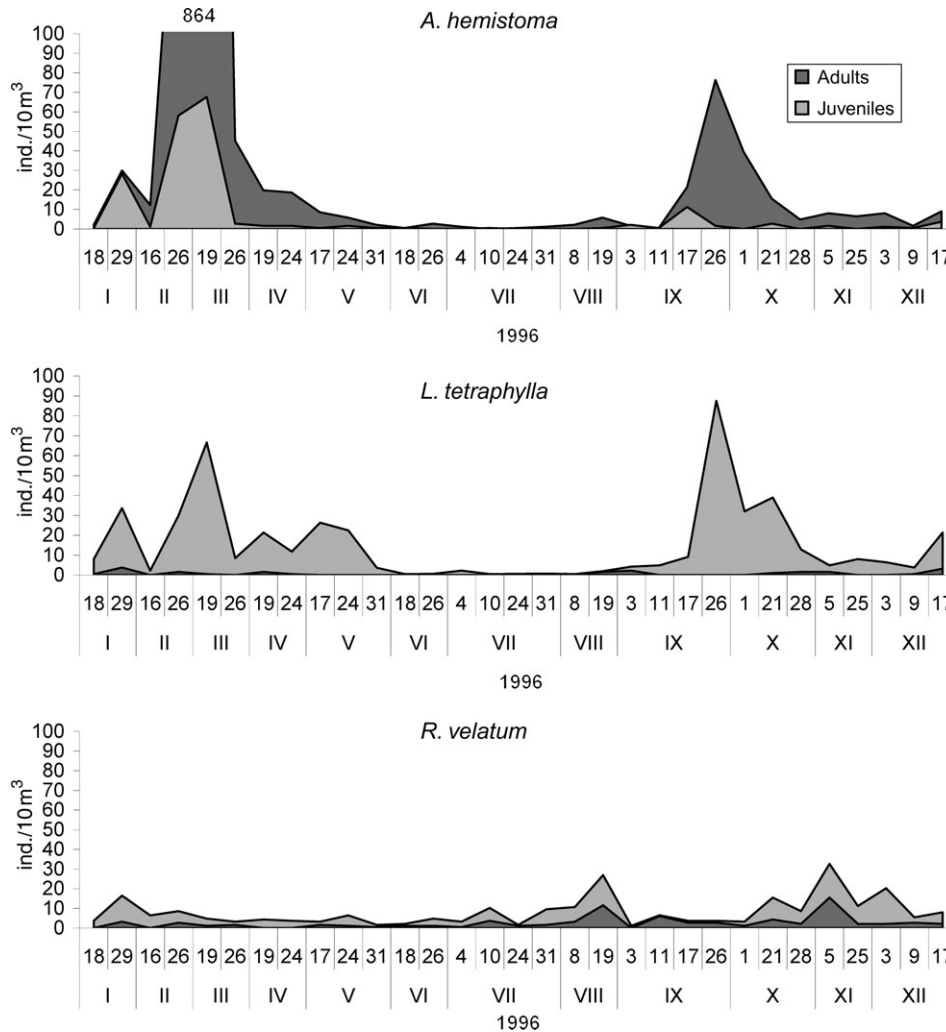


Fig. 5. Distribution of most-abundant hydromedusae (*A. hemistoma*, *L. tetraphylla*, *R. velatum*) and their life stages at Lokrum station in 1996.

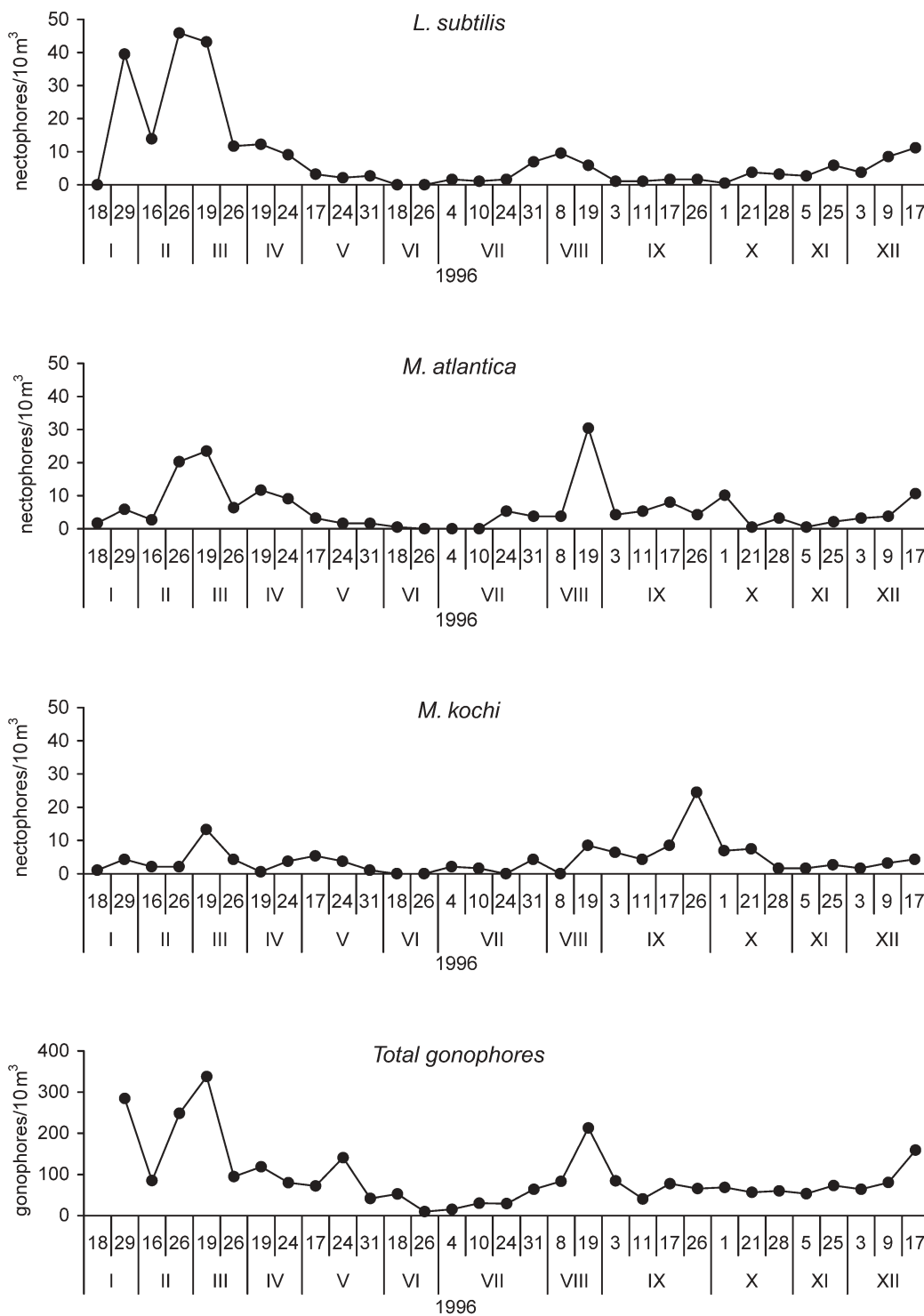


Fig. 6. Distribution of most-abundant calycofiores (*L. subtilis*, *M. atlantica*, *M. kochi*) and total gonophores at Lokrum station in 1996.

abundances of *A. hemistoma* and *L. tetraphylla* were recorded in summer (<4 ind./10 m³). Higher abundances of *R. velatum* were found in August and between October and January (Fig. 5) with the

maximum value on November 5 (30 ind./10 m³). Juveniles were constantly present and accounted for 55%–100% of the population during periods of higher abundance.

Lensia subtilis, *M. atlantica* and *M. kochi* were the dominant calyptophorae (Table II). *Lensia subtilis* was more abundant in winter with a maximum of 46 nectophores/10 m³ on February 26. *Muagiaeaa atlantica* and *M. kochi* showed two annual increases (Fig. 6), one at the end of winter and the other in summer–autumn. Maxima of 30 nectophores/10 m³ of *M. atlantica* and 25 nectophores/10 m³ of *M. kochi* were found on August 19 and September 26, respectively. Two maxima were also observed for total gonophores (Fig. 6): March 19 (340 gonophores/10 m³) and August 19 (214 gonophores/10 m³). The presence of nectophores correlated significantly with that of the total gonophores for *L. subtilis* ($r = 0.87$, $P < 0.001$), *M. atlantica* ($r = 0.75$, $P < 0.001$) and *M. kochi* ($r = 0.35$, $P < 0.01$).

The most frequent and abundant pteropods were *Limacina inflata* and *Creseis virgula* (Table II). *Limacina inflata* had higher abundance from August to December (62–100% juveniles), and again in March (40% juveniles) (Fig. 7). The marked increase of *L. inflata* in August 19 (1021 ind./10 m³) was followed by a rapid decrease, with less than 70 ind./10 m³ at the beginning of September. Periodic increases of *C. virgula* occurred from July to December, with juveniles accounting for more than 60% of the population in this period (Fig. 7).

A maximum value of 136 ind./10 m³ was found on October 21, while values less than 5 ind./10 m³ were found from January to July.

Pelagobia longicirrata was the dominant pelagic polychaete (Table II). Its abundance was highest on April 19 (9 ind./10 m³). Juveniles made up 55–100% of the population from May to July and more than 95% in October and December (Fig. 8).

Sagitta inflata and *S. minima* were the dominant chaetognaths having all of their developmental stages present throughout the year (Table II, Fig. 9). Higher abundance of *S. inflata* was found from August to November (Fig. 9), with a maximum of 554 ind./10 m³ on September 26. Juveniles dominated from June to December, accounting for more than 60% of the population. There was an increase in the abundance of *S. minima* in June and from August to October (Fig. 9), with the maximum value found on August 19 (336 ind./10 m³). Juveniles were most abundant between August and October, contributing 37–51% to the population. *S. setosa* occurred throughout the year (Table II) having densities not higher than 24 ind./10 m³ (March 19). There were periodic increases in abundance of this species from March to April and again from August to November, due to higher occurrence of stages I–III and juveniles and stage I, respectively.

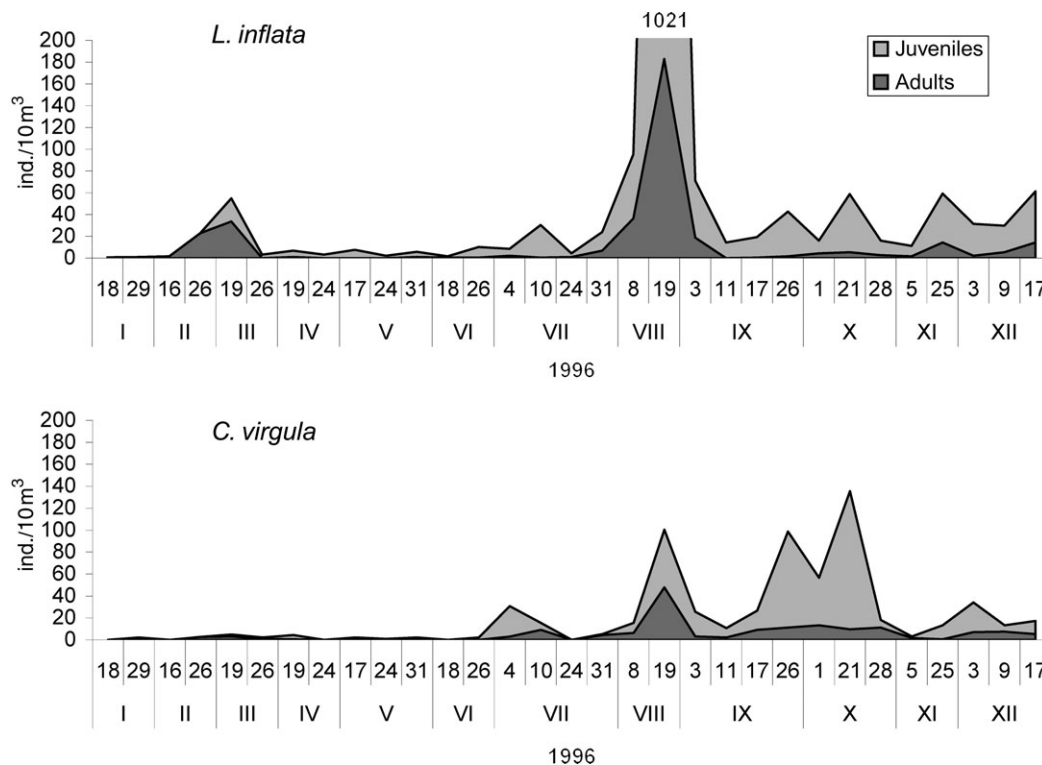


Fig. 7. Annual distribution of most-abundant pteropods (*L. inflata*, *C. virgula*) and their life stages at Lokrum station in 1996.

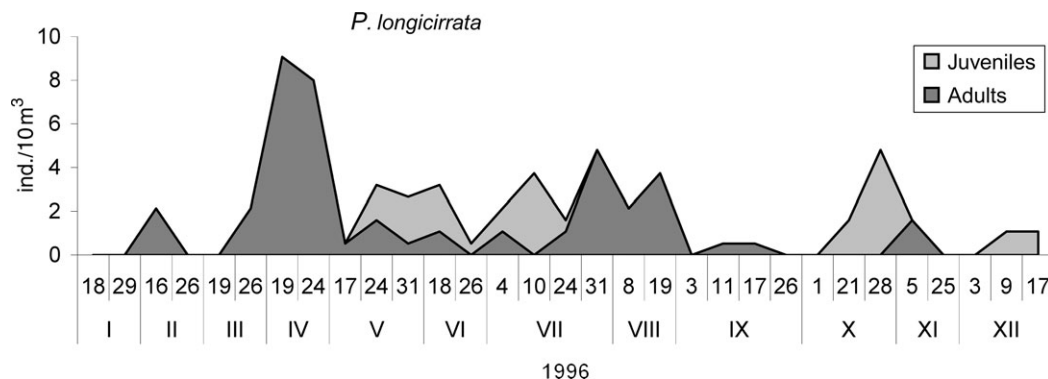


Fig. 8. Distribution of pelagic polychaeta *P. longicirrata* and their life stages at Lokrum station in 1996.

MDS (stress = 0.06) analyses clearly distinguishes two main groups among the 12 dominant species (Fig. 10). Group (A) is composed of species that were most abundant at the end of summer and in autumn: *S. enflata*, *S. minima*, *L. inflata* and *C. virgula*. The abundance of all of these species has a significant positive correlation only with temperature (Table I).

Group (B) consists of species such as *A. hemistoma*, *L. tetraphylla*, *R. velatum*, *M. kochi*, *M. atlantica*, *L. subtilis* and *S. setosa*, generally being most abundant in late

summer–autumn and winter. Among them, only *L. subtilis* had a significant (negative) correlation with temperature. The abundance of *A. hemistoma* and *M. atlantica* are in positive correlation with oxygen saturation (Table I).

Pelagobia longicirrata fit in neither cluster. The only significant correlation for this species was with Chl *a* (Table I).

ANOSIM showed a statistically significant difference between Groups A and B ($R = 0.915$; $P < 0.001$).

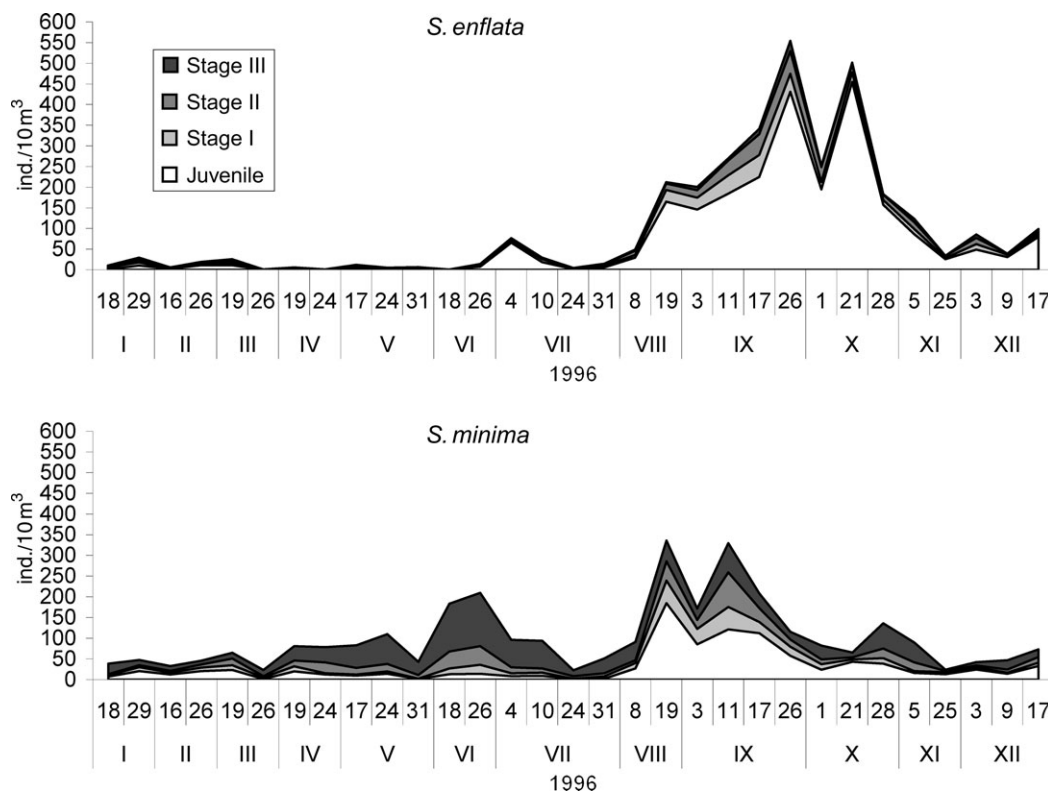


Fig. 9. Distribution of most-abundant chaetognaths (*S. enflata*, *S. minima*) and their life stages at Lokrum station in 1996.

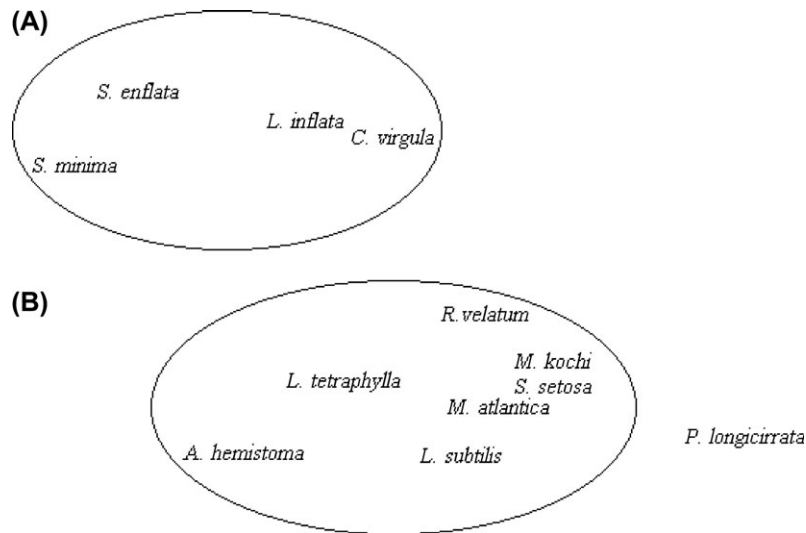


Fig. 10. MDS of most-frequent and abundant species, based on Bray–Curtis similarity coefficient. Stress value: 0.06.

DISCUSSION

Species composition

All hydromedusae, ctenophora, heteropoda and chaetognatha species found in the present study have been previously recorded in the Adriatic Sea (c.f. Batistić *et al.*, 2004). Some of the recorded species such as *Persa incolorata*, *L. meteori*, *Cymbulia peroni*, *S. decipiens* and *S. lyra* are oceanic and mesopelagic. Their appearance in shallow coastal waters occurred sporadically, in winter and spring, when they rise to the surface due to “upwelling” caused by cyclonal gyre (Orlić *et al.*, 1992), and are then carried off by transversal surface currents towards the coast. Margalef’s species richness index varied most in spring. This probably is related to the high fluctuation of hydrographic parameters typical of this season. Thus, the highest index (May) may be owed in part to circulation patterns that enriched coastal waters with oceanic species. The lowest species index (June), on the other hand, might be attributed to the subsequent disappearance of oceanic species from coastal waters, as well as to short-term stress on the whole gelatinous zooplankton community caused by an unusual temperature decrease in the upper layers.

In general, there are notable changes in the species composition and abundance in the communities of calycophorae, pteropoda and polychaeta in the coastal South Adriatic (Table IV). *M. kochi*, for example, the most numerous Adriatic calycophore (Gamulin and Kršinić, 1993), has decreased in abundance and appears to be in the process of being replaced by its allochthonous congener, *M. atlantica* (Table IV). This

latter species is common in the Atlantic Ocean and Western Mediterranean, and progressive dominance of *M. atlantica* over *M. kochi* in the coastal Ligurian Sea (Western Mediterranean) has been documented by fortnightly records from 1985 to 1995 (Licandro and Ibanez, 2000). Suitable hydrographic conditions and the direction of surface currents probably enabled the immigration of *M. atlantica* from the western part of the Mediterranean to the Adriatic Sea. In February 1995, *M. atlantica* was recorded for the first time in the coastal southeastern (Gamulin and Kršinić, 2000) and central Adriatic (Batistić, 1999). Direct measurements of the current at Otranto and in the South Adriatic in winter–spring 1994/1995 (Kovačević *et al.*, 1999) ascertained very prominent mean northward surface incoming currents along the eastern shore of the Strait of Otranto.

The pteropod *Desmopterus papilio*, common in the tropical Atlantic and Indian Oceans and known from the Western Mediterranean (Rampal, 1975), was found at Lokrum in February 1996. This also may be related to enhanced intrusion of Mediterranean water being more pronounced in winter (Zore-Armanda, 1969; Artegiani *et al.*, 1996). Further, *C. acicula* has been the dominant pteropod along the eastern Adriatic coast, accounting for more than 90% of all pteropods (Gamulin, 1979). During this investigation, however, *C. acicula* comprised only 6% of the pteropod population. On the other hand, *C. virgula* and *L. inflata*, were more abundant accounting for 87% of pteropods (Table IV).

Similarly, *P. longicirrata*, very rare species in the Adriatic Sea (Požar, 1972), became the most abundant

Table IV: Historical records of the dominant species of calycothorans, pteropods and polychaetes in the Adriatic Sea, and comparison of their relative abundances (%) in total number of specimens, in earlier and present study in the coastal South Adriatic

| Species | First record in the Adriatic Sea | Relative abundance (%) in studies earlier than 1995 | Relative abundance (%) in this study |
|-------------------------------|--------------------------------------|---|--------------------------------------|
| <i>Muggaea atlantica</i> | 1995 (Gamulin and Kršinić, 2000) | / | 27 |
| <i>M. kochi</i> | (Will, 1844) | >50% (Gamulin and Kršinić, 1993; Lučić and Mikuš, 1994) | 19 |
| <i>Creseis acicula</i> | (Steuer, 1911) | >90% (Gamulin, 1979; Lučić and Mikuš, 1994) | 6 |
| <i>Limacina inflata</i> | (Steuer, 1911) | <1% (Gamulin, 1979; Lučić and Mikuš, 1994) | 63 |
| <i>C. virgula</i> | (Steuer, 1911) | <1% (Gamulin, 1979; Lučić and Mikuš, 1994) | 24 |
| <i>Desmopterus papilio</i> | 1993 (Batistić <i>et al.</i> , 2004) | <0.5% (Batistić <i>et al.</i> , 2004) | 0.02 |
| <i>Pelabobia longicirrata</i> | 1967/1968 (Požar, 1972) | <1% (Požar, 1972) | 57 |

planktonic polychaeta in this study (Table IV). In the earlier investigations, *Tomopteris helgolandica* was the most abundant planktonic polychaeta in the coastal part of the Adriatic Sea (Zei, 1956; Gamulin, 1979).

The same sort of changes in the species composition and abundance were found in the open South Adriatic from 1993 to 1995 (Batistić, 1999; Batistić *et al.* 2004) at a station which, like the Lokrum station, is exposed to the direct influence of water masses originating in the Eastern Mediterranean. In the present context, it seems significant that this period coincides with changes in thermohaline circulation referred to as the EMT (Klein *et al.*, 1999). Observations in the Levantine Sea in 1993 documented exceptional alterations in calanoid copepods abundance and species composition related to the EMT (Weikert *et al.*, 2001). Unfortunately, no data exist about the abundance and species composition of gelatinous invertebrata plankton community in the Eastern Mediterranean in 1990s. The intensity of Eastern Mediterranean influence into the Adriatic depends on the pressure difference between the Atlantic and Mediterranean and, when it is positive, there is a strong inflow into the Adriatic, one indicator of which is higher salinity (Grbec *et al.*, 2002). This was the case in 1993 and 1995, when salinity exceeded 38.5 in intermediate layers of the open South Adriatic (Batistić, 1999; Batistić *et al.*, 2004). In addition, changes observed in the structure and dynamics of the Northern Adriatic copepod community from 1988 to 1995 appeared to be coupled to hydrographic variations induced by climatic forcing (Kamburska and Fonda-Umani, 2006).

There is no doubt that changes in gelatinous zooplankton community in the South Adriatic have been occurred before 1996 and, as we can see from this

study and previous ones (Batistić *et al.*, 2004), these changes are established in the Adriatic Sea. Our data provide only a basic description of contemporary changes in the South Adriatic plankton. A fuller description of the impact of these changes could be an interesting topic for future research.

Annual cycle of gelatinous zooplankton

A few species of chaetognaths, pteropods and cnidarians were responsible for the peaks in abundance of these zooplankton groups, while their life cycle had a large influence on the seasonal distribution of the whole community.

MDS and cluster analyses clearly distinguished two groups of species. Group A species—*S. inflata*, *S. minima*, *L. inflata* and *C. virgula*—were characterized by highest abundance in late summer and autumn. Although the thermocline was less pronounced during this period, the temperature was still high throughout the water column (average 18.4°C). As reflected in the presence of a large number of juveniles, this was a period of intense reproduction for all these species. This relationship with temperature is not unexpected, as temperature is well known to be a prime factor in controlling the seasonality of many zooplankton species (Raymont, 1983; Gilli *et al.*, 1987; Fernández de Puellas *et al.*, 2003), whereas other factors, such as food supply, are also important. Earlier investigations in the Adriatic Sea underlined the importance of food supply in chaetognath distribution (Batistić, 2003; Batistić *et al.*, 2003). Consistent with their nature as carnivores that feed mainly on copepods (Batistić *et al.*, 2003; Kehayias *et al.*, 2005), *S. inflata* and *S. minima* at Lokrum were found to

follow the summer peaks of abundance of neritic and estuarine copepods (Hure *et al.*, 1980; Lučić, 1996). Even though no statistical significant correlation was found between the herbivorous pteropods and Chl *a*, the increase in abundance of *L. inflata* and *C. virgula* did, however, follow the second annual increase in phytoplankton biomass (July to mid-August). Further, the maximum abundance of pteropods coincided with a decrease in phytoplankton biomass (August 19).

Group B included *A. hemistoma*, *L. tetraphylla*, *R. velatum*, *M. kochi*, *M. atlantica*, *L. subtilis* and *S. setosa*. Their annual distribution showed two increases, one in winter and one in late summer–autumn. The high percentage of juveniles of *A. hemistoma*, *L. tetraphylla*, *R. velatum* and *S. setosa* found in both the above periods suggested probably the intense reproduction of these species. The main reproductive periods of *M. kochi*, *M. atlantica* and *L. subtilis* were similar with respect to total gonophore abundance. According to Gamulin and Kršinić (Gamulin and Kršinić, 1993), *L. subtilis* and *M. kochi* reproduce year round and most intensively over spring and summer.

Considering that the two periods of higher abundance—winter and late summer–autumn—are subjected to different temperature regimes, temperature seems not to be the sole factor determining the dynamics of Group B species. Water column stability in winter, for example, promotes the increase of zooplankton, including of gelatinous carnivores (Bouillon *et al.*, 2004). Late summer–autumn increases followed summer spikes of neritic and estuarine copepods (Hure *et al.*, 1980; Lučić, 1996), cladocerans (Brautović *et al.*, 2000) and appendicularians (Lučić, 1998). The highest average net-zooplankton biomass in the Adriatic was found during this period (Benović and Bender, 1983). However, a lower density of copepods which are common prey of gelatinous carnivores, was found at Lokrum in winter (Lučić, 1996). This might be explained by high feeding pressure exerted by hydromedusans and siphonophores. Indeed, hydromedusae, siphonophores and ctenophores are able to decrease zooplankton biomass by more than 20% per day (Deason, 1982; Matsakis and Conover, 1991; Purcell, 1992). Medusae alone can graze 13–94% per day of the copepod stock (Purcell, 1997).

The distribution of the planktonic polychaete *P. longicirrata* fit in neither cluster. Instead, its abundance peaked in spring and summer. The feeding habits of this species are not quite clear but it is possible that, like most polychaetes generally considered as carnivores are in fact omnivorous (Pleijel and Dales, 1991). This might explain the correlation with Chl *a*. Unlike Groups A

and B species, juveniles of *P. longicirrata* were found only twice during the year: from May to August and from October to December. This suggests semi-annual reproduction.

A common characteristic of most Groups A and B species was that their lower abundances coincided with two unusual temperature decreases: ca. 5°C in the upper 10 m on June 18 and again on July 24. This phenomenon could be explained by a large and sudden discharge of freshwater from the nearest hydroelectric power plant during summer when winds blow from the north (Legović *et al.*, 2003). Only species with very wide temperature tolerances, such as *S. setosa*, *S. minima* (Alvarino, 1965) and *P. longicirrata* (Reibisch, 1964) did not exhibit such a dramatic drop in their abundance. Salinity had no discernible impact on the annual distribution of dominant species. Despite the extremely low values at the surface and at 5 m on May 17, most chaetognaths, hydromedusae, polychaetes and calycophores typically are found at greater depths (F. Kršinić, Dubrovnik-Croatia, personal communication) where salinity remains between 36 and 38.

The annual distribution of the dominant species shows some differences when compared with data from other parts of the coastal Mediterranean (Rampal, 1975; Gili *et al.*, 1987; Goy, 1991, 1997; Kehayias *et al.*, 1995; Buecher *et al.*, 1997; Daly Yahia *et al.*, 2003). For example, different annual distributions were found for hydromedusae (Benović, 1971) and calycophorae (Gamulin and Kršinić, 1993) during roughly simultaneous investigations in Naples (Western Mediterranean) and Dubrovnik (South Adriatic, East Mediterranean). These differences likely resulted from the variability to be expected in coastal environments (Walsh, 1976) exposed to different levels of anthropogenic, hydrological and terrestrial influences.

Earlier descriptions of the annual cycle of gelatinous zooplankton in the Mediterranean most often have been based on monthly samples collected over a year (e.g. Gili *et al.*, 1987; Gamulin and Kršinić, 1993). The finer scales are, however, especially important in understanding the temporal distributions of certain gelatinous species, some of which have short life cycles measured only in days. Thus, some calycophores (Carré, 1967), holoplanktonic hydromedusae (Bouillon, 1993) and pteropods (Rampal, 1975) have the potential to increase very rapidly to exceptionally high levels when environmental conditions are favorable and then, just as rapidly, effectively disappear. In this study, for example, the hydromedusan *A. hemistoma* and the pteropod *L. inflata* increased 20 and 15 times, respectively, in less

than 10 days. However, it is important to stress that for *A. hemistoma*, it was difficult to disentangle population growth from a potential abundance increase related to water transport in the winter period when Mediterranean water inflow are more pronounced. Contrarily, the pteropod *L. inflata* showed an increase in abundance during summer, and this increase is probably tied to the local environmental condition, as there is a negligible influence of Mediterranean waters in this season.

A fuller description must await future research, one part of which should involve a more extensive sampling effort on a broader area that evaluates the relative role of point-processes related to population dynamics, and purely advective processes in determining observed zooplankton patterns.

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